ALASKA BOARD OF FISHERIES

Hatchery Committee Meeting

Anchorage | October 14, 2023

On-Time Public Comments

Comments: October 14, 2023 Hatchery Committee Meeting

September 29, 2023

Marit Carlson-Van Dort, Chair
Alaska Board of Fisheries
Board Support Section
P.O. Bos 115526
Juneau, AK 99811-5526

Dear Chair Carlson-Van Dort and Board Members

The Alaskan salmon hatchery operators appreciate the Board's commitment to maintaining annual Hatchery Committee meetings and observance of the Joint Board Protocol on Salmon Enhancement. We look forward to participating in the upcoming October 14 meeting. We think it important for the Board to have these ongoing discussions in order for the Board and the public to remain current on hatchery management, production, and research as stipulated in the Joint Protocol #2002-FB-215.

The notice of public meeting for the Hatchery Committee meeting lists hatchery production levels, research, and discussions of Board authority on hatchery-related matters as topics for this upcoming meeting. The topic of Board authority with regard to hatchery programs has received significant discussion at the Board level in recent years along with extensive testimony and submission of a variety of documents related to issues of production and permitting authority. In support of this likely discussion, we offer the following two documents to accompany this letter:

1) Transcript of the March 7, 2020 testimony to the Board of Fish by John Sund, former Alaska State Legislative Staffer to Representative Terry Gardiner and legal counsel for Southern Southeast Regional Aquaculture Association during the years in which the guiding statutes for the Private, Non-profit Hatchery were formed.
2) Legal memorandum by the firm Ashburn & Mason, P.C. in Anchorage (July. 2018) and submitted to the Board of Fisheries for the March, 2020 Hatchery Committee meeting

These documents provide perspective on legislative intent related to Board authority and seek to answer questions related to the Alaska hatchery program as well as questions of Board process and jurisdiction, hatchery production, regulation, and other issues.

Additionally, we support ongoing updates on the Alaska Hatchery Research Project and Hatchery-Wild Interaction Study. This important research project, initiated in 2012 and scheduled to conclude in 2024, has generated significant findings related to the efficacy of management programs, straying behaviors, genetic stock structure, and relative reproductive success that are directly tied to the pink and chum salmon hatchery programs in Alaska. Prior to this study, much of the literature on hatchery programs is/was focused on other species of Pacific salmon and based on programs that serve different ecological, programmatic, and economic functions. This ground-breaking research supports the success and implementation of the foundational concepts of precautionary management, wild stock priority, and the ADF&G genetic policy that were at the core of the development of the State's hatchery programs.

We, as operators of those State programs, are committed to the concepts of stewardship and sustainability that guide the policy, permitting, and management of these programs. We support annual meetings of the Hatchery Committee and invite any opportunity to discuss the cultural and economic benefits of the Alaskan Hatchery Program.

Sincerely,

Alaska PNP Salmon Hatchery Operators

Tina Fairbanks
Executive Director
Kodiak Regional Aquaculture Association

Geoff Clark
General Manager
Prince William Sound Aquaculture Association

Dean Day
Executive Director
Cook Inlet Aquaculture Association

Mike Wells
Executive Director
Valdez Fisheries Development Foundation

Scott Wagner
General Manager
Northern Southeast Regional Aquaculture Association

Susan Doherty
General Manager
Southern Southeast Regional Aquaculture Association

Katie Harms
Executive Director
Douglas Island Pink and Chum, Inc

Alaska Board of Fisheries
HATCHERY COMMITTEE MEETING
March 7, 2020
Anchorage

Comments
John Sund
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Craig, Alaska

RE: Board Authority: AS 16.10.440(b)

I direct my comments to the discussion regarding the authority of the Board of Fisheries as stated in AS 16.10.440. I believe I can bring a historical perspective and background surrounding the drafting of the section and provide a historical context to assist in the review and discussion.

At the time of the drafting legislation creating and setting up the legal and legislative framework for the Private Non-Profit Regional Aquaculture Associations (PNP); 1976 – 1980, I worked on the legislation and regulations as an attorney for Southern Southeast Regional Aquaculture Association (SSRAA) and staff to the legislature in 1977 and 1979-80.

The Board has wrestled with the authority of the Board regarding the private non-profit hatchery program for many years. The Department of Law has written memorandums to the Board regarding the question of Board authority over the past 20 – 30 years.

The legislation to set up a comprehensive framework for the creation and management of private non-profit hatcheries was adopted over a few years. It was a new endeavor and as the implementation took place various unknown factors arose and the legislature passed new and clarifying statutes to address the issues. The primary legislation was adopted in 1974, 1976, 1977, 1978 and 1979 and a few additional changes in later years.

It was new territory to balance the oversight of the creation of hatcheries operated by private non-profit entities. The use of common property resources and public resources to build hatcheries that produce salmon for harvest in the commercial, sport and personal use fisheries. The challenges included a balance between public input and consideration of use of public assets, the private financing through assessments on commercial fishermen and loans from the state and the need for stability in the planning, production and financing.

There was also a need to proceed with expediency to get the process going and keep it going. There were many unknown challenges to deal with. This had never been done before. It was a new social experiment in a public – private partnership. There were no models in the world to follow. It was new ground for everybody. The initial legislation creating private non-profit hatcheries was one or two sentences adopted in 1974. From there the idea started and different areas of the state began to explore options. The challenges from how to finance to site selection, brood stock egg takes, organization of managing entities needed solutions. Voluntary assessments in Prince William Sound worked for one year but proved to be unreliable. The legislation was amended in 1977, 1978, 1979 and later years. It was a new program and concept. Mandatory assessments to be collected by processors and sent directly to associations was found unlawful in the Wayne Alex case. Legislation was amended to recognize the assessments as a tax payable to the state and deposited in the general fund. The enhancement loan fund needed clarification regarding the accrual of interest on outstanding balances.

Many of these issues came to a head in 1977 – 1978. The 1978 legislature appropriated $100,000 to set up the Aquaculture Policy Study Group. The Letter of Intent for FCC for SCS for CSHB 920 opening paragraph:

> "The Aquaculture Study proposes to clarify statutes authorizing private nonprofit salmon hatcheries so that management authorities such as the Department of Fish and Game and the Board of Fisheries can better understand and implement the intent of the Legislature."

The Aquaculture Study Group organized in July and met in September and later in the fall 1978. Six major areas of concern were chosen to be addressed by the study group:

1. Clearly define the State's policies on Aquaculture – examine existing statutes/ resolutions/policies
2. Stock Management
3. Define roles of organization and groups
4. Land Use problems
5. Cost/Benefit analysis of private and state projects
6. Research Base

As you can see from the list there were a lot of areas of confusion and overlapping jurisdiction and policy and procedures to work through. The ideas, recommendations and concepts from this study group led to many of the provisions adopted in the 1979 legislation. Including the change to AS 16.10.400.

In the 1976. AS 16.10.440 read

> (a) Fish released into the natural waters of the state by a hatchery operator under secs. 400-470 of this chapter are available to the people for common use and are subject to regulation under applicable law in the same way as fish occurring in their natural state until they return to the specific location designated by the department for harvest by the hatchery operator.
>
> (b) The board may promulgate regulations necessary to implement secs. 400-470 of this chapter.

This section created a layer of confusion in terms of how the nonprofit hatcheries were going to operate. The statute vests detailed authority in the Commissioner to implement and manage the creation, operation and permitting of nonprofit hatcheries. How were the nonprofit hatcheries to get permits if the Board of Fisheries is required to promulgate regulations to implement the same sections as delegated to the Commissioner? The decision was to place the implementation of the nonprofit hatcheries and permitting and comprehensive planning with the Commissioner. And leave the allocation of the fish in the common property water to the Board of Fisheries.

AS 16.10.440 was amended to read:

> (a) Fish released into the natural waters of the state by a hatchery operated under AS 16.10.400 – 16.10.470 are available to the people for common use and are subject to regulation under applicable law in the same way as fish occurring in their natural state until they return to the specific location designated by the department for harvest by the hatchery operator.

> (b) The Board of Fisheries may, after the issuance of a permit by the commissioner, amend by regulation adopted in accordance with AS 44.62 (Administrative Procedure Act), the terms of the permit relating to the source and number of eggs, the harvest of fish by hatchery operators, and the specific locations designated by the department for harvest. The Board of Fisheries may not adopt any regulations or take any action regarding the issuance or denial of any permits required in AS 16.10.400-16.10.470.

This amendment is confusing and is causing a great deal of angst among the Board and hatchery operators. What does it mean? The legislature could have just adopted the last sentence and said the Board of Fisheries may not adopt any regulations or take any action. But the legislation includes three carve outs of authority for the Board. Two of the provisions make sense in terms of the Board authority to deal with allocation of fish in the common property. The harvest of fish by hatchery operators and the specific locations. The third provision relating to the source and number of eggs is creating confusion in terms of the management, long term planning and operation of non- profit hatcheries.

My recollection of the history of this section is related to the need to harvest the initial brood stock from wild salmon spawning streams. At the time (1978-79), there was a lot of discussion of how and where to source the initial brood stock and how that may impact the production of wild salmon streams. The selection of the streams for hatchery brood stock involved discussion at the Regional Planning Team, between regional hatchery managers and the Department and the US Forest Service. Access to many streams involved crossing Forest Service land. Setting up temporary camps on streams. Building weirs in the streams to trap salmon. Deciding how many salmon to harvest for hatchery brood stock. Impact of the brood stock taking on the overall production of that stream. It was complicated. And getting it right was important.

This section provided a means for the Board of Fisheries to act upon a permit granted by the Commissioner for the egg take from wild salmon stocks in specific stream. The Board of Fisheries never reviewed or questioned any of the Commissioner decisions on collection of the initial brood stock for hatchery from wild salmon streams either in the state owned and operated hatcheries or the private non-profit hatcheries.

In looking back at this section (b) that is the only conclusion I draw. It was intended for the Board to have an opportunity to look at the gathering of hatchery brood stock from wild salmon streams. The other sections in .440(b) relate to the Board authority for harvest of salmon in the common property including harvest by hatchery operators. The provision dealing with amending permits for source and number of eggs does not fit with the scope of the overall statutory design to place authority for oversight of non-profit hatchery with the Commissioner and allocation of salmon in the common property with the Board of Fisheries.

It is my opinion the reference that the Board may amend a permit issued by the Commissioner relating to the source and number of salmon eggs was intended to apply to the initial egg take of brood stock from the wild streams.

It was not intended to be a vehicle for the Board to step in at any time on a permit by permit basis to amend or revoke permits issued regarding sources and number of salmon eggs taken from stocks returning to the hatcheries or transferred between hatcheries. If that were the case the entire statutory framework for management and operation of non-profit hatcheries is upended. The planning, operations, financing, site selection is placed in limbo. And subject to intervention by the Board of

Fisheries on an ongoing basis. Either through emergency action or through the regular Board cycle. The unknown factor looms very large in every decision. This is what the original planners and drafters of the non-profit hatchery program were trying to avoid.

It is difficult to envision what and how a Board regulation would look like in terms of amending a permit? What criteria would be used? How would the impacts be measured? How would it affect the financial structure of the company? All these issues are considered by the Commissioner when granting the permit. There is a process through the Regional Planning Team, public hearings and staff recommendations to arrive at the decision.

The last sentence in subsection (b) was included as a definitive statement that the Board of Fisheries may not adopt any regulations or take any action regarding the issuance or denial of any permits required in AS 16.10.400 – 16.10.470. When this section is read in the context of the of the statutes dealing with non- profit hatcheries it is clear the legislature put the Commissioner in charge of the non-profit hatcheries. And the Board of Fisheries with the authority to regulate the harvest of salmon in the common property.

There is a robust and comprehensive process set out in the statutes providing for public comment and input into the decision-making structure for managing nonprofit hatcheries. If there is a problem or issue that arises after a permit is issued the Commissioner can make a finding the hatchery is not in the best interest of the public and alter the conditions of the permit under AS 16.10.430. There are examples of the Commissioner using the power granted in the statutes to deal with breaches of permits. The Commissioner closed the Meyers Chuck hatchery due to noncompliance. And, revoked the permits for Alaska Aquaculture due to default on debt. There are ways and means built into the existing statutes to deal with many of the issues of concern.

I strongly recommend the Board not to attempt to use the reference to source and number of salmon eggs in AS 16.10.440(b) as a vehicle to amend permits issued by the Commissioner under the nonprofit hatchery statutes.

ASHBURN & MASON P.C.

LAWYERS

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July 9, 2018

VIA EMAIL: dfg.bof.comments@alaska.gov

Chairman John Jensen
Alaska Board of Fisheries
P.O. Box 115526
Juneau, AK 99811-5526

Re: **Public Comments of Ashburn & Mason, P.C., Counsel for Prince William Sound Aquaculture Corporation In Opposition To May 16, 2018 KRSA et al. Emergency Petition Regarding VDFA Hathcery Production (Comment Due Date July 9, 2018).**

Dear Chairman Jensen and Members of the Board of Fisheries,

Ashburn & Mason, P.C., counsel to Prince William Sound Aquaculture Corporation ("PWSAC"), submits the following opposition and public comments to the above-referenced petition:

INTRODUCTION

Petitioners ask the Board to declare an emergency and reduce the current permitted salmon production at Valdez Fisheries Development Association's ("VFDA") Salmon Gulch Hatchery. The Department of Fish and Game (the "Department") granted VFDA's production permit in 2014, which provided for gradual production increases on a yearly basis. In year three of the permit, Petitioners now ask the Board to declare an

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"emergency" and essentially veto this permit without engaging in the notice and comment rulemaking required by statute. The Petition establishes no "emergency," nor does the Board of Fisheries ("Board") have the statutory authority to veto the Department's prior permit decision regarding salmon production.

A permit granted four years ago does not qualify as an "emergency" under any definition of the word, let alone the strict definition governing emergency petitions under Alaska law. By statute, true regulatory emergencies are held to a minimum and rarely found.[1] The reason for this strict standard is that enacting regulations outside of the notice and comment rulemaking procedures mandated by the Administrative Procedure Act is strongly disfavored. Here, establishing an emergency requires "unforeseen" and "unexpected" threats against fish and game resources.[2] VFDA's long-standing permit is neither unforeseen nor unexpected. The fact that Petitioners chose not to engage in the public process leading to the permit grant does not make the permit "unforeseen."

Even if there were an emergency, the Board lacks statutory authority to grant the relief requested by Petitioners. As set forth in detail below, the legislature invested the Department with the legal duty to oversee all aspects of hatchery creation, operation, and

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[1] AS 44.62.270.

[2] 5 AAC 96.625(f).

production,[3] including but not limited to how many fish hatchery operators are allowed to incubate and release each year. By statute, the Department, not the Board, regulates hatchery activities that directly impact production levels, such as the harvest of eggs from hatchery broodstock.[4] The Board, on the other hand, is tasked with regulating and allocating the harvest of both hatchery and wild salmon among all user groups that the hatcheries were established to serve, including commercial, personal use, sport, subsistence, and hatchery cost recovery.[5] The Department and the Board have respected and abided by this division of labor and authority for over 30 years. To our knowledge, the Board has never before attempted to second guess a decision by the Department to authorize a specific level of egg take in a hatchery permit.

The Petition seeks to disrupt this well-established division of authority by interjecting the Board into the realm of production management. Specifically, the Petition asks the Board to micro-manage egg take levels from hatchery broodstock, which is squarely within the Department's sphere of authority and expertise, and outside the Board's jurisdiction over allocation of harvest levels. The Petition's only ground for this change in the *status quo* is a narrow statutory subsection, AS 16.10.440(b), addressing

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[3] AS 16.10.400-.470; 5 ACC 40.005-.990.

[4] AS 16.10.445; 5 AAC 40.300; 5 AAC 40.340; 5ACC 40.840.

[5] *E.g.*, AS 16.05.251.

the Board's authority to amend hatchery permits regarding the "source and number of salmon eggs." This provision cannot bear the weight Petitioners place on it.

When this statute was enacted in 1979, the legislative's reference to "the source and number of salmon eggs" almost certainly referred to the collection of *wild* salmon eggs, before the hatcheries' cost recovery operations had been fully established. Back in 1979, collection of salmon eggs from wild stocks involved the harvest of wild salmon still swimming out in the ocean. In those early days, egg take had a potential to affect the Board's allocative decisions. By contrast, hatchery egg take today is conducted entirely from returning hatchery broodstock, captured in terminal harvest areas, not out in the Sound, with little or no allocative implications.

Even if the statute could be construed to apply to eggs recovered from returning hatchery broodstock, it is an insufficient legal basis for disrupting the Department's comprehensive regulatory regime, which includes hatchery production planning and detailed permitting requirements. Again, the Board has jurisdiction over harvest levels, and the Department has jurisdiction over all aspects of hatchery production, including egg take levels.[6]

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[6] *E.g.*, AS 16.10.445, granting the Department exclusive authority over "the source and number of salmon eggs taken" by hatchery operators.

The Petition is also premature. The potential effects of hatchery fish straying into wild salmon streams, which is the stated impetus for the Petition, have been closely watched by the Department's biologists over the years. These effects are now the subject of an ongoing, in-depth scientific study. Until the study results are known, it is premature to consider curtailment of hatchery production that has already been permitted by the Department. Further, the Board has already stated its intent to address hatchery issues during its regular fall meeting cycle. These important issues can be addressed at that time where there is full opportunity for public participation and comment.

ABOUT ASHBURN & MASON AND PWSAC

Ashburn and Mason is submitting these comments, which focus on the relevant statutes, regulations, and established administrative practice, as a supplement to the comments submitted directly by the Prince William Sound Aquaculture Corporation ("PWSAC"). Ashburn & Mason has represented PWSAC since its creation in 1974. Our firm worked closely with PWSAC's visionary founders in the legislative process that resulted in the creation of the private nonprofit hatcheries ("PNPs") regional aquaculture associations, now codified at AS 16.10.375, *et. seq.*

PWSAC's founders were commercial fishers and community leaders who were responding to repeated wild salmon run failures, and the resulting economic distress throughout the Prince William Sound region in the early 1970s. Working together, the fishermen, local community representatives, the Department, and key legislators developed an innovative legal framework for the creation and operation of the state's PNPs and regional aquaculture associations.

Over the past 40-plus years, the statewide hatchery system has been a resounding success, and is an integral part of Alaska's world class sustainable fisheries. Alaska's hatcheries have generated tens of millions of dollars of economic benefit every year spread across all user groups, supplementing, but not displacing, the sustained yield of Alaska's wild salmon stocks. In fact, all of PWSACs hatcheries were started with salmon eggs collected originally from local wild stocks. The genetics of all Prince William Sound hatchery fish are therefore traceable back to local streams.

DISCUSSION

I. NO EMERGENCY EXISTS TO JUSTIFY THE PETITION TO RESTRICT VFDA'S PERMITTED EGG TAKE

By statute, true regulatory emergencies, which allow the Board to issue regulation without public notice and comment, are held to a minimum and rarely found.[7] This is because public notice and comment are essential to the fairness and transparency of

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[7] AS 44.62.270.

regulatory rulemaking in Alaska. The explicit state policy against the adoption of emergency regulations is so fundamental to the function of regulatory rule-making that it is codified in the Administrative Procedure Act.[8] The Commissioner's decision to deny the emergency Petition reflects this well-established policy and decades of Alaska law and regulation, and must be respected.

The Petition does not present an emergency. Rather, it challenges a permit granted several years ago. The narrow exception for adoption of emergency regulations is limited to "unforeseen" and "unexpected" threats against fish and game resources.[9] These threats must be so imminent that regulatory intervention cannot wait for the usual notice and comment process under the Administrative Procedure Act.[10] For example, the Board adopted an emergency regulation to reorganize the Chignik fishery in 2005 when the Supreme Court issued a decision invalidating the previous fishery rules just six weeks before the season was slated to open.[11] The Superior Court agreed that the timing of the Supreme Court's decision created a legitimate emergency because no one could

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[8] *Id.*

[9] 5 AAC 96.625(f).

[10] 5 AAC 96.625(f).

[11] As referenced *infra.* at 3-4, the Commissioner currently has standing authority to review petitions for emergency regulation. See, 2015-277-FB. Prior to the adoption of this policy in 2015, the Board retained the authority to review petitions for emergency regulation.

reasonably rely on when the Supreme Court would issue its decision, or what that decision would be. In addition to the "unexpected" and "unforeseen" nature of the Supreme Court's decision, the timing also created a sense of imminence. With less than six weeks before the fishing season opened, the Board "had to act quickly…because it had to have something in place for the June opening."[12]

Here, the Petition fails to demonstrate how VFDA's long-standing permit, or the current conditions in the Sound, present an unexpected or unforeseen situation threatening the salmon fisheries. No acute biological or environmental event has impacted the Sound or Cook Inlet in recent months, creating an unpredictable threat. Rather, the purported justification for an emergency petition is an alleged trend, observed over the last several *years*. There is no reason why the proposed Board action could not have been presented a year ago or, more to the point, why it could not wait until the next regularly scheduled Board meeting, which will provide a fuller and fairer opportunity for interested parties and members of the public to comment and participate in the process.

In short, the Commissioner properly exercised his authority under AS 16.05.270 and 2015-277-FB to determine that the Petition failed to present an emergency under the

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[12] See, *State of Alaska, Alaska Bd. of Fisheries v. Grunert,* 139 P.3d 1226, 1241 (Alaska 2006).

Administrative Procedure Act. For the reasons explained in the Commissioner's June 14, 2018 letter to Petitioners, emergency action is unwarranted under these circumstances.

II. THE BOARD DOES NOT HAVE VETO AUTHORITY OVER HATCHERY PRODUCTION PERMITS

A. The Commissioner Has Primary Authority Over Hatchery Permitting and All Hatchery Operations

1. History and Purpose of the Hatchery Program

The desire of Alaskans to manage their abundant salmon fisheries was a driving force behind Alaska Statehood.[13] The importance of protecting and developing natural resources such as salmon is embedded in the Alaska Constitution, which directs the legislature to "provide for the utilization, development, and conservation of all natural

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[13] *See, e.g.*, *Pullen v. Ulmer*, 923 P.2d 54, 57 n. 5 (Alaska 1996); Alaska Legislative Affairs Agency, *Alaska's Constitution: A Citizen's Guide* (4th ed. 2002) at http://w3.legis.state.ak.us/docs/pdf/citizens_guide.pdf (Many Alaskans concluded "that the notion of the federal government's superior vigilance as a trustee of the public interest was really a cloak for the institutional interests of bureaucrats and the economic interests of nonresident corporations exploiting those resources (principally Seattle and San Francisco salmon canning companies)."); HOUSE COMM. ON INTERIOR AND INSULAR AFFAIRS, *Act Providing for the Admission of the State of Alaska into the Union of 1957*, H.R. REP. No 85-624 (1958) (The Statehood Act "will enable Alaska to achieve full equality with existing States, not only in a technical juridical sense, but in practical economic terms as well. It does this by making the new State master in fact of most of the natural resources within its boundaries . . . ."); Univ. of Alaska Anchorage, Institute for Social and Economic Research, *Salmon Fish Traps in Alaska* (1999), at 14, at http://www.iser.uaa.alaska.edu/publications/fishrep/fishtrap.pdf ("Alaska political entrepreneurs used the [fish] trap issue to rally the citizens of the territory around the quest for statehood.").

resources belonging to the State, including land and waters." It also requires the legislature to make decisions that "provide for the maximum benefit of its people."[14] The Alaska Constitution proclaims that "fish, wildlife, and waters are reserved to the people for common use,"[15] and dictates that "Fish, forests, wildlife, grasslands, and all other replenishable resources belonging to the State shall be utilized, developed, and maintained on the sustained yield principle, subject to preferences among beneficial uses."[16] Further, the Constitution expressly references the goal of "promot[ing] the efficient development of aquaculture in the State," and protecting Alaska's economy from outside interests:[17]

> No exclusive right or special privilege of fishery shall be created or authorized in the natural waters of the State. This section does not restrict the power of the State to limit entry into any fishery for purposes of resource conservation, to prevent economic distress among fishermen and those dependent upon them for a livelihood ***and to promote the efficient development of aquaculture in the State.***

By the early 1970s, salmon runs were in steep decline throughout Alaska. In Prince William Sound, seining did not open at all in 1972 and 1974 due to dangerously

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[14] ALASKA CONST. art. VIII, § 2.

[15] ALASKA CONST. art. VIII, § 3.

[16] ALASKA CONST. art. VIII, § 4.

[17] ALASKA CONST. art. VIII, § 15. The Constitution has since been amended to provide for the limited entry permit system now in place, *See infra* n. 7, but the reference to promoting the "efficient development of aquaculture" remains unchanged.

low wild stock returns. In response, the State of Alaska resolved to restore the salmon fisheries. A constitutional amendment provided the basis for limited entry legislation for commercial fisheries,[18] and the state hatchery program was initiated through the creation of the Fisheries Rehabilitation & Enhancement Division (FRED).[19]

Under AS 16.05.020, the Commissioner must "manage, protect, maintain, *improve, and extend* the fish, game ... of the state in the interest of the economy and general well-being of the State." The Department is further required to: "develop and continually maintain a comprehensive, coordinated state plan for the orderly present and long-range rehabilitation, *enhancement*, and development of all aspects of the state's fisheries for the perpetual use, benefit, and enjoyment of all citizens" and "through rehabilitation, *enhancement*, and development programs do all things necessary to ensure perpetual *and*

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[18] AS 16.43.400 *et seq.* Alaska's limited entry fishery essentially provides that only permit holders may engage in commercial fishing. The granting of these permits, and the management of the commercial fisheries, are tightly regulated by numerous state agencies including the State Commercial Fisheries Entry Commission (CFEC), the Alaska Department of Fish & Game (ADF&G), and the Board of Fisheries (BOF). *See generally Johns v. CFEC*, 758 P.2d 1256, 1263 (Alaska 1988) ("The Limited Entry Act has two purposes: enabling fishermen to receive adequate remuneration and conserving the fishery.").

[19] AS 16.05.092. As explained more fully below, FRED no longer exists as a distinct division within the Department. However, the operation of most or all of the original hatcheries owned and operated by FRED has been transferred to the regional aquaculture associations, under long-term professional services agreements. PWSAC, for example, currently operates the Cannery Creek, Main Bay, and Gulkana Hatcheries, all of which were constructed and initially operated as FRED hatcheries in the early 1970s.

increasing production and use of the food resources of state waters and continental shelf areas."[20] Similarly, the Department is required generally to "manage, protect, maintain, *improve, and extend* the fish, game and aquatic plant resources of the state in the interest of the economy and the general well-being of the state."[21] The Department is also generally charged to do everything possible to assist with hatchery operations.[22]

In addition, the legislature created the Fisheries Enhancement Revolving Loan Fund to promote the enhancement of Alaska's fisheries by, among other things, providing long-term, low-interest loans for hatchery planning, construction, and operation.[23] PWSAC has received significant support from this program over the years, particularly for capital investments.

In 1974, the FRED state-owned and managed hatchery program was expanded to include private ownership of salmon hatcheries with the passage of the Private Non-Profit (PNP) Hatchery Act.[24] The Act stated that its purpose was to "authorize the private ownership of salmon hatcheries by qualified non-profit corporations for the purposes of

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[20] AS 16.05.092(3) (emphasis added).

[21] AS 16.05.020(2) (emphasis added).

[22] AS 16.10.443.

[23] AS 16.10.500-.560; *see generally* Alaska Division of Investments, "Fisheries Enhancement Revolving Loan Fund Program Overview," April 2007 at http://www.commerce.state.ak.us/investments/pdf/FEover07.pdf.

[24] These provisions are now codified at AS 16.10.375 *et seq.*

contributing, by artificial means, to the rehabilitation of the State's depleted and depressed salmon fishery." Further, as noted above, a separate fisheries enhancement loan program was created in 1976 to provide state financing for nonprofit hatcheries.[25]

Over time, the State has transferred operation of some of the FRED hatcheries to other entities, including the nonprofit hatcheries operated by the regional aquaculture associations, concluding that it would be more cost-effective for these hatcheries to be operated by the regional associations. The legislature specifically authorized the sub-contracting of state hatcheries in 1988,[26] acknowledging that after 17 years of the State planning, building and operating hatcheries, Alaska sought an even more efficient way of ensuring a healthy, robust, and sustainable salmon fishery.[27]

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[25] AS 16.10.500 *et seq.; see also State Commercial Fisheries Entry Comm'n v. Carlson*, 65 P.3d 851 (Alaska 2003) ("The state operates a revolving loan fund to support investments in developing and operating fish hatcheries and other fish enhancement projects.").

[26] AS 16.10.480.

[27] Alaska's partnership with the nonprofit hatcheries is unique. Almost all states operate hatcheries of some kind (salmon, trout, walleye, catfish, etc.), but no state operates a hatchery program like Alaska's, and no state works with private nonprofit entities to assist the state government in its hatchery programs. By way of example, California has 21 state hatcheries (http://www.dfg.ca.gov/fish/Hatcheries/HatList.asp), Oregon has 33 state hatcheries (http://www.dfw.state.or.us/fish/hatchery/), and Washington has 91 state hatcheries (http://wdfw.wa.gov/hat/facility.htm), and all of these hatcheries are operated by the government.

Alaska law provides that the hatcheries may only be non-profit.[28] By design, the hatcheries are allowed to recover operating and capital expenses, as well as costs for research and development and expansion of the production system, including wild stock rehabilitation work.[29] The system is designed to provide benefits to the common property resource users. The nonprofit regional aquaculture associations have no stock-holders, owners, or members. Today, five regional aquaculture associations, from Southeast Alaska to Kodiak, including PWSAC, produce hatchery salmon for common property fisheries.

Thus, the Alaska Constitution, combined with numerous statutes, including those creating the Department of Fish and Game,[30] the Limited Entry Act,[31] the Private Non-Profit Hatcheries Act,[32] and the Fisheries Enhancement Revolving Loan Fund,[33] together

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[28] AS 16.10.380.

[29] AS 16.10.455.

[30] AS 16.05.010, *et.seq.*; *see also* 5 AAC 40.100-.990.

[31] AS 16.43.400 *et seq.* Alaska's limited entry fishery essentially provides that only permit holders may engage in commercial fishing. The granting of these permits, and the management of the commercial fisheries, are tightly regulated by numerous state agencies including the State Commercial Fisheries Entry Commission, the Alaska Department of Fish & Game (ADF&G), and the Board of Fisheries (BOF). *See generally Johns v. CFEC*, 758 P.2d 1256, 1263 (Alaska 1988) ("The Limited Entry Act has two purposes: enabling fishermen to receive adequate remuneration and conserving the fishery.").

[32] AS 16.10.375-480.

[33] AS 16.10.500-.560.

demonstrate a strong and long-standing state policy in Alaska of promoting hatchery development for the purpose of enhancing and ensuring the long-term vitality of Alaska's fisheries.

2. The Department Strictly Regulates All Aspects of Hatchery Creation, Operation, and Production

The Alaska Department of Fish and Game has been charged by the Alaska legislature with final authority over how many fish hatchery operations are allowed to incubate and release each year,[34] and to regulate all other details of hatchery operation.[35]

Pursuant to AS 16.10.375, the Commissioner must designate regions of the state for salmon production and develop a comprehensive salmon plan for each region through teams consisting of Department personnel and nonprofit regional associations of user groups. The Commissioner also has the task of classifying an anadromous fish stream as suitable for enhancement purposes before issuing a permit for a hatchery on that stream. As 16.10.400(f).

Of particular relevance to the issue presently before the Board, AS 16.10.400(g) requires a determination by the Commissioner that a hatchery would result in substantial public benefits and would not jeopardize natural stocks. The statutes also require the

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[34] AS 16.10.445; 5 AAC 40.300; 5 AAC 40.340; 5 AAC 40.840.

[35] AS 16.10.400-.470; 5 AAC 40.005-.990.

Department to conduct public hearings near the proposed hatcheries, and to consider comments offered by the public at the hearings before issuance of a permit.[36]

All state hatcheries are operated pursuant to a permit issued by the Department.[37] Standard permit conditions include: (1) provisions that eggs used for broodstock come from a source approved by the Department;[38] (2) no placement of salmon eggs or resulting fry into waters of the state except as designated in the permit; (3) restrictions on the sale of eggs or resulting fry; (4) no release of salmon before department inspection and approval; (5) destruction of diseased salmon; (6) departmental control over where salmon are harvested by hatchery operators; and (7) hatchery location to prevent commingling with wild stocks. [39]

Further, there is an intricate system of basic and annual hatchery plans that are reviewed annually by the Department and provide for performance reviews, and in

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[36] AS 16.10.410.

[37] AS 16.10.400; 16.40.100-.199; 5 AAC 40.110-.240.

[38] AS 16.10.445. This requirement is related to regulations regarding fish transport permitting. *See* 5 AAC 41.001-.100. These regulations provide that no person may transport, possess, export from the state, or release not the waters of the state any live fish unless that person holds a fish transport permit issued by the Commissioner.

[39] *See generally* McGee, *Salmon Hatcheries in Alaska – Plans, Permits, and Policies Designed to Provide Protection for Wild Stocks,* Published for 2004 American Fisheries Society Symposium, at 327.

appropriate cases, permit alterations.[40] The basic management plans include a complete description of the facility, including the special harvest area, broodstock development schedules, and description of broodstock and hatchery stock management.[41]

Year-to-year hatchery production is regulated through the annual management plans (AMPs) approved and adopted by the Department. For example, each year, PWSAC and the other PNPs across the state work with the Department, which ultimately formulates an AMP for each hatchery. That plan, among other things, determines the number of eggs the hatchery will collect, how the eggs will be collected, the number of fish it will incubate, and how many fish will be released from the hatchery.[42] The AMP also addresses how PNPs will conduct their cost recovery harvest at each hatchery and addresses other specifics of hatchery operation.[43]

3. The Board's Proper Role is to Allocate Harvest, Not to Override the Department's Permitting and Production Decisions

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[40] 5 AAC 40.800-990. As noted above, there is also an extensive Regional Comprehensive Planning Program established under AS 16.10.375 and 5 AAC 40.300-.370, with full public participation. This process creates Regional Planning Teams who are charged to "prepare a regional comprehensive salmon plan . . . to rehabilitate natural stocks and supplement natural production . . . ." 5 AAC 40.340.

[41] *See generally* McGee, at 329.

[42] 5 AAC 40.840.

[43] McGee, at 329.

The Board of Fisheries is established by AS 16.05.221, "for purposes of the conservation and development of the fishery resources of the state."[44] In general terms, the Board's duties complement those performed by the Department. While it has broad statutory authority, the Board has historically focused on allocation of fisheries resources between and among the various user groups and gear types. For example, under AS 16.05.251(a) the Board has the power to set time, area, and methods and means limitations on the taking of fish. Under AS 16.05.251(a)(3), the Board also establishes quotas, bag limits, and harvest levels. To the best of our knowledge, however, the Board has always deferred to the Department's expertise and experience with respect to the detailed management of hatchery permitting and production levels.

B. The Board Cannot Override Annual Hatchery Production Permits Issued by the Department

Petitioners contend that AS 16.10.440(b) grants the Board the authority to upend the Department's carefully constructed regulatory framework governing hatchery

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[44] AS 16.05.221.

production.[45] This interpretation of the statute reads it out of context and is inconsistent with its historical origins. Under Alaska law, this statutory provision must be construed in light of the overall statutory scheme governing Alaska's salmon hatcheries,[46] its legislative history and intent,[47] and over 40 years of consistent administrative interpretation and practice, during which the Board (to our knowledge) has never

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[45] AS 16.10.440 provides: (a) Fish released into the natural waters of the state by a hatchery operated under AS 16.10.400 - 16.10.470 are available to the people for common use and are subject to regulation under applicable law in the same way as fish occurring in their natural state until they return to the specific location designated by the department for harvest by the hatchery operator. (b) The Board of Fisheries may, after the issuance of a permit by the commissioner, amend by regulation adopted in accordance with AS 44.62 (Administrative Procedure Act), the terms of the permit relating to the source and number of salmon eggs, the harvest of fish by hatchery operators, and the specific locations designated by the department for harvest. The Board of Fisheries may not adopt any regulations or take any action regarding the issuance or denial of any permits required in AS 16.10.400 - 16.10.470.

[46] *See, e.g. Monzulla v. Voorhees* Concrete Cutting, 254 P.3d 341, 345 (Alaska 2011), *citing In re Hutchinson's Estate*, 577 P.2d 1074, 1075 (Alaska 1978), where the Supreme Court articulated the doctrine of *in pari materia*: the "established principle of statutory construction that all sections of an act are to be construed together so that all have meaning and no section conflicts with another."

[47] *See, e.g. Native Village of Elim v. State* 990 P.2d 1, 5 (Alaska 1999), *Kochutin v. State,* 739 P.2d 170, 171 (Alaska 1987) *citing Hammond v. Hoffbeck*, 627 P.2d 1052, 1056 & n. 7 (Alaska 1981).

attempted to use this statute as the basis for usurping the Department's traditional control over hatchery production.[48]

At the time Section 440(b) was enacted in 1979, the hatchery system was in its infancy. Most hatchery egg take was from wild stocks, not returning hatchery fish, which is how egg take is conducted today. The thinking at the time was that salmon eggs harvested from wild stocks were still a "public resource" while the fish were swimming out in the ocean, and the harvest of wild fish for egg take had allocation implications that could potentially fall within the Board's purview. In contrast, today's egg take procedures are conducted almost exclusively from returning hatchery broodstock that are captured in the special harvest areas directly in front of the hatcheries. At that point, the hatchery salmon cease to be a public resource and their capture and the collection of their eggs have very limited allocative implications. Further, as the Commissioner noted in his January 14, 2018 Memorandum to the Board on the subject of the current Petition, "the

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[48] *See e.g. Marathon Oil Co. v. State, Dep't of Nat. Res.*, 254 P.3d 1078, 1082 (Alaska 2011), *Premera Blue Cross v. State, Dep't of Commerce, Cmty. & Econ. Dev., Div. of Ins.*, 171 P.3d 1110, 1119 (Alaska 2007), and *Bullock v. State, Dep't of Cmty. & Reg'l Affairs*, 19 P.3d 1209, 1219 (Alaska 2001), where the Alaska Supreme Court held that agency decisions based on "longstanding, consistent and widely known" interpretations of agency expertise should be given "great weight."

Board's authority over the possession, transport and release of live fish had not been delegated to the department when AS 16.10.440(b) was amended."[49]

Moreover, the legislative history of Section 440(b) indicates that it was never intended to be used by the Board as back door means of overriding the Department's permitting authority or limiting hatchery production. The Resources Committee's letter of intent on HB 359, which included the language in question, states as follows:

> There are three other major changes made by the bill:
>
> (1) Section 2 of the bill amends AS 16.10.440(a)(b). The amendment clarifies the role of the Board of Fisheries. The role of the Board of Fisheries as envisioned by the original legislation was to regulate the *harvest* of salmon returning to the waters of the state. That role extends to regulating those fish which are returning as a result of releases from natural systems and also from hatchery releases. There are provisions in other specific locations for the harvest of salmon by the hatchery operator for sale, and use of the money from that sale, for the specific purposes as stated in AS 16.10.450. The added language clarifies that the Board of Fisheries may adopt regulations relating to the *harvest* of the fish by hatchery operators at the specifically designated locations. The Board of Fisheries in the past year or two has enacted regulations relating to those harvests for several of the private nonprofit hatcheries in the state.[50]

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[49] Memorandum from Sam Cotton, Commissioner, to John Jensen, Chair, dated January 14, 2018, Re: Emergency Petition to the Alaska Board of Fisheries requesting the Board to reverse a department decision to allow a 20 million increase in the number of pink salmon eggs to be harvested by VFDA in 2018.

[50] House Journal, March 15, 1979, pp. 601-602 (emphasis added).

The exclusive reference to regulation of harvest, and the absence of any mention of production controls, corroborates the conclusion that the legislature never intended to authorize the Board to limit hatchery production.

The Board's traditional function has always been to allocate harvests among competing user groups, not to regulate production of fish. This legislative history, with its emphasis on "harvest," is also consistent with PWSAC's long-held belief (apparently shared by the Department) that Section 440(b) was intended to cover egg take from wild salmon streams, not to apply to egg take from returning hatchery fish.

Further corroboration of this conclusion is found in AS 16.10.445(a), which unambiguously requires the Department, not the Board, to "approve the source and number of salmon eggs taken under AS 16.10.400-16.10.470." Additional evidence that the Department, not the Board, is responsible for regulating hatchery egg take can be found in 5 AAC 41.001, *et. seq.* For example, 5ACC 41.005 prohibits the release of hatchery fish without a permit issued by the Commissioner. Regulation of egg take and release of the resulting salmon fry are obviously two sides of the same coin. The regulatory scheme clearly and consistently assigns exclusive responsibility for regulating those two closely related hatchery activities to the Commissioner.

Given the legislative history, the 30-plus year pattern of administrative interpretation, the anomalous language in Section 440(b) regarding regulations to "amend…the terms of a permit," and the mandate of Section 445(b), it is quite clear that the Board has little or no role in regulating hatchery production, including but not limited to egg take permit restrictions.

Moreover, regulation of hatchery production by the Board would overlap and almost certainly conflict with the comprehensive and detailed hatchery regulations that are currently in place and operating effectively. As noted above, the Department has a rigorous permitting process for new hatcheries, 5 AAC 40.100-.240. There is an extensive Regional Comprehensive Planning program established under AS 16.10.375 and 5 AAC 40.300-.370, with full public participation. By regulation, the responsibility of the Regional Planning Teams is to "prepare a regional comprehensive salmon plan ... to rehabilitate natural stocks and *supplement* natural production . . ." 5 AAC 40.340 (emphasis added). As mentioned earlier, there is also an intricate system of basic and annual hatchery plans that are reviewed annually by the Department, performance reviews, and, in appropriate cases, permit alterations. 5 AAC 40.800-.900. Production levels are carefully monitored by the Department under these regulations and adjusted if necessary for economic or biological reasons. The Department's statutory authority for this intense level of hatchery regulation is quite clear, and there seems to be little room for the Board to insert itself into a very public process that has been working well for many years.

CONCLUSION

Back in the early 1970s, Prince William Sound experienced recurring wild salmon run failures, which caused serious financial distress throughout the region. In response, the framers of the Constitution and the Alaska Legislature took active and far-sighted steps to first establish a state run hatchery system and, shortly thereafter, the private non-profit and regional hatchery regime that has consistently stabilized the runs and enhanced salmon harvests throughout the state since 1976. Overall, Alaska's hatcheries have been a remarkable success and have helped the state's salmon resources to thrive and expand over the past 40 years, creating millions of dollars of positive economic impact, without any demonstrable harm to wild salmon stocks.

From the very beginning, every aspect of Alaska's hatcheries' creation, operation, and production have been closely supervised and regulated by the Department, with harvest area and allocation decisions made by the Board. This division of responsibility has served Alaska well for many years and there is no good reason to abandon it now.

For these reasons, the Board should deny the Petition.

ASHBURN & MASON, P.C.

Matthew T. Findley

for:

A. William Saupe

Laura C. Dulic

September 29, 2023

Alaska Department of Fish and Game

Board of Fisheries, Hatchery Committee

PO Box 115526

Juneau, AK 99811-5526

RE: Comments Regarding Hatcheries for the Board of Fisheries Hatchery Committee

Please accept this letter on behalf of The Conservation Angler (TCA), an international conservation organization focused on restoring runs of wild salmon and steelhead by using science-based measures to reshape fishery and hatchery management. TCA has worked in many rivers across the Pacific Rim and has spent the past three decades conducting conservation and research in the most pristine steelhead and salmon rivers in the world (Kamchatka Peninsula) to better understand the resilience, diversity, and productivity of wild populations.

We submit these comments for consideration by the Hatchery Committee (Alaska Board of Fisheries) in advance of its meeting on October 14, 2023.

Hatcheries have been widely used to propagate salmonids for purposes ranging from harvest to conservation, however, rapid expansion of hatchery production across the North Pacific beginning in the 1980s has also raised numerous concerns about their effects on wild salmonids in freshwater and the ocean. For example, a recent study synthesized peer-reviewed literature on salmonids from across the globe and identified 206 studies that examined whether hatchery fish had an adverse, positive, or neutral effect on wild salmonids (see McMillan et al. 2023, attached). Of those 206 publications, 83% reported some type or level of adverse effect on wild salmonids, most commonly through genetic interactions. Only 3% of the studies reported beneficial effects of hatcheries on wild salmonids, and the remaining 14% either documented no effect or the results were indeterminate. Importantly, McMillan et al. (2023) includes an online database containing all the publications in the review, which the Hatchery Committee may find useful.

The hatchery synthesis also identified 23 publications focused on potential interactions and effects associated with the abundance of pink and chum salmon in the North Pacific Ocean, many of which are from hatcheries, including those located in and around Prince William Sound. Among those studies, 14 reported some type or level of adverse impacts from hatchery salmonids, while three reported no effect.

A subsequent review by Ruggerone et al. (2023) (see attached) synthesized the effects of pink salmon on many organisms in the North Pacific Ocean. They provided strong evidence that pink salmon initiate pelagic trophic cascades and adversely affect the growth, survival, productivity, and abundances of forage fishes, squid, other Pacific salmon, seabirds, humpback whales, and killer whales. This research should interest the Hatchery Committee because of the high number of hatchery pink salmon being released in Alaska and the likely impacts those releases are having on the state's wild fish stocks and commercial, recreational, tribal, and subsistence fisheries.

Thank you for the opportunity to comment and provide research for consideration.

Please reach out if you have any questions.

Sincerely,

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Fisheries Management and Ecology

WILEY

REVIEW

A global synthesis of peer-reviewed research on the effects of hatchery salmonids on wild salmonids

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Abstract

Hatcheries have long produced salmonids for fisheries and mitigation, though their widespread use is increasingly controversial because of potential impacts to wild salmonids. We conducted a global literature search of peer-reviewed publications (1970–2021) evaluating how hatchery salmonids affected wild salmonids, developed a publicly available database, and synthesized results. Two hundred six publications met our search criteria, with 83% reporting adverse/minimally adverse effects on wild salmonids. Adverse genetic effects on diversity were most common, followed by effects on productivity and abundance via ecological and genetic processes. Few publications (3%) reported beneficial hatchery effects on wild salmonids, nearly all from intensive recovery programs used to bolster highly depleted wild populations. Our review suggests hatcheries commonly have adverse impacts on wild salmonids in freshwater and marine environments. Future research on less studied effects—such as epigenetics—could improve knowledge and management of the full extent of hatchery impacts.

KEYWORDS

artificial propagation, hatchery salmonids, hatchery supplementation, salmonid captive-breeding, salmonid enhancement, salmonid stocking

1 | INTRODUCTION

For over one hundred years, hatcheries have been used to propagate and release salmonids across the globe (Jonsson, 1997; Waples, 1991; Zaporozhets & Zaporozhets, 2004), largely to subsidize fisheries, attempt to mitigate for habitat loss and overexploitation (Araki & Schmid, 2010; Hilborn, 1992; Maynard & Trial, 2014) and, more recently, to try to rebuild depleted populations of wild salmonids (Berejikian & Van Doornik, 2018; Hagen et al., 2021; Hess et al., 2012). Hatchery salmonids currently underpin many recreational, commercial, and (in the lower-48 of the United States in particular) legally obligated mitigation and tribal treaty fisheries, but the pervasive reliance on hatcheries remains contentious (Claussen & Philipp, 2022; Harrison et al., 2019; Kleiss, 2004). Although there is substantial evidence that hatchery salmonids generally have lower relative fitness than wild salmonids (Bouchard et al., 2022; Christie et al., 2014; Milot et al., 2013), continuing debate centers on the broad potential effects of releasing hatchery salmonids into nature and their potential impacts on sympatric wild salmonids (see Section 2 and Figure 1 for the definition of effect and impact), particularly when it comes to recovery of threatened and endangered populations (Araki & Schmid, 2010; Paquet et al., 2011; Young, 2013).

Evaluating and synthesizing the breadth of potential hatchery effects is complicated, however, because results may depend on several factors. For instance, while adverse effects on wild salmonids have been commonly reported, others have found beneficial effects (Maynard & Trial, 2014; Miller et al., 1990; Naish et al., 2007), and publications cover a range of potential effects on different "Viable Salmonid Population parameters" (VSP: McElhany et al., 2000)—distribution (Laffaille, 2011), diversity (Bernaś et al., 2014), abundance (Willmes et al., 2018), and productivity of wild salmonids (Nickelson, 2003)—that may occur through different pathways such as ecological or genetic processes (Allendorf, 1991; Flagg et al., 2000; Neff et al., 2011), disease (Lamaze et al., 2014), or fishing (Hilborn & Eggers, 2000; Naish et al., 2007). Further, responses can differ among species (Araki & Schmid, 2010); the existing body of literature encompasses numerous salmonid species, and within species, there can be very different life histories such as individuals that migrate to the ocean and back (anadromous) or remain and mature in freshwater (resident) (Gossieaux et al., 2019; Maynard & Trial, 2014; Naish et al., 2007).

The source broodstock and intent of the hatchery program could also influence the type and magnitude of effects on wild fish. Traditional "production" type hatchery programs generally breed only hatchery individuals, often from a non-local source, and stock them to provide fisheries, and consequently, their effects could differ from modern "supplementation" programs that integrate some wild fish into their broodstock (to reduce genetic impacts) and release fish to enhance fisheries and the number of naturally spawning adults (Araki & Schmid, 2010; HSRG, 2015; Naish et al., 2007, Table 1). Moreover, smaller-scale "recovery" programs, including some captive breeding efforts, that rely solely on wild fish as broodstock to provide a short-term, conservation boost to highly depleted wild populations (Berejikian & Van Doornik, 2018; Janowitz-Koch et al., 2019) may offer more conservation benefits to wild salmonids than longer running supplementation programs that try to achieve multiple goals (Bowlby & Gibson, 2011; Naish et al., 2007).

Finally, large releases of hatchery salmonids also raise the potential for ecological effects in the North Pacific Ocean (Ruggerone & Irvine, 2018). An emerging body of research suggests hatchery salmon have triggered density-dependent responses in several co-mingling populations of wild salmonids, including but not limited to, reduced survival (Fukuwaka & Suzuki, 2000; Cunningham et al., 2018), growth (Kaeriyama et al., 2011), fecundity (Shaul & Geiger, 2016), and body size and abundance (Ruggerone et al., 2012).

The immense body of literature makes it difficult to interpret the information and results succinctly (Araki & Schmid, 2010). Research on the potential effects of hatchery salmonids on wild salmonids dates to the early-1900s and spans numerous species and three continents (Jonsson, 1997; Lichatowich, 2001; Maynard & Trial, 2014; Zaporozhets & Zaporozhets, 2004). In practice, scientists, managers, and policymakers may be familiar with studies in their region and on species they are tasked with managing and conserving but may be unaware of research outside their immediate scope of focus. For example, there have been numerous hatchery studies on Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) that commonly reference one another (Horreo et al., 2014; Nilsson et al., 2008) and there are several publications on brook charr (*Salvelinus fontinalis*) (Bruce et al., 2020; Létourneau et al., 2018; Marie et al., 2010), yet those results are rarely cited or utilized in research on Pacific Salmon and vice-versa (e.g., Tatara & Berejikian, 2012; Wang et al., 2002). Accordingly, while several studies have reviewed hatchery effects on wild salmonids (Fraser, 2008; Naish et al., 2007), few have covered both *Oncorhynchus* and *Salmo* spp. (e.g., Araki & Schmid, 2010; Maynard & Trial, 2014), and to our knowledge, none have attempted to account for the entire breadth of publications for all species across the globe from freshwater to the ocean.

An evaluation of the overall body of peer-reviewed literature seems particularly valuable given the ongoing debate over hatchery practices in the western United States and other regions where salmonid recovery efforts are underway. A synthesis of publications from across the globe, covering various species and spanning freshwater and saltwater ecosystems would consolidate a broad array of literature and findings, and offer comprehensive insight into the patterns and processes of how hatchery salmonids potentially affect wild salmonids (Figure 1). For example, a synthesis could help determine: (1) How many studies have been published and how is the research distributed by year, country, species, and life history? (2) What proportion of publications reported adverse or beneficial hatchery effects on wild fish and how did those results vary by year, country, species, and life history? (3) Do potential effects differ based on the type of hatchery program? (4) Which VSP parameters (abundance, productivity, diversity, spatial distribution: McElhany et al., 2000) are most affected and what are the most common pathways of hatchery influence, such as genetic or ecological processes? and, (5) How many publications have evaluated potential hatchery effects in the open ocean and what are the general results so far? In turn, such an effort would help illuminate gaps in knowledge and areas for future research, increase the breadth of information available to decision-makers, and improve opportunities for collaborative research among scientists across different regions and countries.

2 | METHODS AND SYNTHESIS

2.1 | Objective and focus

Our objective was to collate all relevant peer-reviewed publications from across the globe and synthesize the main results—as presented by the authors—to answer broad-scale questions that are important to those tasked with researching, managing, and conserving salmonids (Figure 1). We also sought to incorporate the publications into an easily accessible database that can serve as a standing resource and be updated by scientists as new information comes to light (Appendix S1). In this effort, we reviewed only publications that explicitly and quantitatively evaluated whether stocking of hatchery salmonids affected the diversity, abundance, productivity (including effects on growth and survival as components of productivity), and distribution of wild salmonids via genetics, ecology, fishing, or disease (e.g., Berejikian & Van

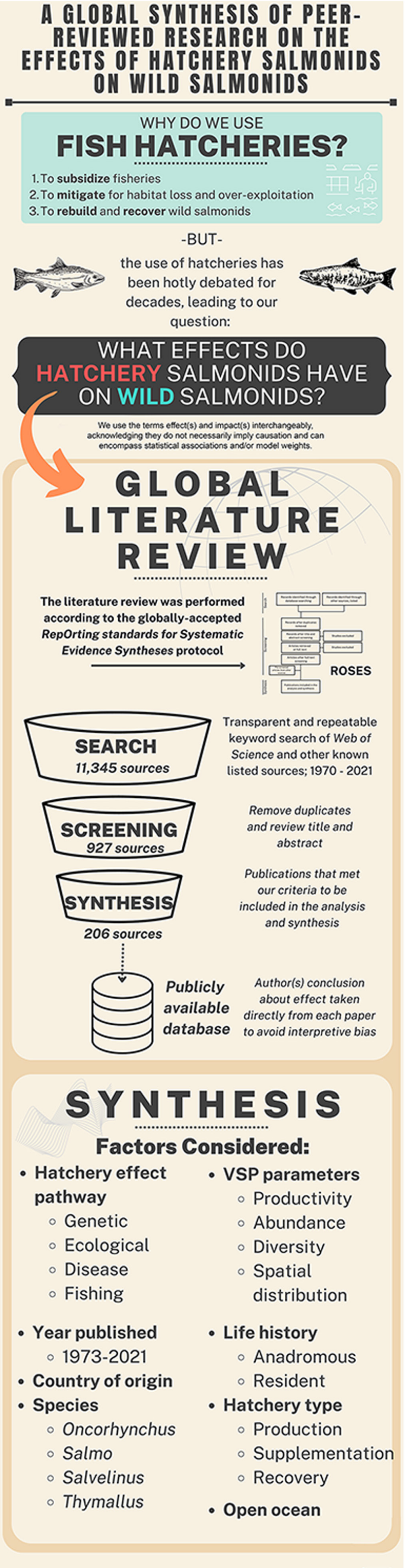

FIGURE 1 Infographic displaying the rationale for the synthesis of research on how hatchery salmonids affect wild salmonids, how we define the terms effect(s) and impact(s), the literature search process, and the factors we considered when evaluating results from each publication. Although we identified 206 total publications, there are 207 total entries because Levin and Williams (2002) was counted twice, once for an adverse effect and once for no effect.

Doornik, 2018; Reisenbichler & Rubin, 1999). We did not seek to review publications that only compared *differences* between hatchery and wild salmonids, such as studies on the relative fitness of hatchery and wild individuals (e.g., Christie et al., 2014) unless the research also directly evaluated whether those effects influenced the recipient wild population of salmonids (e.g., Araki et al., 2009). Similarly, though epigenetic influences (i.e., effects arising through altered gene expression rather than changes to the genetic code) are increasingly recognized as important mechanisms for domestication (Le Luyer et al., 2017), we did not include epigenetic studies here because so far they have not directly addressed impacts to VSP characteristics in wild populations (but see Section 4 for emphasis that this topic deserves greater attention, and future iterations of our database will incorporate relevant studies as they become available). Ours was not a formal meta-analysis of quantitative effects, nor an assessment of fisheries that hatcheries can provide unless the study also examined whether fisheries potentially affected wild salmonids. Last, we use the terms effect(s) and impact(s) interchangeably, acknowledging they do not necessarily imply causation and can encompass statistical associations and/or model weights.

2.2 | Literature search

We conducted a literature search of peer-reviewed global publications focused only on research that directly evaluated how releases of hatchery salmonids potentially affected VSP characteristics of wild salmonids (*Oncorhynchus*, *Salmo*, *Salvelinus*, *Thymallus*) living in nature. We did not find any relevant literature on *Hucho or Coregoninae*. We used a modified search strategy based on guidelines from the Collaboration for Environmental Evidence for conducting a literature synthesis (Haddaway et al., 2018; Pullin et al., 2022: Figure 2). We started our search date with 1970 because preliminary searches found few publications prior to 1970 that matched our criteria (Table 2). Primary publications from 1970 (capturing a ramping up of searchable, relevant research) through May 29, 2021, were discovered via two English language searches in Web of Science (WOS) (Figure 2). We then reviewed a broad suite of publications to identify appropriate search terms that were relevant to our topic of interest and covered the array of descriptors used to characterize potential effects of hatchery salmonids on wild salmonids. Based on this foundation, we conducted a topic search (TS) using the descriptors: TS=(((hatcher* OR supplement* OR stock* OR enhance* OR artificial production* OR captive born OR introduced) AND (salmon* OR salmoni* OR steelhead OR char OR trout OR Oncorhynchus OR Salvelinus OR Salmo OR Grayling)) AND (effect* OR affect* OR outcome* OR respon* OR result* OR reestablish* OR restor* OR recover* OR collaps* OR influence* OR impact* OR chang* OR alter* OR increas* OR decrease* OR strength* OR weak* OR prevent* OR eliminat* OR assist* OR improv* OR reduc* OR replace* OR benefit* OR differ* OR consequenc* OR implicat* OR contribut* OR compensat* OR imped*

TABLE 1 Definition, description, and alternative terms used to classify different types of hatchery programs found in the literature review.

Hatchery type	Source of broodstock	Intent	Also referred to as
Production	Uses all or nearly all hatchery fish for broodstock, often but not always founded on non-local or non-native stock	Produce fish to support fisheries; rarely have conservation intent	Traditional, stocking, planting, releasing, supplementation, ocean ranching
Supplementation	Uses a proportion of wild fish as broodstock to help integrate hatchery and wild gene pool	Enhance fishery and supplement wild/natural populations, often run indefinitely	Supplementation, enhancement, conservation, supportive breeding
Recovery	Uses all or almost all wild fish for broodstock to fully integrate hatchery and wild gene pool	Rebuild wild populations by providing boost in abundance, sometimes no fishery focus, and temporary	Supplementation, enhancement, supportive breeding, captive breeding, conservation

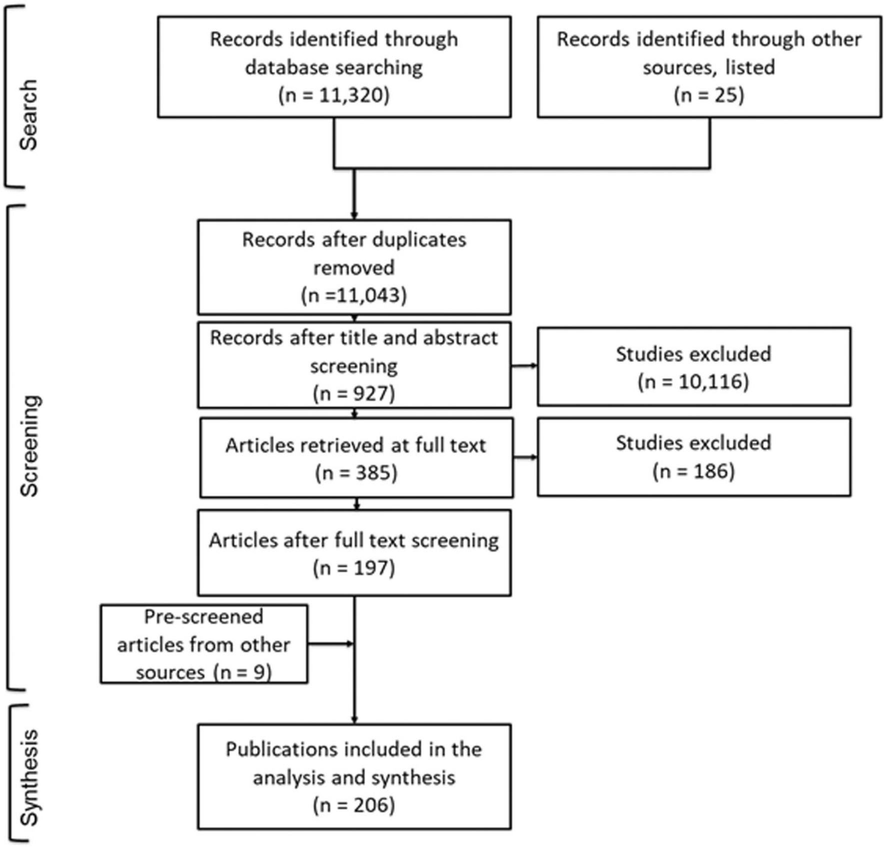

FIGURE 2 Flow diagram of the literature review process based on ROSES (RepOrting standards for Systematic Evidence Syntheses) flow diagram for systematic reviews (Collaboration for Environmental Evidence, 2018).

OR threat* OR caus* OR mask*) AND (gene* OR competition OR divers* OR producti* OR distribut* OR abundan* OR fitness OR demograph* OR evolution* OR ecolog* OR diverge* OR introgress* OR integrity* OR structure* OR life histor* OR portfolio OR size OR tim* OR space* OR spatial* OR densit* OR density dependen* OR growth OR surviv* OR predat* OR composit* OR interbreed* OR status OR trend OR hybrid* OR biomass OR disease* OR rate OR duration OR resilien* OR habitat* OR interspecific OR intraspecific OR regime OR manage*)). Next, we conducted a title search (TI) in WOS using the same descriptors.

2.3 | Selection process and criteria for inclusion

The WOS search revealed 11,320 potential publications, including 10,867 in the topic search and 453 in the title search (Figure 1). Following the decision tree outlined in Figure 2, duplicates were removed, and titles and abstracts were screened manually to identify publications that met the criteria to be eligible for our review (Table 2). To be included, first, the publication had to have been peer-reviewed and provide empirical data or a model that evaluated whether hatchery salmonids, via genetics, ecology,

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TABLE 2 Criteria for inclusion of publications found during the search, including the type and year of the publication, hatchery type, the study focus, and review articles.

Criteria	Include	Exclude
Publication and years	Peer-reviewed in primary literature; 1970–2021	Non-peer-reviewed; prior to 1970
Hatchery type	Any production, supplementation, or recovery hatchery where fish are purposely released into nature	Net-pens where fish are not purposely released into nature
Study focus	Examined genetic, ecological, fishing, and/or disease effects of hatchery salmonids on wild salmonid abundance, productivity, diversity, and distribution	Examined how hatchery rearing and production affected wild salmonid performance, behavior, and traits (e.g., fitness of wild fish vs. hatchery fish)
Review publications	Contain new analyses, previously unpublished data	Summarize existing publications, no new analyses and/or data

TABLE 3 The sub-set of information for each publication that we used in our synthesis and summaries.

Attribute	Definition and/or classification
Year	Year study was published
Location	State, province, country of research
Hatchery species	Species of salmonid(s) that were studied
Life history	Did study focus on anadromous or freshwater resident (including freshwater migratory) species, or both
Habitat	Denotes whether study was conducted in freshwater or ocean or both
Hatchery type and intent	Hatchery classified as production, supplementation, recovery, or a combination thereof based on criteria in Table 1
Hatchery effect pathway	Denotes whether study examines, (1) genetic, (2) ecological, (3) fishing, or (4) disease effects, or combination thereof, on wild fish due to the presence of hatchery fish
Viable Salmonid Population parameter	Denotes whether study evaluates productivity, abundance, diversity, spatial distribution, or combination thereof
Genetic effect	Denotes which genetic attribute was analyzed, including diversity, population structure, effective population size, or a combination thereof
Effect on wild fish	Denotes whether hatchery effect on wild fish is adverse, minimally adverse, indeterminate, beneficial, or no effect if authors did not find any statistically significant effect

Note: See Table S1 in Appendix S1 for full description of all information included in the entire database.

fishing, or disease (i.e., hatchery effect process: Table 3), influenced VSP parameters that are fundamental to the viability of wild salmonids (McElhany et al., 2000). This also included publications that examined intra- and inter-species impacts of large releases of hatchery salmonids into the North Pacific Ocean (e.g., Frost et al., 2020; Ruggerone et al., 2012). Second, publications had to focus on hatchery programs that purposefully released fish into nature for fishing or conservation or both; we excluded publications on the effects of farmed salmon raised in net pens for direct consumption. Third, the search revealed numerous review articles. To minimize potential duplication, we only included reviews that contained new data or new analysis of previously collected data. Fourth, we excluded studies on inter-species impacts of introduced non-native resident salmonids, such as effects of non-native hatchery rainbow trout (*O. mykiss*) on native cutthroat trout (*O. clarkii*) in the United States' Intermountain West, because those results are clearly understood to be negative (Dunham et al., 2004; Hansen et al., 2019; Seiler & Keeley, 2009). Last, after reviewing papers on potential effects of hatchery salmonids in the open ocean, we identified and included an additional nine publications that were not found in the formal literature review (Figure 2).

2.4 | Classification and database of publications

We reviewed the full text of every publication that met our criteria with a strong focus on information that was most relevant to our synthesis, such as the study questions, the location and description of the hatchery programs, and the results of potential impacts on wild salmonids. Next, each publication was entered into a database created in R Core Team (2022), provided in Appendix S1, and classified according to several relevant basic attributes so that each article entry includes associated columns with the authors, year, journal, DOI, the abstract, country, hatchery species, species interaction (e.g., intra- or inter-species hatchery effect), habitat (freshwater or ocean), life history (anadromous or freshwater resident or both), and study approach, which denoted whether it was an observation, model, experiment, or combination thereof (Table S1), but we only used a subset of these attributes in our analysis (Table 3).

We then classified the hatchery type and intent as production, supplementation, or recovery because previous studies (e.g., Berejikian & Van Doornik, 2018; Bingham et al., 2014; Bowlby & Gibson, 2011) and reviews (Araki & Schmid, 2010; Maynard & Trial, 2014; Naish et al., 2007) suggest potential effects on wild salmonids may vary in relation to the goal and broodstock sources of the hatchery program. We used criteria in Table 1 to define: (a) production hatcheries as those that solely or mostly use hatchery fish for broodstock, often but not always consisting of non-local or non-native strains, to produce fish for fisheries; (b) supplementation hatcheries as those that use a mixture of wild and hatchery fish for broodstock to improve genetic integration of the two populations and produce fish both to enhance fisheries and supplement natural spawners (e.g., Naish et al., 2007); (c) recovery hatcheries as those that use all or almost all wild fish for broodstock, including some captive brood programs, and produce fish solely to rebuild depleted stocks of wild salmonids (e.g., Berejikian & Van Doornik, 2018). Less commonly, we classified studies as including a combination of the different types of hatchery programs, such as Chilcote et al. (2011) which evaluated multiple stocks with a mixture of supplementation and production hatcheries.

Classifying the hatchery types was not always clear-cut, however. For instance, some publications used the term supplementation to describe the intent of hatchery programs that used non-local strains to "supplement" fisheries (e.g., Baer & Brinker, 2010; Baillie et al., 2016). Because they used non-local stocks and the hatchery releases were focused on production for fisheries, we classified them as production programs to be consistent with our criteria. In others, it was not clear from where the hatchery brood originated, but it was clear the focus was on fisheries (e.g., Hilborn & Eggers, 2000). Accordingly, we were cautious when classifying publications as supplementation programs unless there was sufficient information on the source of broodstock and intent (e.g., Fernández-Cebrián et al., 2014).

Next, we recorded the pathway of hatchery effect (i.e., genetic, ecological, fishing, disease) and VSP parameter(s) studied. Given the number of genetic publications on diversity, we further classified those studies according to the attribute that was analyzed, including diversity (e.g., Williamson & May, 2005), genetic population structure (e.g., Bruce et al., 2020), effective population size (e.g., Berejikian & Van Doornik, 2018), or a combination thereof such as both population structure and effective population size (e.g., Almodóvar et al., 2020).

We classified the hatchery effect on wild salmonids as adverse, minimally adverse, indeterminate, no effect, or beneficial (Table 3). To avoid any interpretative bias, we recorded the effect(s) directly as declared by the author(s). *Adverse and beneficial* refer to publications where the hatchery effect was determined by the authors to be harmful or helpful to the wild population, respectively. Adverse effects could include but are not limited to evidence of reduced productivity or abundance (e.g., Chilcote et al., 2011), or reduced diversity (e.g., Williamson & May, 2005) via unintended genetic introgression with hatchery fish (e.g., Cordes et al., 2006) or reduced effective population size (e.g., Gossieaux et al., 2019). Beneficial could denote effects such as evidence of increased effective population size (e.g., Hedrick et al., 1995), a demographic boost (e.g., Janowitz-Koch et al., 2019), or increased diversity and abundance from a critical level (e.g., Berejikian & Van Doornik, 2018). *Minimally adverse* refers to publications that found some negative effects on wild fish, but where those negative effects were inconsistent or explicitly reported by the authors as being minimal or slight (e.g., Finnegan & Stevens, 2008), while *indeterminate* refers to publications where both negative and positive effects were found (e.g., Small et al., 2009). *No effect* means the authors did not find a statistically significant effect for their measurement of choice (e.g., Wishard et al., 1984).

Last, we included an *effect summary*, a single sentence that encapsulated how the hatchery effects impacted the wild fish in relation to the VSP parameter(s) of interest. For instance, an effect summary could conclude that hatchery salmonids had a beneficial effect on the wild populations via increased genetic diversity (Berejikian & Van Doornik, 2018) or an adverse effect due to decreased genetic diversity (Bernaś et al., 2014).

2.5 | Questions and synthesis of information

After consolidating the research into a database, we synthesized the distribution of publications from 1970 to 2021 to summarize existing knowledge about how hatchery salmonids affect wild salmonids in freshwater and marine environments across the globe. Although the database contains a range of information which we provide in Appendix S1, hereafter we focus our analysis and results on five specific objectives:

1. To understand how the research effort was distributed, we first summed the total number of publications by year, country, species, habitat type, and life history.
2. Second, to synthesize the overall body of literature on hatchery effects on wild salmonids we summed the number of publications that reported adverse, minimally adverse, indeterminate, no effect, or beneficial effects on wild salmonids, and then calculated the proportion of different potential hatchery effects by year, country, species, and life history.
3. Third, we calculated the proportion of studies for each hatchery effect in relation to the hatchery's source of broodstock and

intent, which was classified as production, supplementation, recovery, or a combination thereof.

4. Fourth, to understand the potential ways hatchery fish impacted wild salmonids, for each hatchery effect we summed the number of publications in relation to the processes that contributed to the hatchery effect (genetic, ecological, fishing, disease, or a combination thereof), the affected VSP parameters (productivity, diversity, spatial distribution, and abundance, or a combination thereof), and if relevant, the type of genetic effect (diversity, population structure, effective population size, or a combination thereof).
5. Fifth, we tallied the number of publications that evaluated hatchery effects in the ocean and summarized the general results.

After evaluating those results, we identified potential data gaps and highlighted areas for future research in the Section 4.

3 | RESULTS

3.1 | Number of publications and database

After eliminating duplicates and reviewing titles, abstracts, and then full papers, we identified 206 relevant articles published between 1970 and 2021 (Figure 2). The literature search accounted for 197 of the publications, while nine studies in the ocean were identified through citations in other publications. One publication, Levin and Williams (2002), was counted twice in each component of the synthesis because the authors found adverse effects on one species and no effects on another; hence, hereafter we refer to 207 as the number of publications. The articles cover a wide range of observational studies, models, and experiments focused on *Oncorhynchus*, *Salmo*, *Salvelinus*, *and Thymallus* species in North America, Europe, and Asia. We also identified 50 review publications on the effects of hatchery fish on wild fish that could provide useful context and discussion points for this synthesis, though only four (Hilborn & Eggers, 2000; Naman & Sharpe, 2011; Ruggerone & Nielsen, 2004; Zaporozhets & Zaporozhets, 2004) provided new data and were therefore included in our synthesis (Appendix S1).

3.2 | Distribution of research by year, country, species, habitat, and life history

Our summary of publications revealed several results about how research was distributed in relation to several factors ranging from time to VSP parameters. First, the number of publications on the effects of hatchery salmonids on wild salmonids was unequal over time (Figure 3a). Publications per year steadily increased from 1973 and peaked at 15 publications in 2012, after which the number of publications per year slightly declined until the end of May 2021, when our search was concluded.

Second, we found publications from 22 different countries (Figure 3b). Among those, over half ($n=113$) of the results focused on salmonid populations in the USA, followed by 20 in Canada, 11 in France, and 10 apiece in Spain and Norway (Figure 3b). Three to five publications each were found for the UK, Switzerland, Sweden, Poland, Russia, and Denmark.

Third, publications covered 15 species; among those, brown trout were the most researched with 39 publications, followed by steelhead ($n=33$), Chinook salmon ($n=28$), and Atlantic salmon ($n=19$), compared to 14 publications on chum salmon, 11 on brook charr, and nine apiece on pink and coho salmon (Figure 3c). We also classified 11 studies as *Oncorhynchus* species, either because the analyses were not species-specific (e.g., Goodman, 2005) or they covered three or more species (e.g., Chilcote et al., 2011). One study was classified as Pacific salmon because they focused on multiple species of salmon in the ocean (Bigler et al., 1996), and we found two studies on grayling and one apiece for Amago salmon (*O. masou*), Arctic charr (*S. alpinus*), cutthroat trout, and golden trout.

Fourth, 181 studies evaluated hatchery effects occurring in freshwater, 23 in the ocean, and three were classified as both because they considered impacts in freshwater and the estuary (Levin & Williams, 2002; Nickelson, 2003). And, twice as many publications focused on anadromous life histories ($n=132$) compared to resident life histories ($n=64$), while only 12 publications included data on both life histories (Figure 3d).

3.3 | Synthesis and distribution of hatchery effects on wild salmonids

3.3.1 | All publications combined

Reported hatchery effects on wild salmonids ranged from adverse to beneficial, but the majority were adverse: 144 (70%) studies reported an adverse effect on wild salmonids and another 26 articles (13%) reported a minimally adverse effect (Figure 4). Thus, 83% of studies reported some degree of adverse effects from hatcheries on wild salmonids. Only seven publications (3%) reported beneficial effects of hatchery salmonids on wild salmonids, while 17 studies (8%) reported no hatchery effects on wild salmonids, and 13 (6%) were classified as indeterminate.

3.3.2 | Hatchery effects by year, country, species, and life history

Adverse or minimally adverse effects predominated the distribution of research across time, space, species, and life history. From 1970 through 2021, most publications each year reported adverse or minimally adverse effects on wild salmonids, except for 1994–1995 (Figure 3a). The first publication to report a beneficial hatchery effect occurred in 1995 followed by another publication in 2006,

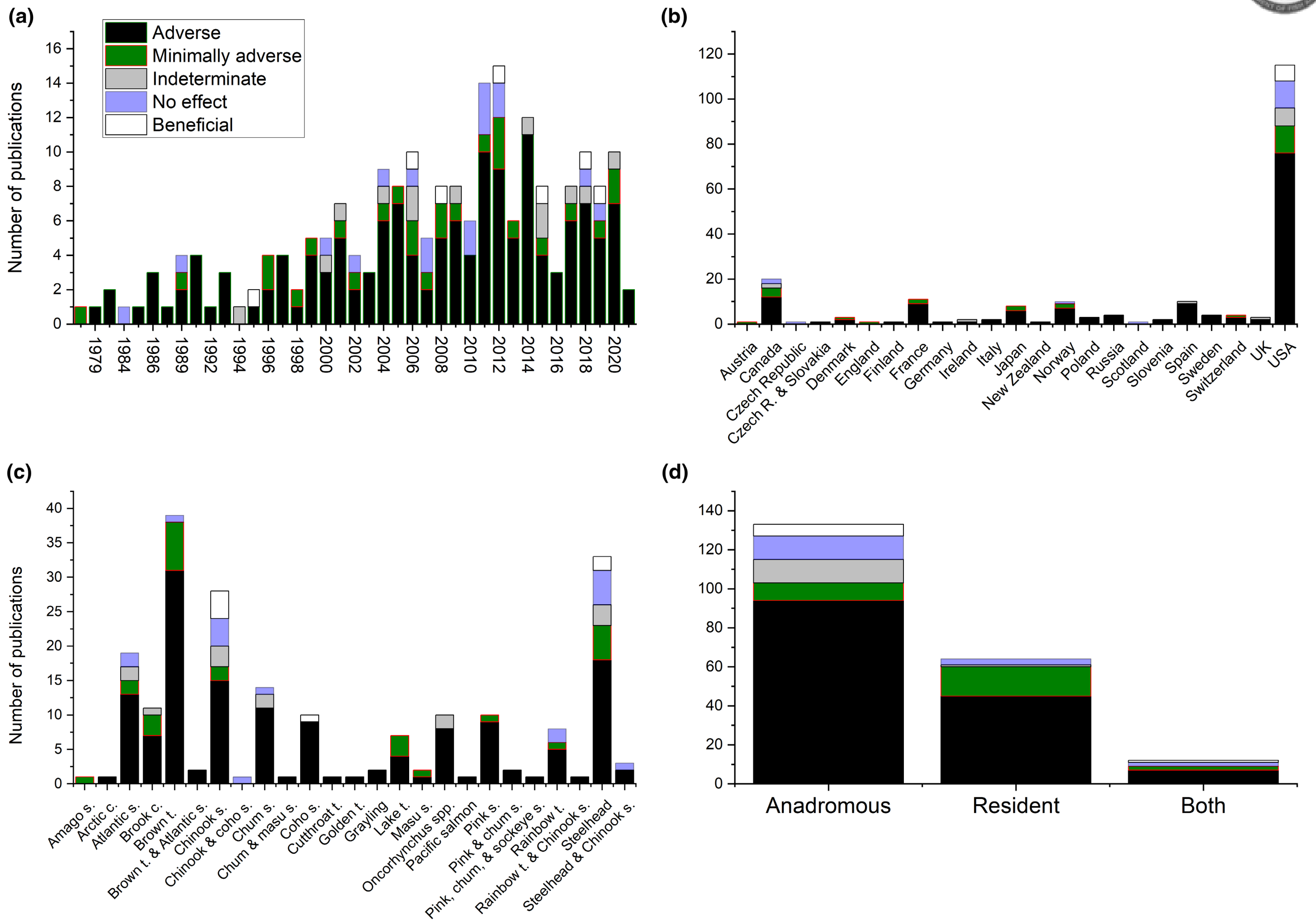


FIGURE 3 Distribution of publications by (a) year, (b) country, (c) species, and (d) life history in relation to the hatchery effect on wild fish, denoted as adverse, minimally adverse, indeterminate, no effect, or beneficial. Adverse and beneficial refer to publications where authors describe the hatchery effect as being negative or positive on the wild population, respectively. A minimally adverse effect refers to publications that found some negative effects on wild fish, but they were inconsistent, while indeterminate refers to publications where hatchery effects included aspects that had both negative and positive effects on the wild population or hatchery effects were almost immeasurable. No effect means that the authors did not find a significant hatchery effect on wild fish for the parameters they measured. In panel c., *Oncorhynchus* spp. refers to studies that focused on *Oncorhynchus* in general or included information on several species. There are 207 total entries because Levin and Williams (2002) was counted twice in each panel, once for an adverse effect on Chinook salmon and once for no effect on steelhead.

with the remaining five reports of beneficial effects being published thereafter as the number of publications increased.

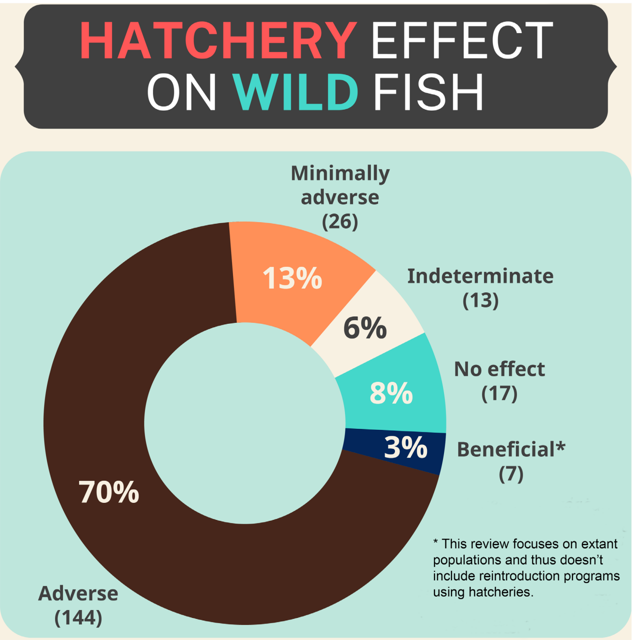
Across the globe, 86 of 113 publications from the USA reported some type of adverse effect (adverse = 74, minimally adverse = 12), but it was also the only country to report beneficial effects (Figure 3b). In Canada and France, 12 of 20 studies and nine of 11 studies reported adverse effects, respectively, compared to nine of 10 in Spain and seven of 10 in Norway (Figure 3b). The Czech Republic and Scotland, with one study apiece finding no effect, were the only countries where an adverse or minimally adverse effect was not found, but overall, reports of no hatchery effect were rare outside North American countries.

For the most studied species, 37 of 38 brown trout publications reported adverse ($n = 31$) or minimally adverse hatchery effects ($n = 7$), compared to 17 of 28 for Chinook salmon (adverse = 15, minimally adverse = 2) and 15 of 19 studies on Atlantic salmon (adverse = 13, minimally adverse = 2: Figure 3c). For steelhead, 23 of 35 found adverse ($n = 18$) or minimally adverse effects ($n = 5$), including one study on "steelhead" from the Great Lakes where they are introduced (Bartron & Scribner, 2004); five of eight studies on resident rainbow trout also found adverse effects. Otherwise, 10 of 11 publications on brook charr and eight of nine each on pink and coho salmon reported adverse or minimally adverse effects, while beneficial hatchery effects were only reported for Chinook salmon, steelhead, and coho salmon.

Adverse and minimally adverse effects accounted for 102 of 132 publications on anadromous life histories and 60 of 64 publications on resident life histories (Figure 3d). Of the few publications that found a beneficial effect, six of seven were documented for the anadromous life history.

3.3.3 | Hatchery effect by hatchery type and intent

Most publications focused on production hatchery programs ($n=143$) and more studies focused on supplementation programs ($n=28$) than recovery programs ($n=17$), while 19 studies accounted for a combination of production and supplementation hatcheries (Table 5). The proportion of studies reporting adverse effects on wild salmonids was 74% for production programs and 64% for supplementation programs. However, another 17% of the studies on production programs found minimally adverse impacts, while no minimally adverse effects were reported for supplementation programs (Table 5). On the contrary, 7% of the publications on supplementation programs found beneficial results and 17% indicated no effect, while 74% of the studies focused on both production and supplementation programs found adverse effects and 16% reported no effect.



* This review focuses on extant populations and thus doesn't include reintroduction programs using hatcheries.

FIGURE 4 Donut plot displaying proportion (and number, in parentheses) of publications by the effect of hatchery salmonids on wild salmonids, including adverse, minimally adverse, indeterminate, no effect, and beneficial. There are 207 total entries because Levin and Williams (2002) was counted twice, once for an adverse effect and once for no effect.

For supplementation programs specifically, one publication reported a beneficial hatchery effect on abundance and productivity of natural-origin Chinook salmon (Fast et al., 2015) and another found releases of hatchery coho salmon increased abundance of naturally spawning fish without appearing to adversely affect wild productivity (Sharma et al., 2006). Nonetheless, adverse results from supplementation hatcheries were multiple and ranged from reduced diversity (Christie et al., 2012), productivity (Buhle et al., 2009), and abundance (Willmes et al., 2018) to altered run timing and spatial distribution (Hoffnagle et al., 2008).

The distribution of effects was more balanced for recovery programs, though the sample size was smaller (Table 5). Of the 17 studies on recovery hatcheries, the proportion of beneficial results (29%) was similar to the combined 30% of studies that found adverse (24%) and minimally adverse results (6%), respectively, while another 12% reported no effect and 29% were indeterminate. Of the five studies that reported beneficial effects from recovery hatcheries, four used all wild fish for broodstock, including two publications on the same long-term experiment on highly depleted populations of steelhead (Berejikian et al., 2008; Berejikian & Van Doornik, 2018) and the two on the same population of Chinook salmon (Hess et al., 2012; Janowitz-Koch et al., 2019). Adverse effects from recovery programs included decreased productivity in steelhead (Araki et al., 2009), reduced genetic structure (Lynch & O'Hely, 2001), and reduced diversity and productivity in Atlantic salmon (Bowlby & Gibson, 2011) and coho salmon (Willoughby & Christie, 2019).

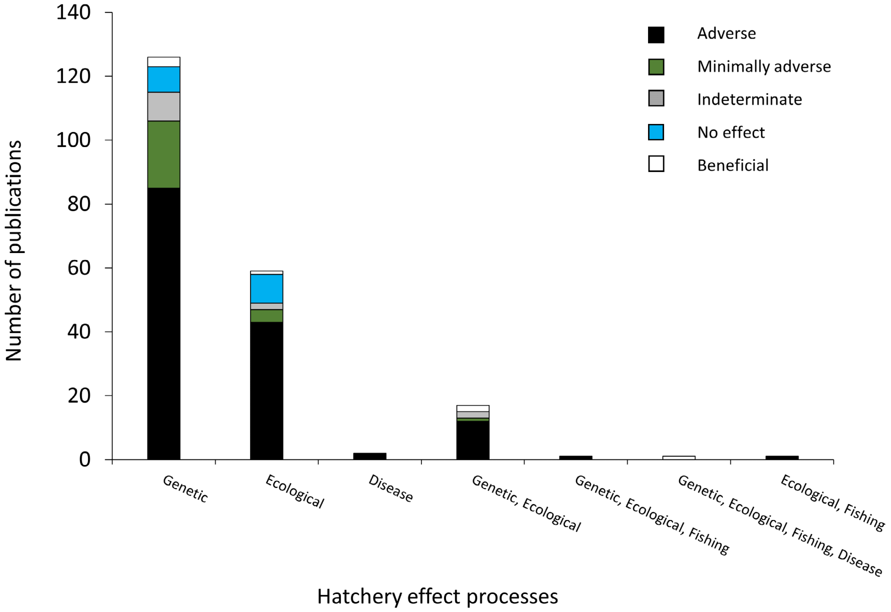


FIGURE 5 Distribution of publications in relation to the different processes through which hatchery fish affected wild salmonids, including ecological, genetic, fishing, disease, or some combination thereof in relation to the hatchery effect on wild population, denoted as adverse, minimally adverse, indeterminate, no effect, or beneficial. There are 207 total entries because Levin and Williams (2002) was counted twice in the ecological category, once for an adverse effect and once for no effect.

TABLE 4 Number of publications by their respective hatchery effect (adverse, minimally adverse, indeterminate, no effect, beneficial) on the Viable Salmon Population (VSP) parameter(s) of wild fish, including abundance (Abun.), distribution (Distr.), diversity (Diver.), productivity (Prod.), and various combinations thereof.

Effect on wild fish	Abun.	Distr.	Diver.	Prod.	Abun. & Distr.	Abun. & Diver.	Abun. & Prod.	Abun., Diver., and Prod.	Diver. & Distr.	Diver. & Prod.	Diver., Prod., & Distr.
Adverse	9 (1)	2	**66**	38 (14, 2)	1	3	14 (4)	4	1	4	1
Minimally adverse	2	1	**20**	3 (1)							
Indeterminate	1		**8**	2			2				
No effect		2	**7**	6 (4)	1		1				
Beneficial	1		1	**2**		**2**	1				
Total	13	5	**102**	51	2	5	18	5	1	3	1

Note: Adverse and beneficial refer to publications where authors describe the hatchery effect as being negative or positive on the wild population, respectively. A minimally adverse effect refers to publications that found some negative effects on wild fish, but they were inconsistent, while indeterminate refers to publications where hatchery effects included aspects that had both negative and positive effects on the wild population or hatchery effects were almost immeasurable. No effect means that the authors did not find a significant hatchery effect on wild fish for the parameters they measured. In cells with parentheses, the number refers to the number of studies in ocean, and if present, the second number after the comma refers to the number of studies in both the ocean and freshwater. Bolded and underlined values represent the VSP parameter with the greatest number of studies for each respective effect on wild fish. There are 207 total entries because Levin and Williams (2002) was counted twice in the productivity category, once for an adverse effect and once for no effect.

3.3.4 | Hatchery effect pathways and genetic effects

More publications (*n* = 126) tested or evaluated how hatchery salmonids affected wild salmonids via genetics than other pathways, and most reported adverse (*n* = 85) or minimally adverse effects (*n* = 21), while fewer were indeterminate (*n* = 9), found no effect (*n* = 8), or reported a benefit (*n* = 3) (Figure 5). Adverse effects also predominated (*n* = 44) among the 60 ecological studies, and 12 of the 17 articles focused on a combination of genetic and ecological processes found adverse results. Potential disease and fishery effects were far less studied. Outside of a review by Naish et al. (2007), we found only two publications that evaluated potential effects of disease and parasites (Lamaze et al., 2014; Robinson et al., 2020) and three that included fishery effects as a component of their research (Baer & Brinker, 2010; Fast et al., 2015; Hilborn & Eggers, 2000).

The strong genetic focus is why one VSP parameter, diversity, was also commonly represented in 102 publications, 86 of which reported adverse (*n* = 66) or minimally adverse effects (*n* = 20) (Table 4). This was particularly true for brown trout, where 35 of 39 publications focused on diversity. An additional 13 studies included genetic diversity as a component and 12 found adverse effects. Of the 115 genetic-centric studies, most focused on potential effects on population structure (*n* = 59), followed by various measures of genotypic/allelic diversity (*n* = 25) and effective population size (*n* = 7). The remaining 10 genetic articles were combinations of population structure, diversity, and effective population size.

Examples of adverse genetic effects included, but were not limited to, changes in population structure (Ayllon et al., 2006; Thaulow et al., 2012) stemming from an increased frequency of hatchery-origin alleles in wild populations (Caudron et al., 2009; Létourneau et al., 2018), reduced effective population size in wild populations with hatchery releases (Almodóvar et al., 2020; Hagen et al., 2021), replacement of wild salmonids by hatchery salmonids (e.g., Quiñones et al., 2013; Reisenbichler & Rubin, 1999), and reduced resistance to parasitic infections (Lamaze et al., 2014). In the single beneficial publication on diversity, a recovery hatchery program increased the effective population size in an endangered population of salmon (Hedrick et al., 1995), although as mentioned below, benefits to diversity were found in other publications that measured multiple VSP parameters.

After diversity, most publications focused on productivity, abundance, and a combination of productivity and abundance (Table 4). Of the publications on productivity, 30 were conducted in freshwater, 18 in the ocean, and three in both freshwater and an estuary. In freshwater, 22 of 30 studies found adverse effects on the productivity of wild salmonid populations (e.g., Chilcote et al., 2011; Jonsson et al., 2019; Skaala et al., 1996), while two apiece found no effect (e.g., Courter et al., 2019) or were indeterminate (e.g., Riley et al., 2005). In addition, nine of 13 studies on abundance and 14 of 18 studies on productivity and abundance in freshwater reported adverse effects, such as reduced productivity and abundance of wild salmonid populations (e.g., Byrne et al., 1992; Young, 2013) and reduced abundance and individual

TABLE 5 Number of publications (proportion in parentheses) and hatchery effect on wild fish by hatchery type.

Hatchery type	Adverse	Minimally adverse	Indeterminate	No effect	Beneficial
Production	108 (75%)	24 (17%)	4 (3%)	7 (5%)	0 (0%)
Supplementation	15 (64%)	0 (0%)	3 (11%)	5 (18%)	2 (7%)
Recovery	4 (24%)	1 (6%)	5 (29%)	2 (12%)	5 (29%)
Production, supplementation	14 (74%)	1 (5%)	1 (5%)	3 (16%)	0 (0%)

Note: Hatchery types include: production, supplementation, recovery, or a combination of production and supplementation or supplementation and recovery. Production refers to hatcheries that use all or nearly all hatchery fish for broodstock, which are often from a non-local source, and focus on producing fish for fisheries; supplementation refers to programs that integrate local wild and hatchery fish for broodstock to enhance fisheries and supplement wild populations; and a recovery program focuses strongly on conservation and uses mostly or all wild fish (fully integrated) to try and rebuild wild populations by providing a boost in abundance (often temporary). There are 207 total entries because Levin and Williams (2002) was counted twice in the production and supplementation category, once for an adverse effect and once for no effect.

condition of wild juveniles (Noble, 1991). The six remaining publications that reported benefits to abundance and productivity or a combination thereof all occurred in freshwater (e.g., Berejikian & Van Doornik, 2018; Janowitz-Koch et al., 2019). Effects on distribution and combinations of parameters including distribution were less represented than the other three VSP parameters (e.g., Hoffnagle et al., 2008; Love Stowell et al., 2015; Table 4).

3.3.5 | Hatchery effects in ocean

Hatchery effects on salmonids in the ocean involve competition for prey, potentially leading to reduced growth, body size and fecundity, delayed maturation, lower productivity, and fewer wild salmon. We found 23 studies on potential hatchery effects. Thirteen of those examined hatchery effects on local populations of wild salmon in the ocean, of which nine (69%) were adverse, one (8%) was minimally adverse, and three (23%) found no effect (Table S2). One of the three no-effect publications focused explicitly on potential juvenile competition in nearshore habitats during early marine residence (Sturdevant et al., 2011), while the other two focused on adult hatchery Chinook salmon production (Ohlberger et al., 2018; Nelson et al., 2019). Most other publications examined correlations between hatchery chum salmon and pink salmon and the productivity and growth wild adult salmon in the ocean (e.g., Cunningham et al., 2018; Frost et al., 2020; Ward et al., 2017).

We also included 10 studies that examined total salmon density effects on wild salmon in which hatchery salmon were an important component (additional studies involving density dependence at sea are available); nine (90%) of these studies reported adverse effects of density dependence on wild salmon while inferring an adverse effect of abundant hatchery salmon stemming from production hatcheries in Asia and North America (Table S2). Declines in the growth of all salmon species across most of their range are the most commonly observed effect of density dependence, including hatchery production (Bigler et al., 1996; Oke et al., 2020). Though not included in our analyses because it did not explicitly evaluate hatchery fish and in contrast to most results, Shuntov et al. (2019, 2020) argued that competition for prey at sea is minimal because prey biomass is exceptional and because salmon consume a small fraction of the available prey. However, this assessment cannot explain the density-dependent biennial patterns observed in Pacific salmon metrics (growth, abundance, productivity, maturation) in response to the biennial abundances of highly abundant pink salmon (Ruggerone et al., in press; Ruggerone & Connors, 2015; Ruggerone & Nielsen, 2004), of which many are hatchery fish (Ruggerone & Irvine, 2018).

4 | DISCUSSION

Hatcheries are used worldwide to produce salmonids for purposes ranging from providing fish for harvest to rebuilding endangered stocks and meeting Treaty responsibilities (Araki & Schmid, 2010; Maynard & Trial, 2014; Naish et al., 2007), but a strong dependence on hatcheries has also generated controversy and debate (Brannon et al., 2004; Claussen & Philipp, 2022; Harrison et al., 2019; Holt et al., 2008). Clarity in this discourse is partly obscured, however, by the sheer volume of complex research that dates back several decades, covers numerous species, and spans three continents, which makes it difficult to interpret succinctly the existing weight of evidence. We sought to provide a transparent, reproducible, and updatable synthesis and database of the current global research evaluating the impacts of hatcheries on wild populations, while purposefully not delving into the complex social and political desires or tribal Treaty and mitigation legal obligations surrounding hatcheries. Our review of over 50 years of peer-reviewed publications on how hatchery salmonids affect wild salmonids found most research reported adverse or minimally adverse hatchery effects across time, species, and countries, even for supplementation-type hatcheries, while reports of beneficial effects on wild salmonids were scarce except for a few very specific situations (e.g., Berejikian & Van Doornik, 2018; Hess et al., 2012). We hope this database serves as a useful standing resource that can be used and built upon to improve the breadth of science incorporated into decision-making.

Prior reviews have summarized overarching hatchery practices and processes, identified potential adverse impacts, and evaluated the role of hatcheries in salmonid fisheries and recovery (Fraser, 2008; Jonsson, 1997; Maynard & Trial, 2014; Naish et al., 2007). More similar to Miller et al. (1990) and Araki and Schmid (2010), we attempted to census the balance of existing peer-reviewed literature and provide summaries of each publication (Appendix S1). Miller et al. (1990) reviewed 316 hatchery projects, including numerous supplementation programs, across the western USA and Canada and in New England states working with Atlantic salmon. Of those, only 25 projects, or 8%, successfully supplemented existing runs of wild salmonids, and while adverse impacts to wild stocks were reported or postulated for almost every type of hatchery situation where the intent was to rebuild wild runs. The authors also suggested a bias toward not reporting negative or unsuccessful results. Two decades later, Araki and Schmid (2010) synthesized 266 hatchery case studies covering several species of fish, including 70 on salmonids, 51 of which (72%) reported adverse impacts ranging from deleterious effects of hatchery rearing on fitness in nature to reduced genetic variation in populations of hatchery fish. Our review of 208 publications found 70% reported adverse hatchery effects and another 13% found minimally adverse effects, while just 3% reported beneficial effects. Although we likely missed some relevant publications despite a transparent search process and did not include research on reintroductions using hatchery salmon (e.g., Liermann et al., 2017) or domestication effects on wild fish reared in hatcheries (e.g., Christie et al., 2016), the overall balance of results across three reviews and hundreds of studies appear relatively similar.

One possible reason for the preponderance of adverse effects across time, space, and species is most publications in our review assessed traditional, production hatcheries that focused on producing fish for fisheries, often but not always from non-local broodstock. Adverse effects on wild salmonids from such programs are well documented (Almodóvar et al., 2020; García-Marín et al., 1999; Marie et al., 2010). This was particularly true for brown trout, the most studied species, where many publications evaluated possible genetic effects of non-local hatchery stocks across Europe, often finding adverse genetic impacts (Araguas et al., 2017; Hansen et al., 2009; Thaulow et al., 2012). However, adverse effects also accounted for 63% of the publications that evaluated potential impacts from supplementation programs that use some or mostly wild fish and frequently employ breeding protocols to try to reduce deleterious genetic effects (Hutchings, 2014; Neff et al., 2011; Pinter et al., 2019).

Adverse effects from supplementation programs could be related to a suite of factors that are not dissimilar from production programs. For example, supplementation broodstock is generally derived from local populations to reduce potential genetic impacts; however, a review of 51 estimates of annual productivity from six studies on four salmon species found the relative fitness of early-generation hatchery individuals was about half that of wild fish (Christie et al., 2014), while another found hatchery salmonids displayed lower genetic variation than wild populations (Araki & Schmid, 2010). Interbreeding with individuals that have lower fitness and less diversity, among other differences, can reduce the diversity (Hagen et al., 2021), effective population size (Christie et al., 2012; Hagen et al., 2021), and productivity of wild populations (Goodman, 2005; Jonsson et al., 2019; Reisenbichler & Rubin, 1999). Depending on the intensity and duration of stocking, the gene pool of the wild population may eventually be compromised by high levels of hatchery influence, as evidenced by studies on brown trout in Europe (Fernández-Cebrián et al., 2014; Hauser et al., 1991; Pustovrh et al., 2012) and brook charr in North American (Létourneau et al., 2018); in the extreme, hatchery salmonids may replace wild fish (Largiadèr & Scholl, 1996; Quiñones et al., 2013).

In addition, although a key goal of supplementation hatcheries is to enhance opportunities for harvest, in some populations and years large numbers of returning hatchery salmon escape fisheries or are allowed intentionally to spawn, leading to many more total salmon than can be supported by the habitat and heighten density-dependent effects (HSRG, 2020; ISAB, 2015). We found studies where hatchery juveniles reduced the abundance and productivity of wild juveniles (Nickelson et al., 1986; Warren et al., 2014). Competition for habitat likely contributed to declines in wild coho salmon on the Oregon coast, USA, where density-dependent effects were five times greater for hatchery salmon than wild salmon and the productivity of several wild populations decreased as hatchery releases increased (Buhle et al., 2009; Nickelson, 2003). Adverse effects may thus depend on genetic and ecological pathways and the intensity of stocking, and such effects may be more common than anticipated if supplementation programs do not meet their own goals for reducing risk (e.g., targeted levels of wild integration into broodstock) and limitations of habitat capacity are not considered (Anderson et al., 2020). Regardless, interbreeding with less fit individuals and increased competition for habitat may help explain why both production and supplementation programs negatively influenced productivity of several populations of wild steelhead (Chilcote et al., 2011), and why a long-term effort to increase natural-origin Chinook salmon did not find a positive effect on abundance after releases were ceased (Scheuerell et al., 2015; Venditti et al., 2018).

Hatcheries can also benefit wild salmonids, though the situations appear nuanced. For instance, hatcheries have helped re-establish extirpated populations of salmonids (Galbreath et al., 2014), prevent extinction (Kline & Flagg, 2014), and jump-start recolonization following dam removal (Liermann et al., 2017). While those efforts did not meet the criteria for inclusion in our synthesis (e.g., effects on wild fish could not, or were not, evaluated due to extirpation or near extinction levels of abundance), in the publications we reviewed nearly all benefits occurred when recovery-type programs were used to provide a demographic boost to endangered populations of salmonids. Examples include small releases of hatchery smolts from a short-term, temporary captive-broodstock program to increase abundance and diversity of steelhead populations that were almost extirpated (Berejikian et al., 2008; Berejikian & Van Doornik, 2018), and a carefully controlled hatchery program that bred only wild fish to boost abundance of a highly depleted population of Chinook salmon (Hess et al., 2012; Janowitz-Koch et al., 2019). However, two of the four beneficial studies reported on the same populations, which tilts

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the proportion of results given the relatively small number of publications, and other publications warn that even improved hatchery practices can still pose significant ecological and genetic risks to wild fish over the long term (Oosterhout et al., 2005), such as competition for food and habitat (ISAB, 2015) and reduced genetic diversity and divergence from the wild population (Bingham et al., 2014). Consequently, beyond 4–6 generations a loss in fitness can outweigh any increase in abundance from hatchery production and cause the population to decline (Bowlby & Gibson, 2011). Nonetheless, our review, like others (Maynard & Trial, 2014; Naish et al., 2007), suggests the balance of effects for recovery hatcheries is less skewed, with as many studies reporting beneficial or no effects as adverse ones.

Within the array of publications we reviewed, most research focused on hatchery effects that occurred via genetic interactions and found adverse impacts on wild salmonids, such as reduced diversity (García-Marín et al., 1999; Perrier et al., 2013; Willoughby & Christie, 2019) and altered genetic structure of wild populations (Valiquette et al., 2014; Weigel et al., 2019; Wenne et al., 2016), though adverse effects on growth (Hasegawa et al., 2014, 2018; McMichael et al., 1997), productivity (Buhle et al., 2009; Nickelson, 2003) and abundance (Nickelson et al., 1986; Quiñones et al., 2013; Willmes et al., 2018) via ecological or both ecological and genetic processes were also reported. The frequency of adverse genetic impacts may have consequences for the resilience of wild fish moving forward. As an example, research on brown trout found long-term supplementation significantly reduced genetic diversity among locations and compromised the conservation of local genetic variation (Fernández-Cebrián et al., 2014), which threatened biodiversity in their southern range (Cagigas et al., 1999; Horreo et al., 2014; Splendiani et al., 2019). A tremendous amount of money and effort has been invested in restoring habitat to improve population productivity and increase carrying capacity (ISAB, 2015), and help offset future effects from climate change (Beechie et al., 2013; Bilby et al., 2022), an action demonstrated to increase wild fish abundance more effectively than species-specific stocking efforts (Radinger et al., 2023). Because the resilience of salmonids also depends on their functional genetic capacity to survive and reproduce in a changing environment (Kardos et al., 2021), future research could help illuminate the extent to which, if any, alterations to genetic diversity may influence returns on habitat investments where both hatchery and wild fish co-exist.

Our literature review also revealed an extensive body of research focused on potential effects of annual releases of 4.5 billion hatchery Pacific salmon into the North Pacific Ocean, which represents 40% of the total mature and immature salmon biomass in the North Pacific Ocean (Ruggerone & Irvine, 2018). The combination of publications on the specific abundance of hatchery salmon and overall abundance of hatchery and wild salmon at sea suggest heightened abundances, particularly of hatchery chum salmon and pink salmon, have triggered density-dependent effects in wild populations resulting in reduced growth, body size, fecundity, productivity, and abundance, and delayed maturation (Table S2). For example, research has found adverse effects of hatchery or total chum salmon abundance on the growth, productivity, and abundance of wild chum salmon (Frost et al., 2020; Kaeriyama et al., 2011; Ruggerone et al., 2012), of total hatchery and wild pink salmon and chum salmon on body size, age, productivity, and abundance of Chinook salmon across their range (Cunningham et al., 2018; Oke et al., 2020; Ruggerone et al., in press), and of hatchery pink salmon on productivity of wild sockeye salmon populations in British Columbia and Alaska (Connors et al., 2020). While it is difficult to disentangle correlation and causation, the strong biennial patterns in abundant pink salmon cannot be explained by the environment alone (Batten et al., 2018; Ruggerone & Connors, 2015; Ruggerone et al., in press) and, consequently, concerns for wild salmon have led scientists to call for international discussions, limits on hatchery production, and hatchery taxes (Holt et al., 2008; Malick et al., 2017; Peterman et al., 2012).

Considering the balance of the research herein, we selected four topics that remain underrepresented and seem important to clarifying science and management opportunities moving forward. First, effects on genetic diversity of wild salmonids are well studied but investigation of epigenetic effects as a possible biological pathway for these (and other) effects has only begun (Koch et al., 2022). Christie et al. (2016) found a single generation in a hatchery environment altered the expression of over 700 genes in steelhead. Other research has found similar results (Leitwein et al., 2022), even in the absence of genetic differentiation between wild and hatchery populations (Le Luyer et al., 2017), and the potential for the epigenetic changes to be passed along to offspring (Leitwein et al., 2021; Venney et al., 2023). Though the duration of impacts remains unclear it is hypothesized that heritable epigenetic effects may alter the evolutionary trajectory of wild populations, which is a critical issue to evaluate where hatchery salmonids are allowed to or are able to breed with wild salmonids (Skinner & Nilsson, 2021). Second, future research could illuminate the adaptive consequences of genetic changes sustained by wild salmonids (Neff et al., 2011) and whether accumulated effects inhibit their capacity to keep pace with climate change (e.g., Munsch et al., 2022) or respond positively to habitat restoration efforts. Third, large-scale experiments that evaluate multiple VSP parameters before, during, and after supplementation, such as Berejikian and Van Doornik (2018), are scarce, but well-designed experiments could help parse out natural spatial and temporal variability in environmental capacity from hatchery effects and offer greater clarity regarding the risks and benefits of hatchery programs.

Last, few publications evaluated disease or fishery effects despite demonstrated mechanisms of influence, such as decreased resilience to parasites associated with hatchery genotypes (see, Lamaze et al., 2014) and mixed stock fisheries on abundant hatchery stocks that are unsustainable for wild stocks (Naish et al., 2007). It is possible our search string did not fully capture the breadth of literature on fishery effects, or such analyses are less frequently published in peer-reviewed journals. Naish et al. (2007) analyzed fishery data from management reports and described a long history of overharvesting weaker wild stocks in intensive hatchery fisheries, which ultimately led to changes in fishery policy in the United States, but direct references to studies that met our criteria were rare. Understanding how such impacts have and continue to affect wild stocks could provide further insight, though in some cases identifying potential changes to wild populations may require a longer-term perspective using historical data (e.g., McMillan et al., 2022).

5 | CONCLUSION

We created an easily accessible database focused on publications that examined potential effects of hatchery salmonids on wild salmonids, and then synthesized the large body of research to better understand how studies and potential hatchery impacts were distributed in relation to time, space, species, habitat, hatchery type, and other factors. Except in a few specific situations when recovery hatcheries were used to boost the abundance of wild salmonids threatened with extinction, hatchery effects on wild salmon were predominantly adverse across time, species, and countries, even when using more modern supplementation hatchery programs and practices. In addition, evidence indicates large releases of hatchery chum and pink salmon in the North Pacific Ocean alter the growth, survival, and abundance of wild salmonids that rely on the same common pool prey resource. These results have implications for conserving and sustaining wild salmonids and for extensive investments in salmon recovery across the globe. In conclusion, while there is a long history of debate over the widespread use of hatcheries, our results were consistent with prior reviews by Miller et al. (1990) and Araki and Schmid (2010), the combination of which clearly indicate that, from a scientific standpoint, hatcheries typically pose numerous risks that commonly result in negative impacts to the diversity, productivity, and abundance of wild salmonid populations. These negative impacts likely limit the efficacy of habitat restoration efforts aimed at rebuilding wild salmonid populations and the adaptive capacity of wild salmonids to keep pace with a changing environment, especially climate warming.

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CONFLICT OF INTEREST STATEMENT

The authors declare there are no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article in the database provided in Appendix S2.

ETHICS STATEMENT

The manuscript has not been submitted for publication or published in another journal and because the manuscript is a review of prior publications on fish, information on ethical treatment of humans and animals is not applicable.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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FEATURE ARTICLE: REVIEW

From diatoms to killer whales: impacts of pink salmon on North Pacific ecosystems

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ABSTRACT: In response to a climate regime shift in 1977 and general heating of the North Pacific Ocean, pink salmon *Oncorhynchus gorbuscha* abundance reached record highs during 2005–2021, comprising 70% of all Pacific salmon. Pink salmon are approximately 25 times more numerous in odd- than even-numbered calendar years in some major North Pacific ecosystems, a unique demographic pattern analogous to repeating whole ecosystem treatment–control experiments. We found compelling examples indicating that in odd years, predation by pink salmon can initiate pelagic trophic cascades by reducing herbivorous zooplankton abundance sufficiently that phytoplankton densities increase, with opposite patterns in even years. Widespread interspecific competition for common-pool prey resources can be dominated by pink salmon, as indicated by numerous biennial patterns in the diet, growth, survival, abundance, age-at-maturation, distribution, and/or phenology of ecologically, culturally, and economically important forage fishes, squid, Pacific salmon and steelhead trout *Oncorhynchus* spp., seabirds, humpback whales *Megaptera novaeangliae*, and endangered southern resident killer whales *Orcinus orca*. In aggregate, the evidence indicates that open-ocean marine carrying capacity in the northern North Pacific Ocean and Bering Sea can be mediated by top-down forcing by pink salmon and by ocean heating, and that large-scale hatchery production (~40% of the total adult and immature salmon biomass) likely has unintended consequences for wild salmon, including Chinook salmon *O. tshawytscha*, and many other marine species. Further investigation of the effects of pink salmon on other species will increase our knowledge of ecosystem function and the important role top-down forcing plays in the open ocean

Pink salmon returning to Prince William Sound, Alaska hatcheries have contributed to record-setting abundances in recent years and to impacts on other marine species.

Photo: Preston and Teresa Cole, https://taps-photography.pixels.com/

KEY WORDS: North Pacific ecosystems · *Oncorhynchus gorbuscha* · Competition · Trophic cascade · Carrying capacity · Climate change · Ocean heating · Ecosystem services

1. INTRODUCTION

Some upper trophic level species play crucial roles in the natural histories of other species and the structure and function of ecosystems. Such interactions have been well documented in terrestrial (Carpenter et al. 1995, Painter et al. 2015), freshwater (Carpenter

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et al. 1985, Naiman et al. 1988, Ellis et al. 2011, Beschta & Ripple 2019), and nearshore marine environments (e.g. Paine 1977, Estes et al. 1998, Christianen et al. 2023), primarily from treatment–control experiments. This has been poorly documented in the open ocean, where experiments are generally impractical because of the great spatial scales, challenging logistics, and expense. Although considerable progress has been made in identifying top-down effects in ocean ecosystems (e.g. Baum & Worm 2009), most inferences have been based on before–after comparisons of change following predator removals or additions. Examples include the slaughter of great whales in the 19th and 20th centuries in the North Pacific and Southern Oceans (Springer et al. 2003, 2006, Roman et al. 2014), the collapse of cod *Gadus morhua* stocks in the NW Atlantic (Frank et al. 2005), and the invasion of killer whales *Orcinus orca* into the eastern Canadian Arctic (Breed et al. 2017, Matthews et al. 2020).

Pink salmon *Oncorhynchus gorbuscha* in the North Pacific Ocean (NPO) exhibit a unique, exaggerated biennial alternation between high and low abundance that can be viewed as a simple, natural treatment–control 'experiment' (Ruggerone & Nielsen 2004), even though all variables cannot be controlled. Many pink salmon populations are predictably much more abundant in odd-numbered calendar years than in even-numbered years (Irvine et al. 2014), thus in this analogy, odd years are equivalent to treatment years and even years are equivalent to control years. The biennial cycles repeat over many decades (Fig. 1), creating reliable replication that can be used to identify effects of pink salmon on the ecosystem. A growing body of evidence suggests that biennial patterns in the biology of many marine species in the NPO can be linked directly and indirectly to pink salmon, and that pink salmon can initiate pelagic trophic cascades.

Our goal here is to synthesize information on those biennial patterns and evaluate evidence that they are caused by direct and indirect effects of pink salmon. Such evidence provides novel information about the influences of top-down predation on the structure and function of open ocean ecosystems, and has important biological and policy value for understanding the ocean's carrying capacity. If, for example, the forage demand of billions of additional salmon released from industrial-scale hatcheries pushes closer to the ocean's carrying capacity, this may have deleterious effects on wild salmon as well as non-salmon species, such as decreased survival rate, productivity, and body size (e.g. Cooney & Brodeur 1998, Perry et al. 1998). Governments and managers often assume hatchery and wild populations do not compete for prey (Holt et al. 2008), or with other species in pelagic food webs, yet the overall benefits and costs of hatchery production to ecological and societal well-being is a matter of considerable debate (e.g. Kaeriyama & Edpalina 2004, Harrison & Gould 2022).

We show that pink salmon can have major top-down impacts on species and food webs that include 5 major taxa — phytoplankton, zooplankton, fishes, marine birds, and marine mammals — over vast regions of the NPO, and through a transhemispheric teleconnection on terrestrial ecosystems in the southern hemisphere (Table 1). In aggregate, the weight of evidence leads to a robust conclusion: pink salmon can exert strong top-down effects on a common pool of prey resources that affect many other species and influence pelagic ecosystems of the NPO. These effects, in turn, may affect human subsistence and cultural, recreational, and economic values in both the northern and southern hemispheres. The examples of direct and indirect effects of pink salmon presented here are likely not the only ones that exist, and other researchers with multi-year data sets might seek additional biennial patterns waiting to be found, and explanations for them.

2. BACKGROUND

Pink salmon life history characteristics are uniquely suited for testing hypotheses about top-down interactions with other marine species. These fish are widely distributed throughout epipelagic waters of the NPO; e.g. those from eastern Kamchatka, Russia, migrate eastward to approximately 150° W (Radchenko et al. 2018), suggesting that they have the potential to interact with species across the Bering Sea (BS) and Gulf of Alaska (GOA), including North American salmon. Major populations spawn in Alaska, British Columbia (BC), Puget Sound (WA), the Russian Far East, and northern Japan (Takagi et al. 1981). Their overall abundance increased steadily after the mid-1970s, reaching unprecedented levels during 2005–2021, when annual abundance averaged 522 million adults, or nearly 70% of all Pacific salmon (Fig. 1). Approximately 82 million adult pink salmon per year (16% of total) originated from hatcheries during 2005–2015 (Ruggerone & Irvine 2018).

Pink salmon have benefited from climate change, beginning with a major climatological regime shift in 1977 (Mantua et al. 1997) and heating of the NPO, as indicated by a strong positive correlation between

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Table 1. Evidence for interactions between pink salmon and plankton, forage fishes, squid, Pacific salmon, seabirds, and whales. Evidence includes biennial or cyclic patterns, and positive (+) and negative (–) correlations (Pearson's correlation or linear regression) when available. Biennial patterns without correlation analyses indicate negative effects of pink salmon on other species. For seabirds, biennial patterns with correlation analyses apply only to omnivores: for planktivores, biennial patterns in Births, Productivity, and Phenology indicate positive correlations with pink salmon. See Section 3 and Supplement 2 at www.int-res.com/articles/suppl/m719p001_supp2.xlsx for details. SH: southern hemisphere; NH: northern hemisphere; NP: North Pacific; AI: Aleutian Islands; BS: Bering Sea; GOA: Gulf of Alaska; PWS: Prince William Sound; SOG: Strait of Georgia; AK: Alaska; BC: British Columbia; OR: Oregon; WA: Washington; WC: West Coast; R: river; I: island

Species	Diet	Growth	Fecundity	Births	Productivity	Abundance	Age-at-maturation	Distribution	Phenology	Body condition	Ecosystem	Population location
Plankton												
Phytoplankton						Biennial, +					BS, AI, central NP	
Zooplankton		Biennial, +				Biennial, –					BS, AI, central NP	
Forage fishes and squid												
Herring		Biennial, –				–					PWS, Sitka Sound	PWS, Sitka Sound
Atka mackerel		Biennial, –									AI	AI
Sand lance						Biennial					Salish Sea	Salish Sea
Pacific Ocean perch						Biennial, –					GOA	GOA
Squid spp.						Biennial					BS, W NP	BS, W NP
Berryteuthis anonychus						Biennial, – and cyclic					BS, GOA	BS, GOA
Pacific salmon												
Sockeye	Biennial	Biennial, –	Assumed –		Biennial, –	Biennial, –	Biennial, +				NP, BS, Salish Sea	Kamchatka, AK BC, WA, PWS
Chum	Biennial, –	Biennial, –	–		Biennial, –	Biennial, –	Biennial, +	Biennial, –		–	NP, BS, Kuril I, Salish Sea	Japan, Russia, Norton Sound, Kuskokwim R, Yukon R, Bristol Bay, SE AK, BC, Salish Sea, WC
Coho	Biennial	Biennial, –	Biennial, –		Biennial, –						W NP, GOA, Salish Sea	SE AK, Kuskokwim R, Russia, SOG
Chinook	Biennial	Biennial, –	–		Biennial, –	Biennial, –	–				NP, BS, Salish Sea	Kamchatka R, Yukon R, Kuskokwim R, Nushagak R, Columbia R, Central AK, SE AK, Salish Sea, AK, BC, WA, OR
Steelhead	–	–			–	Biennial, –					NP	Thompson R, Keogh R, Chilcotin R (BC), Columbia R
Pink	Biennial					Biennial and cyclic					NP, BS, Salish Sea, PWS	Russia, Japan, AK BC, WA
Seabirds												
NH Seabirds	Biennial		Biennial, –	Biennial, –	Biennial, –				Biennial, –	Biennial, –	BS, AI, GOA, PWS	Buldir I, Chowiet I, Pribilof Is, PWS
SH Seabirds						Long-term, –				Biennial, –	BS	Australia, Tasmania
Whales												
Humpback whale				Biennial							SE AK	SE AK
Killer whale				Biennial	Biennial					Biennial	Salish Sea	Salish Sea / WC

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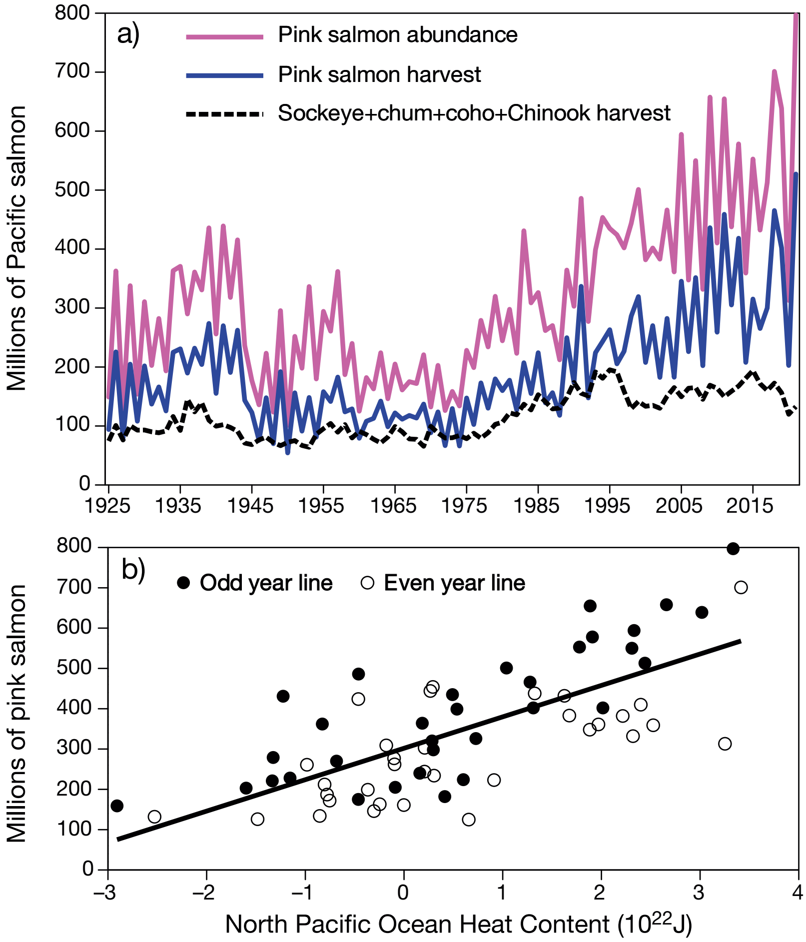

Fig. 1. (a) Annual abundance of adult pink salmon (catch plus spawners) returning from the North Pacific Ocean; commercial harvest of pink salmon; and the combined commercial harvest of sockeye, chum, coho, and Chinook salmon in Asia and North America, 1925–2021 (Ruggerone & Irvine 2018, Ruggerone et al. 2021, NPAFC 2022a). (b) Relationship between pink salmon abundance (odd and even years combined) and annual heat content for the North Pacific Ocean (0–700 m) during the year of juvenile pink salmon entry to the ocean, 1955–2021 (linear regression, df = 1, 65, $p < 0.001$, $R^2 = 0.51$; updated from Radchenko et al. 2007, NOAA 2022)

the Ocean Heat Index in the year they go to sea and adult abundance in the following year (Fig. 1b), and the use of ocean temperature to forecast adult returns (Radchenko et al. 2007, Krovnin et al. 2021, Bugaev et al. 2022). Pink salmon numbers are increasing in the Arctic (Dunmall et al. 2016, Farley et al. 2020), and they recently colonized the North Atlantic Ocean and Barents Sea following intentional stocking by Russia in the White Sea region (Sandlund et al. 2019, Diaz Pauli et al. 2023, Lennox et al. 2023).

Pink salmon have a fixed 2 yr anadromous life cycle in which they spawn in rivers during summer and fall, emerge as fry and emigrate to sea in spring, migrate over 5500 km, and then return to spawn and die after 1 winter at sea (Heard 1991). Odd- and even-year lines are separate, genetically isolated populations. Most notably, they have a unique, exaggerated biennial pattern of abundance in many regions of the NPO. For example, pink salmon sampled in the central BS were approximately 25 times more abundant in odd years than in even years during 1990–2010 (Davis 2003, Morita & Fukuwaka 2020). Potential mechanisms supporting the biennial fluctuations include negative interactions between odd- and even-year lines at sea and in fresh water (Heard 1991), and genetic adaptations of the odd-year line to warmer spawning temperatures (Beacham & Murray 1988).

Growth of pink salmon is relatively slow during the first 8 mo at sea but accelerates after winter, leading to prodigious consumption to fuel a rapid 5-fold increase in body weight by the time they spawn in summer to early fall (Heard 1991, Karpenko & Koval 2012). In the ocean, young pink salmon feed on various zooplankton species, primarily large calanoid copepods and euphausiids, and increasing amounts of squids and forage fishes as they grow (Brodeur 1990, Karpenko et al. 2007, Davis et al. 2009, Graham et al. 2021). Pink salmon <500 g consume zooplankton and small fishes; those >500 g consume zooplankton, fishes, and juvenile squid; and those >1000 g also consume adult squid (*Berryteuthis anonychus*) in spring and summer after overwintering at sea (Davis 2003, Aydin et al. 2005, Shaul & Geiger 2016). Their forage demand during 2005–2021 averaged approximately 4.35 × 10^6 Mt yr^{-1}, based on the methodology of Cooney & Brodeur (1998) and updated abundance values. About 90% of the forage demand occurs in oceanic rather than coastal habitats, especially during their second spring/summer at sea when they consume squid and small fishes and grow rapidly. A key question given such high consumption is whether the bottom-up processes supporting pink salmon are sufficient to also support other marine species.

Scientists have searched for biennial patterns in atmospheric and physical oceanographic variables that might underpin the biennial patterns observed and summarized here, but none have been found. Physical variables that have been associated with interannual and decadal-scale changes in primary, secondary, and/or tertiary production — Northern Hemisphere Zonal Index, solar radiation flux, surface wind speed, sea surface temperature (SST), salinity, density, nutrient levels, integrated mean water column temperature, average winter sea ice extent in the BS, vertical stability index, North Pacific Index, North Pacific Gyre Oscillation, Pacific Decadal Oscillation, and Southern Oscillation Index — have displayed no systematic biennial variability (e.g. Polovina et al. 1995, Mantua et al. 1997, Shiomoto et al. 1997, Sugimoto & Tadokoro 1997, Kobari et al. 2003, Brown et al. 2011, Jorgensen 2011, Litzow et al. 2020a, Thoman et al. 2020, Belkin & Short 2023). Recently, Ohlberger et al. (2023, their Fig. 5g) presented a time series of average summer SST in the BS between 1962 and 2020 that revealed a weak biennial pattern in 1976–1998. Since then, summer SST has been highly irregular between years, unlike the highly regular biennial patterns in biological variables we summarize here.

3. THE EVIDENCE

3.1. Pelagic trophic cascades

Evidence of trophic cascades in open ocean ecosystems is uncommon, although here we document 5 compelling examples, linked to pink salmon, from the NPO and BS spanning multiple decades. The cascades flow downward from pink salmon to large copepods to diatoms: diets of pink salmon include large copepods, primarily *Neocalanus* spp., that consume diatoms in the BS (Davis et al. 2005, Karpenko et al. 2007, Campbell et al. 2016).

In the most recent example, Batten et al. (2018) used continuous plankton recorder data to develop indices of abundance of phytoplankton (primarily large diatoms) and zooplankton (primarily large calanoid copepods) in the BS and Aleutian Islands region during summer, 2000–2014. Three lines of evidence suggested that predation by maturing pink salmon during spring and summer altered the abundance of large copepods, which in turn altered the abundance of diatoms. First, copepods were less abundant and diatoms more abundant in odd years of higher pink salmon abundance (Fig. 2a–c). Second, diatom abundance was negatively correlated with copepod abundance, and copepod abundance was negatively correlated with adult pink salmon abundance (Fig. 2d–f). Third, in 2013, when pink salmon abundance was exceptionally low for an odd year, copepod abundance rebounded to high levels that year and diatom abundance was low (Fig. 2a–c). Evidence for a trophic cascade was strong in both the southcentral BS and eastern Aleutian Islands region, although reduced or absent in the western Aleutian Islands. These findings illustrate the importance of variability in pink salmon abundance and its effects across the ecosystem, which in that study was greater than physical oceanographic variability, according to the authors.

Earlier studies also found evidence of direct effects of pink salmon on summer plankton standing stocks in the central subarctic NPO and the eastern BS. Sugimoto & Tadokoro (1997) reported negative correlations between zooplankton biomass anomalies and Asian pink salmon abundance, and between chlorophyll *a* (chl *a*) concentration (a proxy for phytoplankton biomass) and zooplankton, during 1954–1981. They suggested that top-down predation by pink salmon increased interannual variations in zooplankton and in turn phytoplankton, whereas bottom-up factors were more important at decadal or longer scales. Toge et al. (2011) also reported a positive correlation between chl *a* concentration in the central BS and regional pink salmon abundance during 2002–2008 while noting the apparent trophic cascade through zooplankton.

Pink salmon are usually, but not always, more abundant in odd than even years, and plankton communities reflect those shifts in abundance. Shiomoto et al. (1997) quantitatively sampled pink salmon in the BS, and macrozooplankton (mostly copepods) and chl *a* just south of the central Aleutian Islands during 1985–1994. Early in their research (1985–1988), few differences existed between even- and odd-year pink salmon numbers, macrozooplankton biomass, or chlorophyll concentrations. However, beginning in 1989, odd-year pink salmon abundance and chl *a* notably increased while odd-year macrozooplankton biomass declined. We found negative correlations between the estimates of Shiomoto et al. (1997) of maturing pink salmon abundance and macrozooplankton biomass (Pearson's correlation, $p = 0.040$), and between their macrozooplankton biomass and chl *a* levels ($p = 0.086$). The authors also reported that zooplankton biomass in the central NPO remained low throughout summer of odd years after maturing pink salmon had migrated into the BS, an observation that is consistent with relatively low summer/fall marine scale growth of Bristol Bay sockeye salmon *Oncorhynchus nerka* in odd years (Ruggerone et al. 2005).

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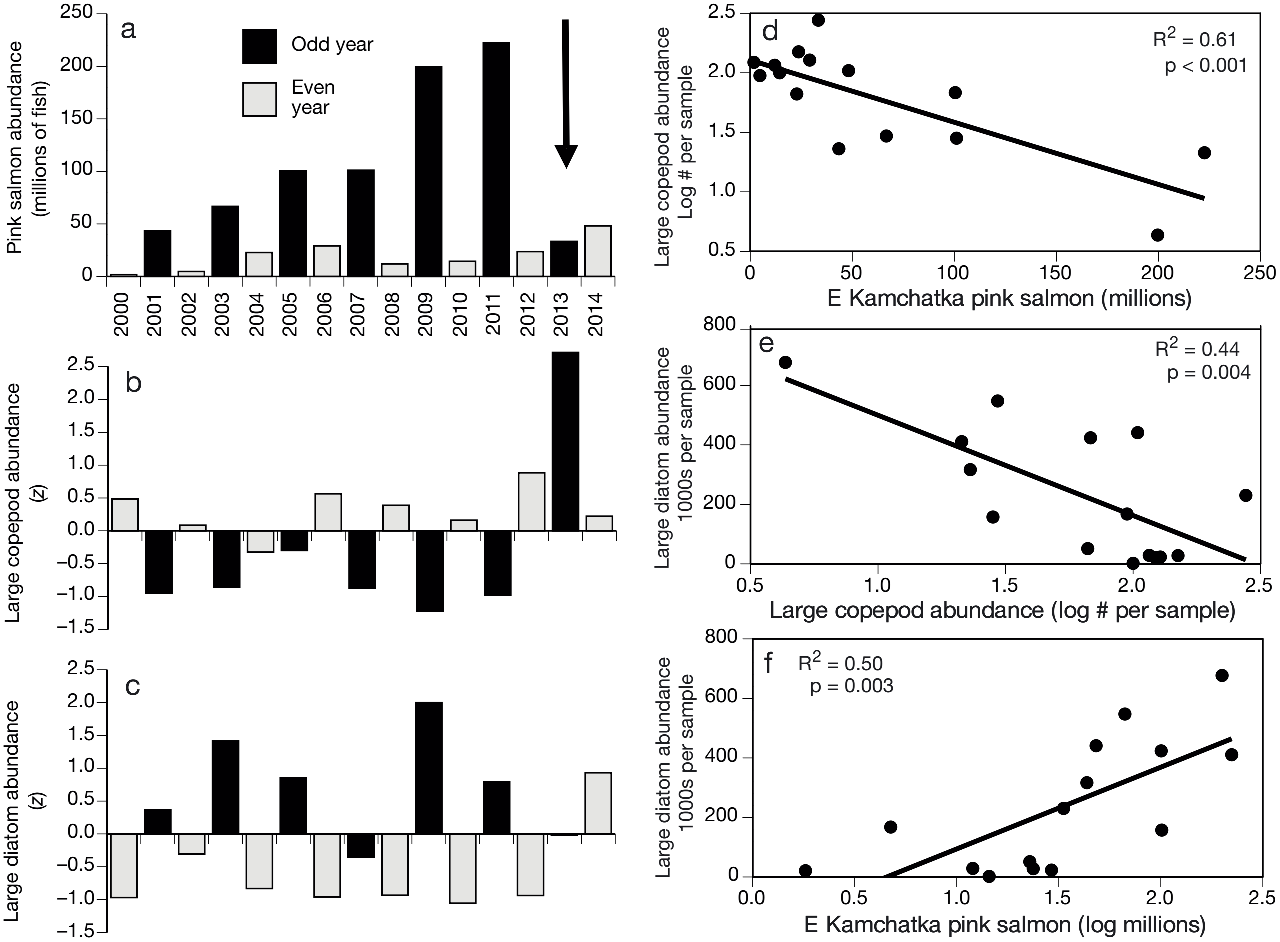

Fig. 2. Three lines of evidence supporting the pink salmon trophic cascade hypothesis in the southern Bering Sea and Aleutian Islands. (a) Biennial pattern of eastern Kamchatka pink salmon, the primary population in this region. (b) Normalized abundance of large copepods. (c) Normalized abundance of large diatoms. (d) Relationship between abundances of eastern Kamchatka pink salmon and large copepods. (e) Relationship between abundances of large copepods and diatoms. (f) Relationship between abundances of eastern Kamchatka pink salmon and large diatoms in 2000–2014. In 2013 (arrow in panel a), pink salmon abundance declined sharply, zooplankton abundance increased substantially, and diatom abundance declined. In 2014, diatom abundance was high for an even year, possibly in response to the marine heatwave that was occurring at the time (DiLorenzo & Mantua 2016). Redrawn from: Batten et al. (2018)

The trophic cascade described here requires tight coupling between phytoplankton and zooplankton, such that changes in the standing stock and grazing pressure by the herbivorous zooplankton have measurable effects on phytoplankton abundance. It then would be expected that in even years of relatively low pink salmon abundance, and thus higher copepod abundance, food limitation might have consequences for copepod growth and body size. A 20 yr study from 1979 to 1998 identified biennial patterns in the abundance of *Neocalanus cristatus*, *N. plumchrus*, and *N. flemingeri* in the central subarctic Pacific and attributed them to pink salmon predation (Kobari et al. 2003). Notably, they also documented biennial patterns in the growth of those copepods, with growth higher in odd years of lower copepod abundance. In addition, they found a positive correlation between body size of *N. cristatus*, the largest of the 3 species, and chl *a* concentration.

3.2. Forage fishes

3.2.1. Pacific herring

As with many forage fishes, Pacific herring *Clupea pallasii* are widely distributed and highly important to marine ecosystems (Surma et al. 2018). Herring are also important to Indigenous people and subsistence fishermen (Thornton & Moss 2021), and they support commercial fisheries.

Sitka Sound, Alaska, has one of the largest herring populations in North America. We found that herring growth (proportional increase in mean annual body weight) was lower in 5 adult herring age groups when emigrating from Sitka Sound in the spring of odd years and returning in the following even years compared with those emigrating in even years, 1996–2018 (Fig. 3a). The magnitude of year-to-year variation in herring growth was negatively correlated with that of adult pink salmon abundance (Prince William Sound [PWS], Southeast Alaska (SEAK), and BC stocks) for each herring age group, especially younger fish (Fig. 3b). Adult herring emigrate from Sitka Sound in spring after spawning and feed in offshore continental shelf waters, possibly from PWS to BC (D. Hay pers. comm.), where in odd years they may encounter fewer zooplankton prey during spring, summer, and fall as a result of

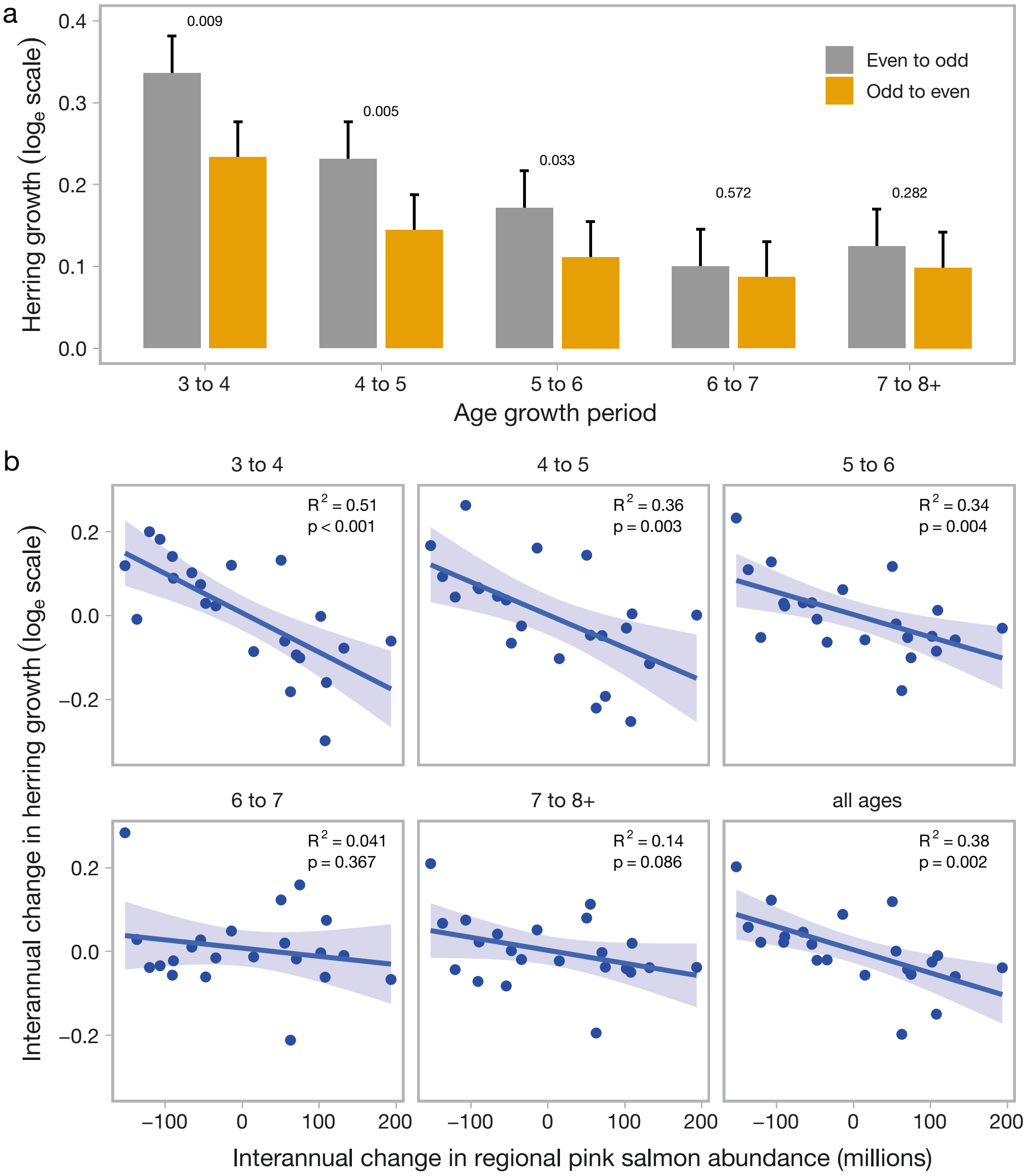

Fig. 3. (a) Biennial pattern in age-specific annual proportional increase in mean weight (growth index, ±95% CI) of adult herring returning to Sitka Sound, Alaska, from 1996 to 2018; and (b) relationships between the magnitude of year-to-year variation of age-specific mean growth of herring and the magnitude in year-to-year variation in abundance of pink salmon returning to North America, where interannual change (G) in year $i = G_i - \text{avg.}(G_{i-1}, G_{i+1})$. In panel (a), 'Even to odd' refers to proportional growth from even to odd years (e.g. $\log_e$[weight-at-age in year t+1/weight-at-age in year t]); t-test p-values are shown above each growth period in (a), and linear regression statistics are shown in panel (b). Herring weight-at-age measured in the commercial fishery prior to spawning. Data sources: S. Dressel unpubl. data, Hebert (2019), Ruggerone & Irvine (2018)

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numerous maturing pink salmon. These relationships were weaker during the previous 16 yr period (not shown), possibly because several year classes failed to produce many herring and because the magnitude of variation in pink salmon abundance was smaller.

In PWS, herring recruitment declined sharply after the 'Exxon Valdez' oil spill in 1989, and the population has yet to recover, leading to several studies of factors inhibiting recovery. A statistical examination of 19 hypotheses for the lack of recovery and subsequent analyses found competition with hatchery pink salmon (up to 600 million released per year) had the greatest support (Deriso et al. 2008, Pearson et al. 2012). This conclusion was based on the large reduction in herring spawning biomass associated with hatchery releases, sympatry of pink salmon fry and age-1 herring in nearshore habitats during late spring and summer, diet overlap, and field studies indicating reduced food intake by juvenile herring in the presence of juvenile pink salmon. Other studies have found equivocal support for this hypothesis, but recommended further study of pink salmon effects on the PWS food web (Cooney 1993, Ward et al. 2017, 2018).

3.2.2. Sand lance

Sand lance *Ammodytes personatus* recruitment and abundance in the Salish Sea were 13 times higher in odd versus even years, corresponding with the strong biennial pattern of pink salmon (Baker et al. 2019). In this region, maturing pink salmon are approximately 45 times more abundant in odd years, leading to exceptionally high abundances of juvenile pink salmon in the following even year that may reduce sand lance prey (Osgood et al. 2016, Sisson & Baker 2017).

3.2.3. Atka mackerel

Atka mackerel *Pleurogrammus monopterygius* are important prey of Pacific salmon and other fishes, marine birds, and marine mammals and the target of a commercial fishery in the Aleutian Islands (Davis 2003, Lowe et al. 2018). Atka mackerel feed heavily on *Neocalanus* spp. and euphausiids (Yang 1999, 2003, Rand et al. 2010), a diet that overlaps extensively with that of pink salmon.

Matta et al. (2020) found a conspicuous biennial pattern in the growth of Atka mackerel otoliths (an index of annual body growth; Fig. 4): a Pearson's negative correlation between otolith growth and the abundance of eastern Kamchatka pink salmon (p = 0.005), and a positive correlation between otolith growth and the abundance of large copepods (p = 0.023). The abundance of large copepods in the region of their study was negatively related to pink salmon abundance (p = 0.002).

3.2.4. Pacific Ocean perch

Pacific Ocean perch (POP) *Sebastes alutus* is a long-lived, commercially important rockfish that mainly occupies continental slope and shelf habitats from California to Japan (Hulson et al. 2021). POP are considered to be semi-demersal, but limited sampling at sea indicates larvae and juveniles inhabit

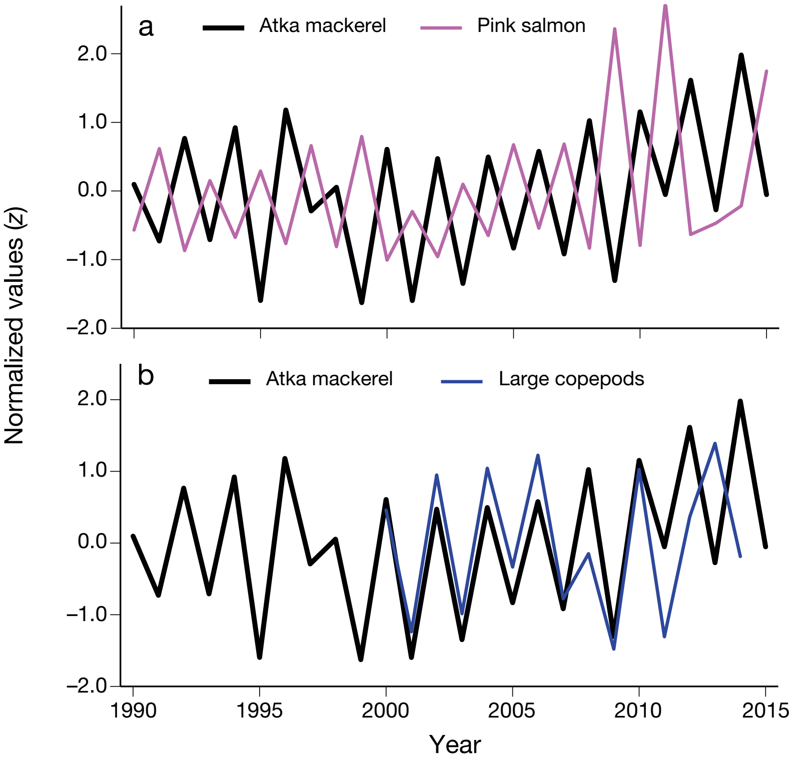

Fig. 4. Relationships between anomalies in otolith growth of Atka mackerel and (a) the normalized abundance of eastern Kamchatka pink salmon (negative), and (b) the abundance of large copepods (positive) in the central Aleutian Islands. Pink salmon data from Ruggerone & Irvine (2018); Atka mackerel and large copepod data from Matta et al. (2020) and M. Matta and S. Batten, with permission

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epipelagic waters far from adult habitats (Kendall et al. 2007, Boldt & Rooper 2009). Juvenile POP primarily consume copepods.

We analyzed age-2 POP recruitment estimates from the GOA (Hulson et al. 2021) and found a pronounced biennial pattern from 1999 through 2019, corresponding to a period of relatively high POP abundance and high interannual variation in numbers of pink salmon returning to North America (Fig. 5). Age-2 POP recruits (typically <160 mm) averaged 45% fewer fish in odd (101 million fish) versus even years (183 million fish) during 1999–2019, suggesting a negative interaction with pink salmon during the growing season (Fig. 5), even though abundances of both species increased after 1977. Over the 43 yr period 1977–2019, approximately 50% of the interannual variability in age-2 POP abundance was explained by interannual variation in the abundance of pink salmon, which also consume copepods, and POP female spawning biomass 2 yr earlier (Fig. 5). Ortiz & Zador (2022) also reported that POP recruitment in the Aleutian Island region exhibited a biennial pattern; abundances of age-3 POP were often higher in odd years.

3.3. Squid

Subadult and adult squid are highly important prey of many fishes, birds, and marine mammals in the NPO (Aydin 2000). For example, large proportions of salmonid diets were squid (subadult and adult *Berryteuthis anonychus*, <150 mm) in the Subarctic Current region of the GOA during 1994–1998: e.g. pink (40–80% of prey weight), sockeye (>85%), coho *O. kisutch* (>95%), and Chinook salmon *O. tshawytscha* (100%), and steelhead *O. mykiss* (50–100%) (Kaeriyama et al. 2004). Bioenergetic modeling indicated a substantial increase in salmon growth when consuming high-energy *B. anonychus*, which is especially important to maintaining growth as temperature increases (Aydin 2000), particularly among larger salmon (Beauchamp 2009). *B. anonychus* is the most abundant squid in the GOA and is distributed primarily south of 53° N and west from North America to about 160° W.

The primary effect of pink salmon on *B. anonychus* abundance appears to be via predation on subadults and adults, rather than competition with juveniles for prey (Shaul & Geiger 2016). In the northwestern GOA, the abundance of *B. anonychus* paralarvae

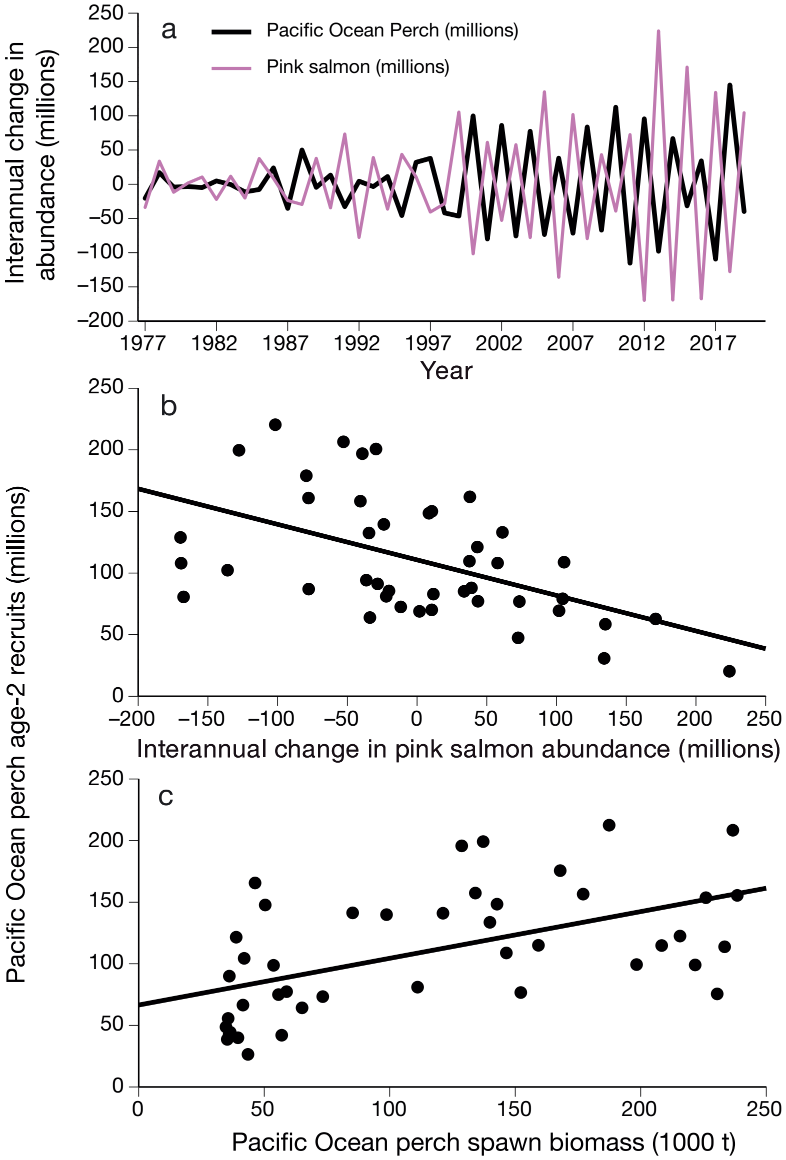

Fig. 5. (a) Interannual change in abundances of age-2 Pacific Ocean perch (POP) in the Gulf of Alaska and pink salmon returning to North America during 1977–2019; and regression-corrected plots of (b) age-2 POP recruits in relation to interannual change in abundances of North American pink salmon ($p < 0.001$) and (c) age-2 POP recruits in relation to the parent spawning biomass ($p = 0.019$). Cochrane-Orcutt multiple regression accounted for autocorrelation ($R^2 = 0.50$; overall df = 2, 39; $p < 0.001$). Interannual change in abundance (A) in year $i = A_i - \text{avg.}(A_{i-1}, A_{i+1})$. Data source: Hulson et al. (2021)

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was negatively correlated with maturing pink salmon abundance during the previous year, as expected from predation by maturing pink salmon on the parent squid (r = –0.55, p = 0.009, Jorgensen 2011). Over a 19 yr period, paralarvae were 95% less abundant in even versus odd years, leading to fewer adult squid in the following odd year (Jorgensen 2011). Jorgensen (2011) could not explain the biennial pattern using oceanographic variables. *B. anonychus* appears to have a 2 yr life cycle, which leads to a strong and consistent biennial cycle when combined with predation by biennial pink salmon. In odd years when pink salmon are highly abundant, squid are less common in diets of all salmon species in the BS (Fig. 6) and the Alaska Gyre in the GOA (Aydin 2000, Kaeriyama et al. 2004).

B. anonychus are critical prey for marine fishes, birds, and mammals, such that substantial predation by pink salmon on squid, as in spring and summer of odd years, can reverberate through the offshore ecosystem (Aydin 2000). Furthermore, the 2 yr lifespan of *B. anonychus* and predation on them by biennially-abundant pink salmon sustains and perhaps exacerbates biennial patterns in squid abundance.

3.4. Pacific Salmon

Biennial variation in the abundance of pink salmon may lead to biennial feeding patterns by other species of Pacific salmon if they are out-competed for common prey, as detailed below. For example, in odd years when pink salmon are typically most abundant, Davis (2003) found that over a 10 yr period, Chinook, sockeye, and pink salmon in the BS consumed fewer nutritionally valuable prey such as squid, fishes, and euphausiids, and all salmon species consumed more low-calorie prey than in even years (Fig. 6). Those high-quality prey are among the principal conduits of energy flow through pelagic food webs that include zooplankton, forage fishes, squids, salmon, seabirds, and marine mammals (Brodeur et al. 1999, Aydin 2000).

Stable isotope signatures of Chinook and coho salmon and steelhead have been used as evidence that they typically feed on higher trophic level prey than pink salmon, and thus there is little direct competition between them (Welch & Parsons 1993, Kaeriyama et al. 2004, Johnson & Schindler 2009). However, diet composition of pink salmon during the second year at sea is more accurate for identifying potential competition with salmon species that consume squid and fishes than stable isotope signatures, which fail to reflect the consumption of squid and fishes by pink salmon during their second year at sea when forage demand is especially great. Muscle isotope signatures require many months after a diet shift from plankton to fish and squid to be partially detected, and years to accurately reflect the new diet (e.g. Madigan et al. 2021; see Text S1 in Supplement 1 at www.int-res.com/articles/suppl/m719p001_supp1.pdf).

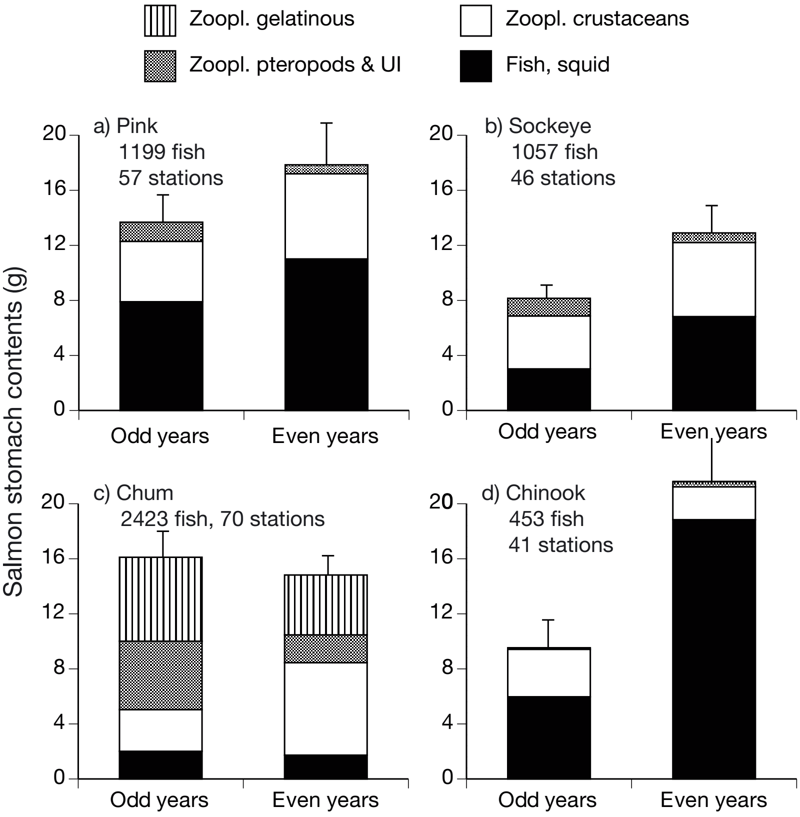

Fig. 6. Mean weights of stomach contents from (a) pink, (b) sockeye, (c) chum, and (d) Chinook salmon sampled in the central Bering Sea during odd and even years, 1991–2000 (UI = unidentified). Error bars: SE. Data source: Davis (2003)

3.4.1. Sockeye salmon

Sockeye salmon migrate long distances during their 2 or 3 yr at sea where they can interact with nearby and distant populations of pink salmon. For example, Bristol Bay sockeye salmon range from the Kamchatka Peninsula to Kodiak Island (Myers et al. 2007, Habicht et al. 2010, Espinasse et al. 2020), and ocean age-1 Fraser River, BC, sockeye salmon have been observed in the central NPO (176.2° E) approximately 4000 km from their natal river (Neville & Beamish 2022).

Among Pacific salmon species, sockeye salmon have the greatest diet overlap with pink salmon (Brodeur 1990, Kaeriyama et al. 2000, Qin & Kaeriyama 2016). Both species are primarily planktivores, but each can switch to higher trophic level prey such as small fishes and squid as they grow in their second season at sea. During a 10 yr study in the central BS (52–58° N), the diet of sockeye salmon averaged 47 % fish and squid, 44 % zooplankton, and 9 % other prey by weight (Fig. 6). However, in odd years, when pink salmon were approximately 40 times more abundant, total prey weight consumed per sockeye salmon declined 36 % versus only 23 % among pink salmon. In odd years, the consumption of energy-rich fishes and squid declined 50 to 58 % in sockeye salmon, respectively, but only 25 to 32 % in pink salmon (Fig. 6; Davis 2003). Likewise, in odd years, consumption of higher caloric-value euphausiids and copepods declined 46 to 50 % in sockeye salmon compared with only 37 to 48 % in pink salmon, respectively. In contrast, lower caloric-value pteropods and amphipods increased in diets of both sockeye (13 %) and pink salmon (72 %) in odd years. These data suggest that pink salmon were able to consume fishes, squid, and energy-rich zooplankton more effectively than sockeye salmon when availability of these key prey was limited (Ruggerone et al. 2003).

In the western NPO, only trace amounts of squid were observed in the stomachs of sockeye and pink salmon during odd years, whereas both species contained 50 times more squid by weight in even years during 1956–1963 (Ito 1964). This observation, which preceded the large increase in pink salmon abundance after the 1977 regime shift, occurred when Asian pink salmon abundance averaged 67 % more fish in odd (200 million) versus even years (120 million; Ruggerone & Irvine 2018).

Despite the tremendous amount of research on sockeye salmon over the past 75 yr, and the odd–even year differential in consumption of squid noted above, interactions between them and pink salmon were largely unknown until the early 2000s (Peterman 1982, Bugaev et al. 2001, Ruggerone et al. 2003). In the past 20 yr, however, a growing body of evidence indicates that pink salmon influence the growth, age, survival, and abundance of sockeye salmon throughout their range in North America.

A quantitative analysis of 47 sockeye salmon populations, representing approximately 90 % of all sockeye salmon ranging from the Fraser River in southern BC to the Kuskokwim River region in southwestern Alaska, found strong associations between sockeye salmon productivity ($\log_e$ recruits per spawner) in brood years 1976–2009 and NPO pink salmon abundance and SST during early life at sea (Connors et al. 2020). Based on these relationships, it was estimated that a 119 million increase in pink salmon abundance (i.e. 1 SD above the mean) was associated with a 9 % decline in sockeye salmon productivity in the BS and the GOA, and a 21 % decline in productivity in BC and SEAK (Fig. 7a), whereas a 1.5°C increase in SST (1 SD) was associated with a 23 % increase in sockeye salmon productivity in the BS and a 9 % increase in the GOA, but with a 12 % decline in BC and SEAK. The mean annual return of approximately 82 million hatchery pink salmon during 2005–2015 was estimated to reduce sockeye salmon productivity by 5 % in the BS, 6 % in the GOA, and 15 % in BC and SEAK.

Sockeye salmon have a diverse life history, especially in northern areas, that can mask detection of biennial pink salmon effects. Sockeye salmon typically enter the ocean after spending 1 or 2 winters in freshwater, then return to their natal rivers to spawn after 2 or 3 winters at sea, thereby encountering both odd-year (abundant) and even-year (few) pink salmon. Therefore, age-specific analyses of sockeye salmon are often needed to unravel the apparent effects of pink salmon on sockeye salmon growth, age-at-maturation, survival, and abundance.

Analyses of annual and seasonal sockeye salmon scale growth at sea revealed strong interactions with pink salmon. For example, over a 43 yr period, odd-year scale growth of Bristol Bay sockeye salmon averaged 6.2 and 10 % less than adjacent even-year growth during the second and third years at sea, respectively (Fig. 8a; Ruggerone et al. 2003, 2016a). Scale growth declined with increasing abundances of pink salmon returning to Russia (the primary overlapping population), explaining 33 and 58 % of second- and third-year scale growth variability, respectively, during 1965–2009 (Fig. 8b; Ruggerone et al. 2016a). Analysis of seasonal scale circuli measurements indicated that the biennial divergence in sockeye salmon growth began in early spring (third season at sea) or late spring (second season at sea) and continued through summer and fall; no biennial pattern was detected during winter when most pink salmon were distributed farther south than

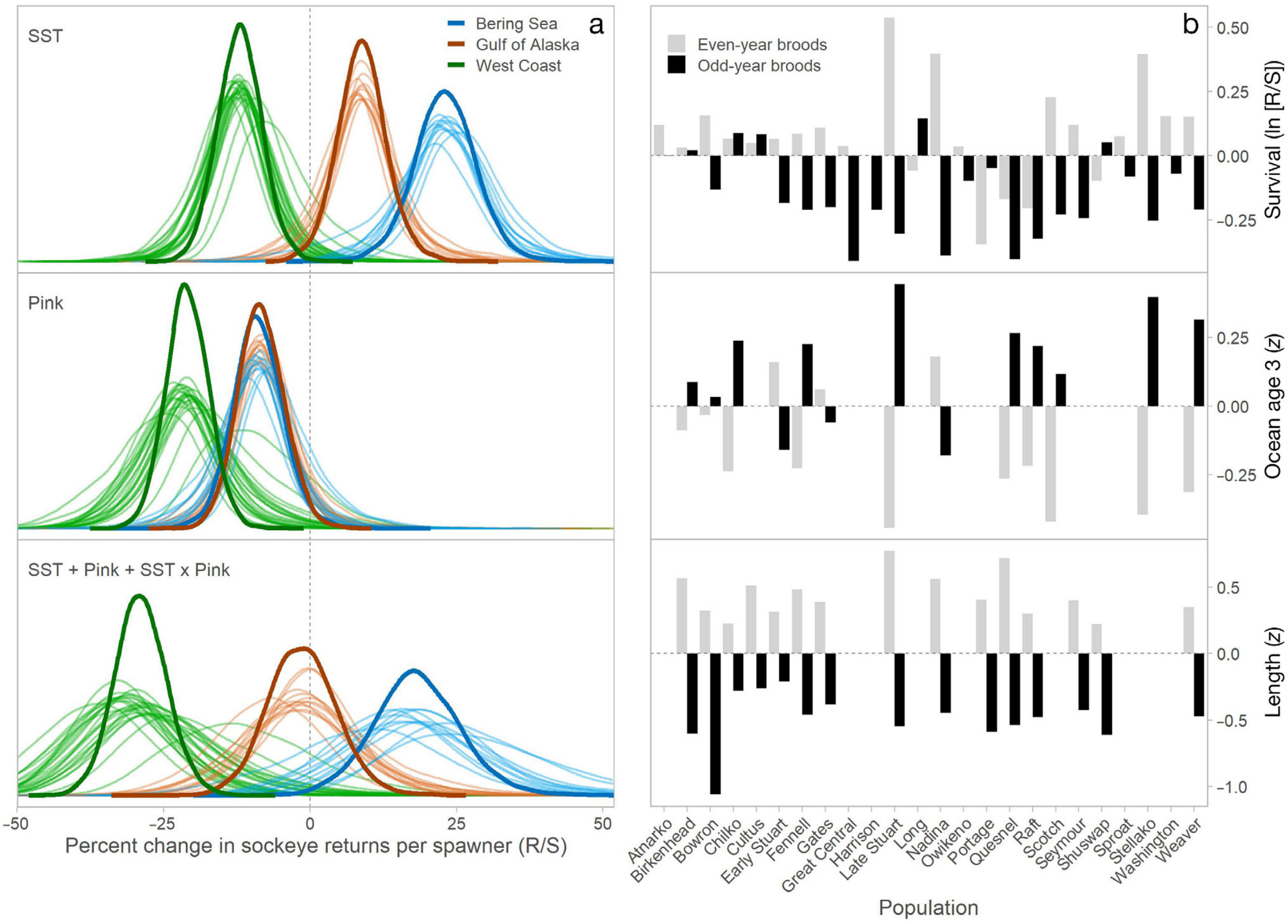

Fig. 7. (a) Posterior probability distributions of the predicted effect of sea surface temperature (SST; top), pink salmon competitors (middle), and the combined effect from all covariate terms (bottom), on survival of 47 sockeye salmon populations originating from the Bering Sea, Gulf of Alaska, and west coast of North America (Southeast Alaska and British Columbia). Posterior hyperdistributions of the covariate effects are in bold lines, with individual stock-specific posterior distributions illustrated by the thin lines. Covariate effects are standardized (i.e. per standard deviation unit increase in each covariate), which equates to 1.5°C SST and 119 million pink salmon above the mean. (b) Mean survival (top), proportion of ocean age-3 sockeye salmon in the adult return (middle), and length-at-age of 24 sockeye salmon populations from British Columbia and Washington state during odd- versus even-numbered brood years, 1978–2005 (bottom). Values are normalized (*z*) relative to the entire data time series, except survival, which is the mean residual ($\log_e$ recruits per spawner) from the recruitment relationship. Data sources: Ruggerone & Connors (2015), Connors et al. (2020)

sockeye salmon (Ruggerone et al. 2005). Biennial patterns in sockeye salmon scale growth were not observed during the first year at sea or during the homeward migration, presumably because abundance of pink salmon is low in Bristol Bay (Ruggerone & Irvine 2018). Biennial scale growth of sockeye salmon returning to watersheds in the GOA region (Chignik, Cook Inlet, PWS, Copper River, and SEAK) was also observed during the second and third years at sea (low growth in odd years), but not consistently during the first year at sea (P. Rand & G. Ruggerone unpubl. data).

Size-at-age of returning Bristol Bay sockeye salmon was negatively correlated with both abundance of Russian pink salmon during the year prior to return and abundance of Bristol Bay sockeye salmon during the year of return, 1958–2003 (Ruggerone et al. 2003, 2007). Eight sex- and age-specific statistical models explained on average 45% of the variability in adult sockeye salmon length. The models indicated that competition with pink salmon reduced the length of female sockeye salmon more than that of males, suggesting a possible adverse effect on future abundance because salmon fecundity is associated with body size (Quinn 2005). A recent analysis of Bristol Bay sockeye salmon size-at-age over a 60 yr period, which considered SST, also found that pink and sockeye salmon abundance had the greatest ex-

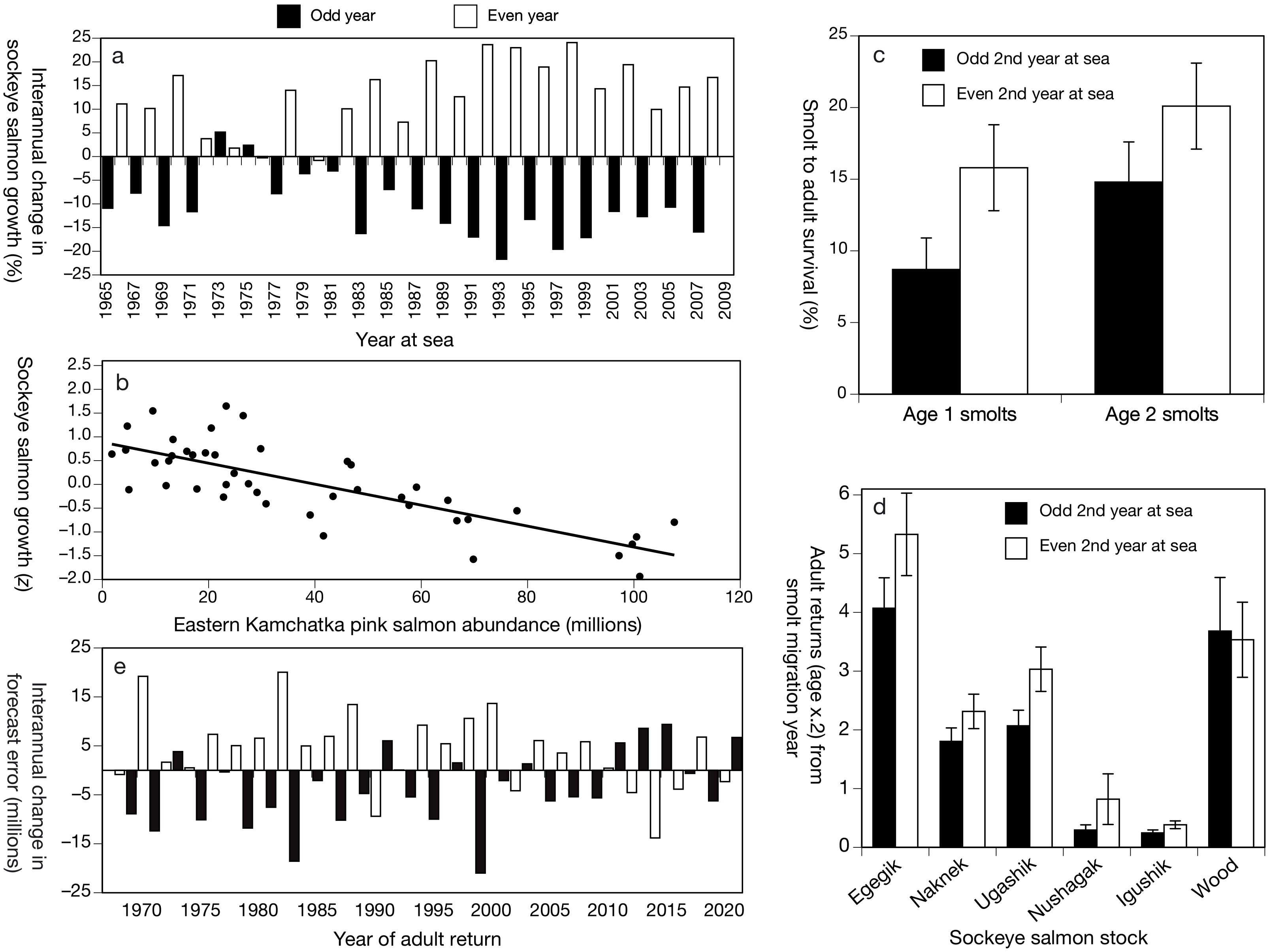

Fig. 8. Examples of biennial patterns and correlation analyses among Bristol Bay sockeye salmon (a,b) testing the hypothesis that pink salmon affect sockeye salmon growth at sea, (c) smolt to adult survival, (d) adult returns from smolt migrations, and (e) adult sockeye salmon forecast error, 1968–2021. Interannual change in scale growth or forecast error (G) in year $i = G_i$ − avg. (G_{i-1}, G_{i+1}). Mean scale growth values in (a,b) represent Kvichak, Egegik, Naknek, Ugashik, and Wood River stocks during the third year at sea, 1965–2008. Second-year growth shows similar patterns (not shown). Smolt-to-adult survival (c) is the annual mean for Kvichak, Egegik, and Ugashik stocks, 1977–1997. Mean annual adult returns of ocean age-2 salmon (d) are from odd- or even-year smolt migrations, 1977–2019, excluding 1999 as an extreme outlier. Error bars are ±1 SE. Updated from Ruggerone et al. (2003, 2016a)

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planatory power (Ohlberger et al. 2023). Oke et al. (2020) reported a negative correlation between body size of sockeye salmon in Alaska (128 populations, up to 60 yr) and the abundance of pink salmon in the NPO.

Smolt to adult survival of Bristol Bay sockeye salmon was significantly lower for fish entering the southeastern BS during even years compared with odd years, 1977–1997 (Fig. 8c, $p < 0.02$; Ruggerone et al. 2003). Specifically, smolt survival declined 35 %, on average, when they entered Bristol Bay in even years and competed with highly abundant Russian pink salmon during their second year at sea (odd year). Survival of younger age-1.2 salmon declined 59 % compared with 30 % among age-1.3 and age-2.2 salmon and 19 % among age-2.3 salmon that interacted with pink salmon in both odd (second year) and even (third year) years at sea.

Age-specific adult sockeye salmon returns to Bristol Bay from odd- versus even-year smolt migrations also revealed apparent interactions with pink salmon (Ruggerone et al. 2003). Adult returns of ocean age-2 sockeye salmon from 6 stocks declined 21 %, or 3.3 million adults per even year, on average, in 1977–2019 when they competed with abundant odd-year pink salmon during their second growing season at sea (Fig. 8d). Ocean age-2 sockeye salmon primarily interacted with pink salmon during a single second year at sea, i.e. either abundant pink salmon in an odd year or few pink salmon in an even year. Adult returns of ocean age-3 sockeye salmon declined only 6 % when emigrating in even years (odd second year) because ocean age-3 sockeye salmon interacted with both even- and odd-year pink salmon. Overall, during 1977–2019, approximately 85 million fewer adult sockeye salmon returned from even-year smolt migrations that encountered abundant pink salmon in the following year than from odd-year smolt migrations that encountered fewer pink salmon.

Interannual variation in forecast error (i.e. error relative to error during the 2 adjacent years) was used to further test the hypothesis that pink salmon affect the survival and abundance of Bristol Bay sockeye salmon (Ruggerone et al. 2016a). Forecast error of southeastern Bristol Bay sockeye salmon (Kvichak, Naknek, Egegik, and Ugashik stocks) was biased high during even-numbered years (avg. 4.0 million fish yr^{-1}), and biased low during odd-numbered years (avg. −3.9 million fish yr^{-1}), 1968–2021 (Fig. 8e). High-biased forecasts in even return years reflect interaction with abundant pink salmon during the previous odd year in which sockeye salmon growth is reduced (Fig. 8a,b); seasonal scale-growth measurements demonstrated little effect of pink salmon during the homeward migration (Ruggerone et al. 2005, 2016a). Likewise, low-biased forecasts in odd return years reflect interaction with fewer pink salmon and greater sockeye salmon growth during the previous even year (Fig. 8a,b). After standardizing forecast error relative to adjacent years, forecasts in even years were biased high in 63 % of the years and biased low in 22 % of the years. Interannual variation in forecast error increased with interannual variation in the abundance of eastern Kamchatka pink salmon during the previous year, 1968–2008 (linear regression, $p < 0.01$, $r = 0.41$, after accounting for autocorrelation). Forecast error was greater for ocean age-2 than for ocean age-3 sockeye salmon because age-2 sockeye salmon interact with either odd-year or even-year pink salmon, whereas age-3 sockeye salmon interact with both pink salmon lines (Ruggerone et al. 2016a). Interannual variation in forecast error shifted after 2009 (Fig. 8e), possibly reflecting an increase in the proportion of sockeye salmon spending 3 rather than 2 winters at sea in response to younger age of smolts (Nielsen & Ruggerone 2009, Cline et al. 2019) and the exceptional abundance of Bristol Bay sockeye salmon since 2014 (Ruggerone et al. 2021).

Interannual variation in forecast error of northwestern Bristol Bay sockeye salmon (Wood River, Nushagak, and Igushik stocks combined) was also biased high in even years (avg. 0.79 million fish yr^{-1}) and biased low in odd years (avg. −1.06 million fish yr^{-1}), 1968–2021. This pattern was not as consistent nor as strong as it was for the southeastern stocks, possibly reflecting the more easterly distribution of Wood River (Bristol Bay, Alaska) sockeye salmon in the NPO and less interaction with eastern Kamchatka pink salmon (Ruggerone et al. 2016a).

The annual return of sockeye salmon to Bristol Bay exceeded 50 million fish from 2015 to 2021 at the same time when pink salmon returns to Russia were exceptionally large (Ruggerone et al. 2021). We hypothesize that this counterintuitive relationship occurs because Bristol Bay sockeye salmon encounter few pink salmon during their first season at sea (Ruggerone et al. 2003, 2005, 2016a) and because both species in the north have benefited from recent marine heatwaves, especially during early life at sea (e.g. Ruggerone et al. 2005, 2007). Greater sockeye and pink salmon abundance, however, led to reduced growth during late life at sea and reduced adult size-at-age of sockeye salmon. Our findings suggest that early growth at sea is critical to salmon survival and subsequent abundance, but that reduced growth at later marine life stages can also affect survival, although to a lesser extent. For Bristol Bay sockeye salmon, favorable early marine conditions have likely overwhelmed competition effects with pink salmon during the second and third seasons at sea (Connors et al. 2020).

This pattern of abundance is reversed among sockeye salmon in the south. Sockeye salmon in BC and SEAK have encountered unfavorable early and late marine conditions in recent decades, leading to declining survival and abundances (Connors et al. 2020). An analysis of up to 36 sockeye salmon populations from Puget Sound, WA, through SEAK during the past 55 yr revealed that high abundance of NPO pink salmon in the second year of sockeye salmon life at sea was associated with lower sockeye salmon productivity, reduced adult length-at-age, and delayed maturation (Ruggerone & Connors 2015). While accounting for SST, they predicted that an increase from 200 million to 400 million pink salmon would lead to a 39% reduction in productivity of Fraser River sockeye salmon, an estimate that is consistent with that of Connors et al. (2020). Furthermore, biennial patterns in sockeye salmon life history characteristics were significant: productivity was low, length-at-age was small, and age-at-maturation was delayed when sockeye salmon encountered highly abundant pink salmon (Fig. 7b). The greatest statistical support for models occurred when sockeye salmon were aligned to interact with immature pink salmon during their second season at sea and continued to interact with maturing pink salmon as they migrated to their natal river. Less support was found for negative interactions during the first season at sea. In contrast, McKinnell & Reichardt (2012) found some support for negative effects of juvenile pink salmon in northern BC on first-year scale growth of Fraser River sockeye salmon, but no support in the Strait of Georgia.

Several studies reported evidence for adverse effects of adult pink salmon on the growth and survival of juvenile sockeye salmon. Marine survival rate residuals of Babine Lake (Skeena River, BC) sockeye salmon were inversely related to the abundance of adult pink salmon returning to northern BC during the year of sockeye smolt emigration to sea in 1961–1977 (Peterman 1982). Sockeye salmon survival was positively correlated with juvenile pink salmon abundance in the year of outmigration. Thus, Babine Lake sockeye salmon may experience both compensatory and depensatory mortality in relation to pink salmon. In PWS, productivity of sockeye salmon returning to the Copper River, Coghill Lake, and Eshamy Lake in 1981–2011 was inversely related to abundance of returning hatchery pink salmon, but no effects were found on wild pink, chum *O. keta*, or Chinook salmon (Ward et al. 2017, 2018). In support of the competition hypothesis, Martinson et al. (2008) reported decreased scale growth of sockeye salmon emigrating from the Karluk River (Kodiak Island, AK) during years when large numbers of adult pink salmon returned to the same area, while providing some evidence for diet overlap between juvenile sockeye salmon and adult pink salmon.

Russia produces approximately 15% of the annual sockeye salmon returns from the NPO (Ruggerone & Irvine 2018). Bugaev et al. (2001) reported that the length and weight of sockeye salmon returning to the Ozernaya River (Kuril Lake, Kamchatka) during 1970–1994 was reduced in years when the ocean abundances of Kamchatka pink salmon were high. The effect of pink salmon abundance on sockeye growth was greater than that of sockeye salmon abundance, owing to the much higher abundance of pink salmon. Additional studies provided evidence that trophic competition between pink and sockeye salmon at sea influenced the growth of Russian sockeye salmon ([Krogius 1960, Birman 1985] in Bugaev et al. 2001). Sano (1963) found that both the size of sockeye and pink salmon caught in the western NPO and the average weight of their stomach contents were smaller in odd years, when pink salmon abundance was high.

3.4.2. Chum salmon

Chum salmon are highly abundant and widely distributed in the NPO (Myers et al. 2007). Most fish (60%) are from hatcheries in Japan, Russia, and Alaska (Ruggerone & Irvine 2018). They enter the ocean as young-of-the-year fry during spring and primarily consume zooplankton while typically spending 3 or 4 yr at sea (Graham et al. 2021). Their unusually large stomach is uniquely adapted to process large quantities of low-calorie gelatinous plankton (cnidarians, ctenophores, and salps), which is thought to be an evolutionary response to reduce competition with other salmon species, especially highly abundant pink salmon (Welch 1997).

Despite this adaptation, there is evidence for competition between chum and pink salmon. For example, in odd years when maturing pink salmon are highly abundant in the BS during June and July, zooplankton abundance has been found to be negatively correlated with pink salmon abundance (Section 3.1). Consequently, in odd years, chum salmon consumed 40% more low-calorie gelatinous zooplankton and

30 % more pteropods, and 40 % less high-calorie prey than in even years when few pink salmon were present, 1991–2007 (Fig. 6; Tadokoro et al. 1996, Davis 2003, Kaga et al. 2013). Furthermore, in odd years, the distribution of immature chum salmon shifts southeastward from the BS (e.g. a 50 % reduction in abundance in the BS) to the eastern NPO, based on Japanese research in 1972–2000, presumably to find higher densities of prey (Azumaya & Ishida 2000, Davis 2003).

Besides changes in chum salmon diet and distribution, a number of studies reported additional effects of competition between chum and pink salmon. For example, chum salmon sampled in the BS exhibited reduced second- and third-year body growth, reduced condition factor, and lower gonad weight (maturity rate index) with increasing local abundance of pink salmon in the previous year, 1971–2010 (Morita & Fukuwaka 2020); slower growth was linked to delayed maturation (Morita & Fukuwaka 2007). Lipid content of chum salmon in the BS was negatively related to local pink salmon abundance (2002–2007) after accounting for chum salmon body size; pink salmon abundance had a greater effect on lipids than chum salmon abundance (Kaga et al. 2013). In the central NPO south of the Aleutian Islands (1959–1995), third-year scale growth of chum salmon was negatively correlated with abundance of Asian pink salmon (Walker et al. 1998). In the western NPO, prey weight consumed by chum salmon was 27 % lower during odd years when maturing pink salmon were abundant (Sano 1963), and feeding rates of immature chum salmon near the Kuril Islands were lower in years of high juvenile pink salmon abundance (Ivankov & Andreyev 1971). However, Shuntov et al. (2017) argued that positive correlations over time between pink and chum salmon weights and pink and chum salmon numbers in the Sea of Okhotsk and the western BS were evidence that environmental factors drove size and abundance rather than competition for prey; there is considerable debate about how applicable those results are to other geographic regions (Shuntov et al. 2017).

Likewise in western Alaska, scale growth of Kuskokwim River (1968–2010), Yukon River (1965–2006), and Bristol Bay (1965–2006) chum salmon was negatively correlated with pink salmon abundance, especially during their third and fourth years at sea; these and other studies also considered oceanographic variables (Agler et al. 2013, Frost et al. 2021). Productivity of Norton Sound chum salmon was negatively correlated with Asian pink salmon abundance in addition to chum salmon abundance (Ruggerone et al. 2012). Scale growth of chum salmon returning to SEAK (1972–2004) and to southern BC (1971–2010) was negatively correlated with the abundance of pink salmon or pink and chum salmon (Yasumiishi et al. 2016), and to the combined biomass of pink, chum, and sockeye salmon during each year at sea (Debertin et al. 2017).

In the Salish Sea, where maturing pink salmon are approximately 40 times more abundant in odd versus even years, chum salmon exhibited strong biennial variations in abundance, size, age-at-maturity, and productivity (recruits per spawner), consistent with the hypothesis of competition for food with pink salmon (Gallagher 1979, Ruggerone & Nielsen 2004, Litz et al. 2021). Overall, chum salmon returns were 32 % lower in high pink salmon years (odd) compared to low pink salmon years (even) during the last 5 decades (Litz et al. 2021). This pattern was reinforced by early maturation of chum salmon produced from odd-year broods that interact with adult and juvenile pink salmon (15 % more age-3 than age-4) compared with those produced from even year broods (17 % more age-4 than age-3). Scale growth of Quilcene River (Salish Sea) chum salmon during the third season at sea (1973–2004) was negatively correlated with the combined abundances of pink and chum salmon while also considering the effect of climate indices (Yasumiishi et al. 2016). Likewise, scale growth of Puget Sound chum salmon (brood years 1997–2012) was negatively correlated with local pink salmon abundance during the first year at sea and with NPO pink salmon abundance during the third year (Anderson et al. 2021). In the Strait of Georgia during 1966–1969, chum salmon fry were smaller in even years when pink salmon fry were abundant versus odd years when few juvenile pink salmon were present (Phillips & Barraclough 1978), and fry-to-adult survival of Fraser River chum salmon declined 44 % (from average of 1.53 to 0.85 % survival) when they entered marine waters in even-numbered years with numerous juvenile pink salmon, 1961–1979 (Beacham & Starr 1982). Chum salmon on the Washington (USA) coast, where few pink salmon spawn, also exhibited biennial patterns in abundance, age, and productivity, suggesting that factors such as intra- and interspecific competition occurring in the northeast Pacific contributed to those patterns (Ruggerone & Nielsen 2004, Debertin et al. 2017, Litz et al. 2021).

3.4.3. Coho salmon

Coho salmon typically spend approximately 16 mo at sea, and many individuals from North America migrate into the GOA and the eastern NPO (Godfrey et al. 1975, Myers et al. 1996). Coho salmon occupy a somewhat higher trophic level than pink salmon because they eat more fishes and squid throughout their life (Welch & Parsons 1993, Kaeriyama et al. 2004, Johnson & Schindler 2009). However, diet overlap between them increases during the second season at sea as pink salmon grow and begin to capture small fishes and squid (Ito 1964, Pearcy et al. 1984, Brodeur et al. 2007). Consumption of squid by pink salmon becomes more pronounced during their final 2 or 3 mo at sea, especially after they reach 1 kg (Davis 2003, Aydin et al. 2005). Maturing coho salmon also consume some zooplankton, but depend primarily upon energy-rich squid.

Over a period of 50 yr (1970–2019), the average weight of coho salmon caught in the SEAK troll fishery declined with increasing biomass of pink salmon harvested in North America (an index of abundance) and increased with broad-scale SST, as indexed by the Pacific Decadal Oscillation (PDO; Shaul & Geiger 2016). An updated version of the statistical model used by Shaul & Geiger (2016) explained 68% of the variability in average annual coho salmon weight, which exhibited a strong biennial pattern that was opposite of adult pink salmon abundance (Fig. 9). Interannual variation in coho salmon weight explained by adult pink salmon biomass was slightly greater (55%) than variability explained by the PDO (45%).

The most likely mechanism responsible for those relationships involves predation by maturing pink salmon on squid (*B. anonychus*), a key prey of maturing coho salmon. The biennial life cycles of pink salmon and squid contribute to distinct biennial abundances of maturing squid that are consumed by a single cohort of ocean age-1 coho and pink salmon (Jorgensen 2011, Shaul & Geiger 2016). Thus, evidence indicates that predation by abundant odd-year pink salmon leads to fewer squid available to maturing coho salmon in odd years (Kaeriyama et al. 2004, Jorgensen 2011) and to their reduced growth and body size (Shaul & Geiger 2016). Adult coho salmon weight was explained by average North American pink salmon biomass 2 and 4 yr earlier, owing to a long-term influence of distinct even- and odd-year

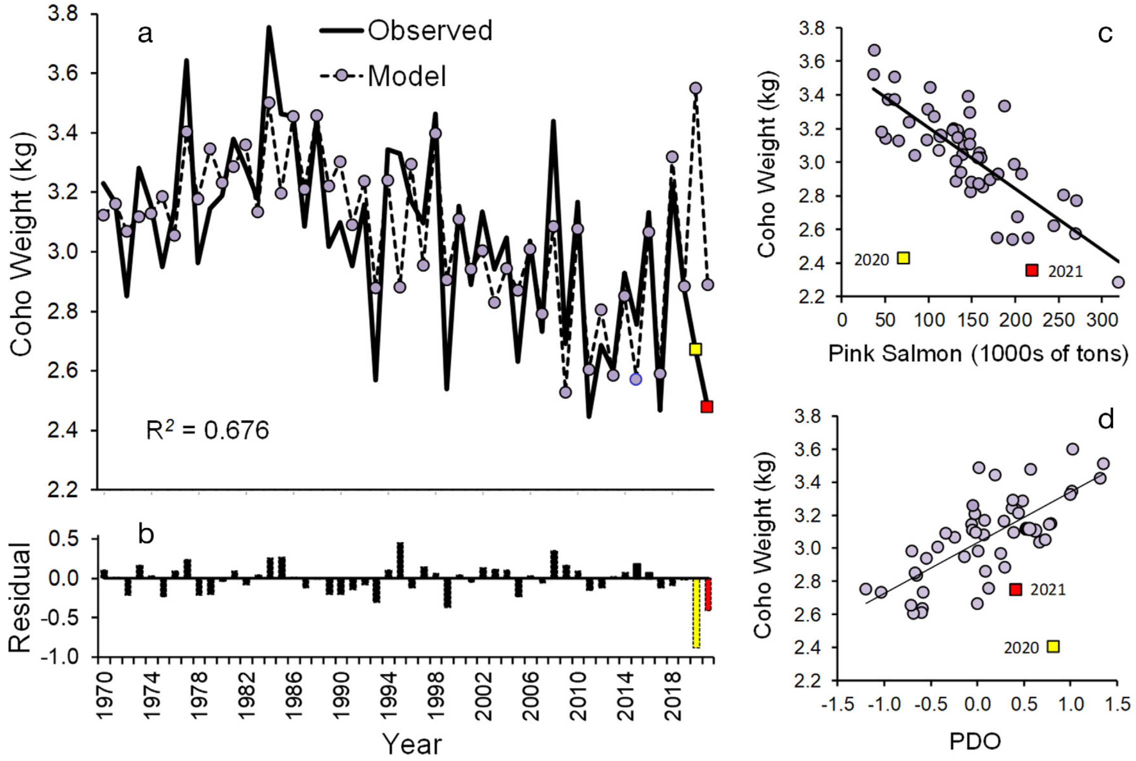

Fig. 9. Southeast Alaska troll-caught coho salmon average dressed weight (ocean age-1) compared with (a) predicted weight based on a multiple regression model with 2 variables: the standardized April–March Pacific Decadal Oscillation (PDO) Index (average for lag 0, 2, and 4 yr) and the standardized average commercial catch of pink salmon in North America (excluding the Bering Sea and Aleutian Islands) lagged by 2 and 4 yr. (b) Model residuals. Also shown are partial residual plots for (c) pink salmon abundance and (d) the PDO index. The multiple-regression model developed by Shaul & Geiger (2016) using 1970–2014 data was refitted for 1970–2019, with 2020 and 2021 values indicated on the partial residual plots by yellow and red squares, respectively

pink salmon lines preying on even- and odd-year lines of maturing squid. In the season of coho maturation, it is possible that pink salmon were too small (<1 kg) to strongly influence squid abundance during winter through late spring when coho salmon began intensive feeding on squid. High average PDO values during the year of maturation and 2 and 4 yr earlier were positively correlated with coho salmon weight, presumably through increased abundance of squid in response to warmer conditions associated with positive PDO index values.

Pink salmon biomass was linked to additional population characteristics of coho salmon in SEAK. Coho salmon survival at sea (1990–2014) was negatively correlated with both pink salmon biomass ($r = -0.58$, $p < 0.05$) and coho salmon body length ($r = -0.67$, $p < 0.05$), which was influenced by pink salmon abundance (Shaul & Geiger 2016). The ratio of female to male coho salmon was lower in odd years ($p = 0.012$), and the per capita egg biomass of maturing coho salmon, which provides an index for the reproductive potential of the spawning coho salmon population, was negatively correlated with pink salmon biomass ($r = -0.60$, $p < 0.05$). The investigators provided evidence that coho salmon body size and survival were primarily influenced during late marine life when coho salmon are offshore. These findings suggest that pink salmon adversely affect both coho salmon survival and future coho salmon abundance by reducing the reproductive potential of the survivors through a combination of lower egg biomass and lower survival of female versus male coho salmon in odd years (Shaul & Geiger 2016).

After 50 yr of strong correlation, the pink salmon–climate statistical model of Shaul & Geiger (2016) failed to predict the extremely low body size of SEAK coho salmon in 2020 (2.67 kg) and 2021 (2.48 kg), both of which followed warm conditions during 2016–2020 and poor GOA pink salmon returns on the even-year line in 2016 and 2018 (Fig. 9). However, total pink salmon returns to North America and Asia in 2018 and 2019 (avg. 670 million fish) were the largest consecutive years on record since 1925 when records were first kept (Ruggerone et al. 2021), raising the question of whether Asian pink salmon, which are typically west of most SEAK coho salmon, may have contributed to the small size of coho salmon in 2020 and 2021. Lastly, the PDO index covers a large region of the NPO and may not have reflected mesoscale effects of marine heat waves in the GOA region.

Studies in other regions are consistent with the findings of Shaul & Geiger (2016), indicating an adverse effect of pink salmon on coho salmon growth, survival, and abundance. Ogura et al. (1991) also reported that final-year growth rates of coho salmon in the western NPO, 1978–1987, were lower in odd years when maturing pink salmon were highly abundant. In the Kuskokwim River in western Alaska, commercial coho salmon harvests in odd years averaged 33 % less (avg. 225 000 coho salmon) compared with even years (avg. 336 000 coho salmon) during 1965–2007 (*t*-test, $p < 0.001$, Ruggerone & Nielsen 2009). Further south in the Strait of Georgia, where diet overlap of juvenile coho and pink salmon was high during 1998–2009, the proportion of coho salmon with empty stomachs increased approximately 37 %, and the abundance and survival of hatchery coho salmon by September declined approximately 73 and 80 %, respectively, in even years when juvenile pink salmon were highly abundant (Beamish et al. 2010).

3.4.4. Chinook salmon

Subadult Chinook salmon have been found extensively in offshore areas of the NPO and BS, where they overlap with pink salmon (Major et al. 1978, Myers et al. 1996; Text S1). Diet overlap between Chinook and pink salmon can be considerable, especially during the second season at sea for pink salmon, when they are large enough to consume squid and small fishes. The small energy-rich squid *B. anonychus* is a major component in the diet of Chinook salmon (and other salmon species) in the GOA, central NPO, and central BS, and is also consumed heavily by maturing pink salmon in these same waters. For example, during a 10 yr study in the central BS (52–58° N), the diet of Chinook salmon averaged 80 % fish and squid, 19 % zooplankton, and 1 % other prey by weight, and the diet of pink salmon averaged 60 % fish and squid, 34 % zooplankton, and 6 % other prey (Fig. 6; Davis 2003). In odd-numbered years, when pink salmon were approximately 40 times more abundant than in even years, total prey weight consumed per Chinook salmon declined 56 % versus only 23 % among pink salmon (Fig. 6). In odd years, Chinook salmon consumed 72 % less squid and 44 % less fish, but 44 % more euphausiids compared with even years (Fig. 6). In odd years, pink salmon consumed 32 % less squid, 25 % less fish, and 29 % less zooplankton compared with even years (Fig. 6). These data suggest that pink salmon consumed fishes and squid more efficiently than Chinook salmon when availability of key prey was low. Other studies indicate that the degree of overlap in the consumption of squid, small fishes, and euphausiids varies with region (Davis et al. 2009, Qin & Kaeriyama 2016). Collectively, this evidence suggests that pink salmon may directly and indirectly affect Chinook salmon growth and survival by consuming the same prey and by altering the food web that supports small fishes, squid, and zooplankton consumed by Chinook salmon.

Chinook salmon harvests, abundances, and average body sizes in northern regions where freshwater habitat is mostly intact have been declining for several decades (Bigler et al. 1996, Lewis et al. 2015, Ohlberger et al. 2018, Welch et al. 2021), and several studies have suggested Chinook survival and growth may be inversely related to pink salmon abundance at sea (e.g. Cunningham et al. 2018, Oke et al. 2020). We examined the time series of annual Chinook salmon commercial harvests in Alaska and BC from 1952 to 2021. Commercial harvests reflect fishing effort, based on abundance predictions and fishery regulations (PSC 2022), and can provide a first-order approximation of abundance, although they can also be confounded by changes in fishery regulations and effort over time. Consistent with the hypothesis that pink salmon affect Chinook salmon, we found that harvest trends during the 70 yr period were opposite those of pink salmon abundance trends (Fig. 10a).

Body size of adult Chinook salmon in Alaska also declined with increasing abundance of pink salmon since 1952. Average weight of commercially caught Chinook salmon was relatively stable over time when abundance of pink salmon was low during 1952 to 1975 (Fig. 10b). Immediately after the 1977 ocean regime shift, body size of Chinook salmon reached its maximum (9.3 kg) and then declined steadily over time as pink salmon abundance increased (Fig. 10b). Chinook salmon body size reached the long-term minimum during 2015–2021 (avg. 5.7 kg) when pink salmon abundance was peaking (564 million yr^{-1}) and when marine heat waves became more frequent (Ross et al. 2021). We note, however, that these trends in size and commercial harvest can be confounded with other long-term trends in oceanographic and freshwater processes, and so should be interpreted with caution. Also, the Japanese salmon fishery on the high seas removed, on average, 334 000 Chinook salmon per year from 1955 to 1980, then harvests declined steadily until its termination in 1991 (NPAFC 2022a). Most of the Chinook salmon had originated from western and central Alaska (Rogers et al. 1984; Text S1), suggesting that Chinook salmon harvests in Alaska would have been even higher during the period when pink salmon abundance was low. Other factors contributing to long-term declines in catch and size of North American Chinook salmon have been hypothesized, including size-selective predation by resident killer whales (Ohlberger et al. 2018, 2019; Text S1).

Lewis et al. (2015) demonstrated a consistent decline in Alaskan Chinook salmon length-at-age and age-at-maturation over a 30 yr period while noting the potential influence of competition for prey with other salmon species. Our analyses of these data

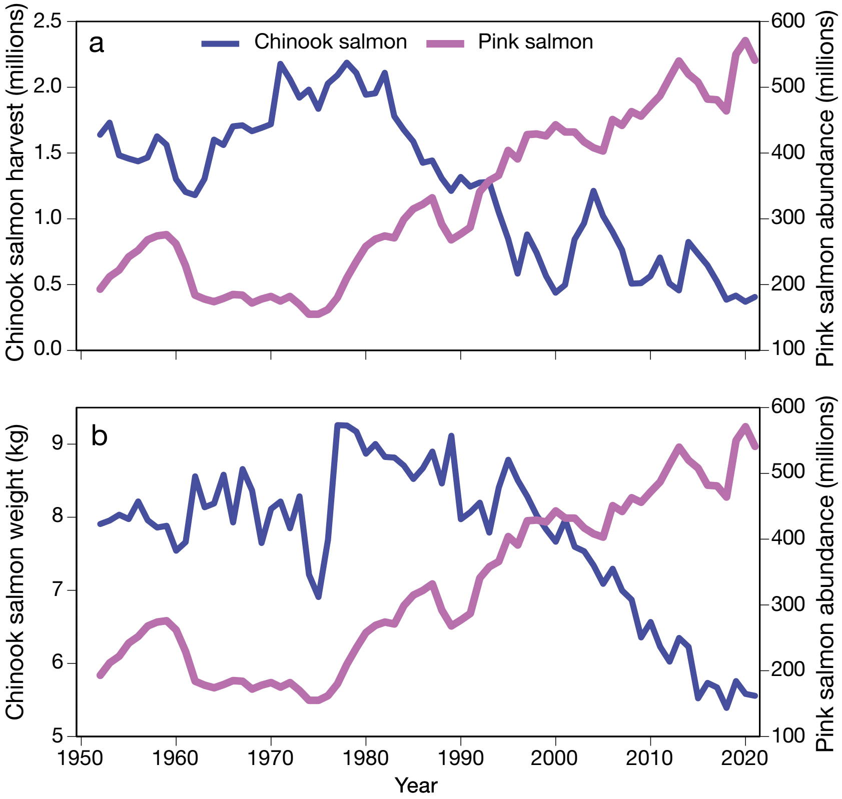

Fig. 10. Time series of (a) Chinook salmon commercial harvests in Alaska and British Columbia, and (b) average weight of Chinook salmon in Alaskan harvests in relation to average pink salmon abundance returning from the North Pacific Ocean 1 to 4 yr prior to the Chinook salmon harvest during 1952–2021 (e.g. harvest in year 2000 was related to average pink salmon abundance during 1996–1999, corresponding to the period of species overlap and potential direct and indirect effects of pink salmon). Data sources: Ruggerone et al. (2010, 2021), Ruggerone & Irvine (2018), NPAFC (2022a)

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and the aggregate length of troll-caught Chinook salmon reveal that mean length of age-1.4 Chinook salmon from all 11 populations declined coincident with increasing pink salmon abundance, although the relationship was weak in 2 populations (Table S1, Fig. S1.1). The populations ranged from the Yukon River in the northeastern BS to the Copper River in the northeastern GOA, and the Unuk River in SEAK. Likewise, average length of 9 of 10 age-1.3 populations of Chinook salmon declined with increasing pink salmon abundance, including 4 weak relationships (Table S1). Average age of 4 of 5 Chinook salmon populations declined with increasing abundance of pink salmon, including 1 weak relationship (Table S1). In the Yukon River, the decline in body size led to a 24–35% reduction in the reproductive potential of female Chinook salmon since the 1970s (Ohlberger et al. 2020). In the Kamchatka River, Russia, scale analysis of Chinook salmon revealed biennial growth patterns during the first and second years at sea, 1935–1955, that may have been related to pink salmon (Grachev 1967).

Analyses of survival across the entire life cycle of Chinook salmon found support for the adverse effect of pink salmon on 2 Yukon River populations using a Bayesian life-cycle model (Cunningham et al. 2018), but no support using dynamic factor analysis of data from 15 populations throughout Alaska (Ohlberger et al. 2016); those studies also considered a number of other variables. Both studies aligned pink salmon abundance with the second season at sea (brood year plus 3 yr) of Chinook salmon rather than each year in which Chinook salmon interact with pink salmon. In contrast, while also considering the effect of oceanographic variables, moderate to strong support was found for an adverse effect of Russian pink salmon abundance on annual scale growth of Yukon, Kuskokwim, and Nushagak Chinook salmon during the third and fourth years at sea over a period of 30 yr or longer (Ruggerone et al. 2016b; Supplement 2 at www.int-res.com/articles/suppl/m719p001_supp2.xlsx). Survival of 2 of the 3 major stocks of Chinook salmon in western Alaska declined with the running 2 yr abundance of Russian pink salmon during the third and fourth years at sea. The percentage of age-6 (age-1.4) and older Chinook salmon in each stock declined with increasing abundance of pink salmon, but support was weak in 1 stock. The decline over time in abundance, growth at sea, and the proportion of older Chinook salmon led the investigators to hypothesize that mortality during late marine life had increased in response to competition with pink salmon and to predation by salmon sharks and other marine predators (Manishin et al. 2021).

Lastly, in the Japanese high seas salmon fishery in the western/central BS and NPO, we found a biennial pattern in the catch of Chinook salmon during 1955–1981. The mean catch in odd years (254000 ± 40000 fish [SE]) was 39% lower than the catch in even years (417000 ± 60000 fish, *t*-test, $p = 0.03$). Chinook salmon catch was negatively correlated with pink salmon catch (linear regression, $r = -0.63$, $p < 0.001$; Text S1, Fig. S1.2). Scale pattern analysis indicated that most of the Chinook salmon originated from western and central Alaska.

Chinook salmon growth and survival may also be affected by pink salmon in coastal seas. In the Salish Sea, subyearling ocean-type Chinook salmon smolts released from 13 hatcheries experienced a 59% decline in marine survival, on average, when released during even years compared with those released during odd years, 1984–1997 (Fig. 11a; Ruggerone & Goetz 2004). Juvenile pink salmon were highly abundant in even years (avg. ~8 million odd-year spawners, 1983–1996) but rare in odd years (<0.5 million even-year spawners). Additional analyses of over 53 million coded-wire-tagged Chinook salmon indicated that the biennial mortality pattern was established during the first year at sea, i.e. within the Salish Sea. No biennial pattern in Chinook salmon survival was observed along the Washington coast and southern Vancouver Island, where few pink salmon spawn. During 1972–1983, overall survival of juvenile Chinook salmon was high and tended to be highest when emigrating with juvenile pink salmon in even years, a change from 1984–1997 possibly related to the 1982–83 El Niño and a shift from predation- to competition-based mortality (Ruggerone & Goetz 2004). Subsequent analyses of subyearling and yearling hatchery Chinook salmon from 1983 to 2012 found lower density-dependent survival and fewer adult returns of hatchery Chinook salmon when released into the Salish Sea during even years when juvenile pink salmon were abundant (Kendall et al. 2020). In odd years, when few juvenile pink salmon were present, density-dependent survival of Chinook salmon was not apparent and survival was higher. From 1970 to 2015, abundance and size of adult natural-origin Chinook salmon in the Salish Sea were negatively correlated with pink salmon abundance (Losee et al. 2019).

Diet overlap between juvenile pink and Chinook salmon in the Salish Sea is relatively low, and researchers hypothesized that pink salmon indirectly influenced Chinook salmon growth and survival (Ruggerone & Goetz 2004, Kendall et al. 2020). Several lines of evidence support a hypothesis of trophic

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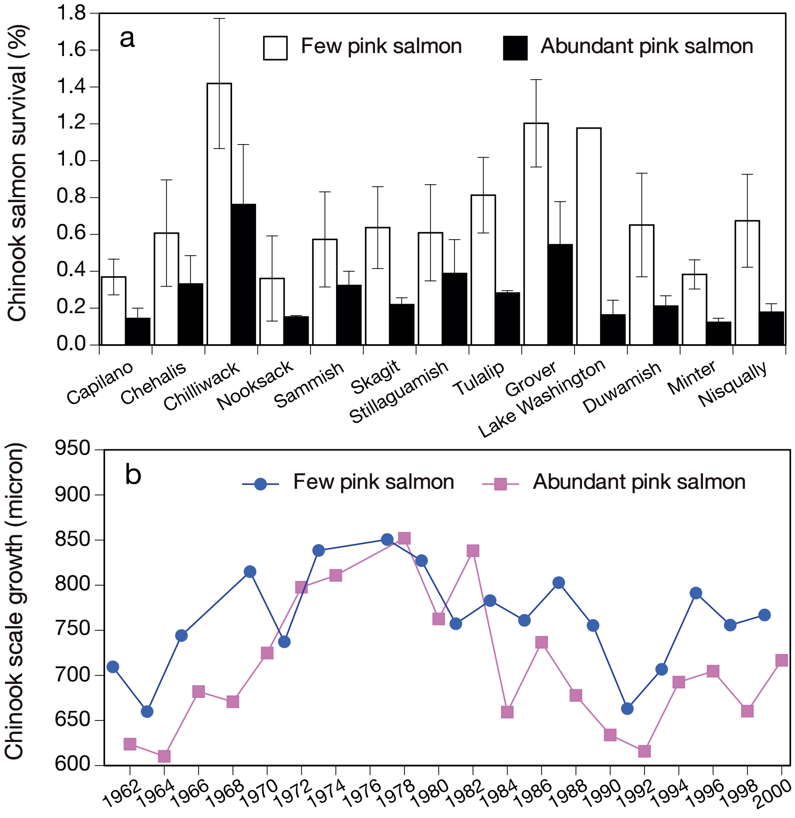

Fig. 11. (a) Mean smolt to adult survival (±1 SE) of subyearling Chinook salmon (tagged ocean type) released from 13 hatcheries in the Salish Sea (Washington and British Columbia) during even years (numerous juvenile pink salmon) and odd years (nearly zero juvenile pink salmon), 1984–1997, and (b) mean early marine scale growth (circuli 11 to 34) corresponding to residence in the Salish Sea of adult Skagit River Chinook salmon (ocean type) during even and odd years, 1961–2000. Data sources: Ruggerone & Goetz (2004); Text S1

interaction. (1) Juvenile pink salmon enter the Salish Sea approximately 2 mo before subyearling Chinook salmon. (2) We found that first-year marine scale circuli measurements of surviving adult Skagit River Chinook salmon were 7% narrower, on average, during even years than odd years, 1961–2000 (*t*-test, $p < 0.01$, df = 35, Fig. 11b; Text S1). (3) During 1983 to 1997, returning coded-wire-tagged Chinook salmon were smaller at age and tended to delay maturation when released into Salish Sea watersheds in even years when juvenile pink salmon were abundant (Ruggerone & Goetz 2004). (4) Early marine growth and survival of Salish Sea Chinook salmon increased with fewer juvenile pink salmon (Claiborne et al. 2021).

Approximately 11–38% of Chinook salmon sampled for genetic stock identification in the southeastern BS during 2005–2010 originated from the Pacific Northwest, raising concern that climate warming may be shifting salmon from the Pacific Northwest into a crowded BS where temperatures are cooler (Larson et al. 2013). In support of this hypothesis, Buckner et al. (2023) analyzed the growth of 48 stocks of Chinook salmon returning to hatcheries and spawning grounds in the Columbia River Basin, Oregon coast, and Washington coast (brood years 1976–2013), and found that growth of subyearling and yearling far-north migrating Chinook salmon was negatively associated with pink salmon abundance. The effect of pink salmon on Chinook salmon growth was stronger than that of the tested oceanographic variables (see their Fig. 4). Growth of subyearling Chinook salmon populations that did not migrate as far north was also negatively associated with pink salmon abundance, but to a lesser extent; growth of yearling Chinook salmon in the southern distribution area was not associated with pink salmon abundance.

3.4.5. Steelhead

Steelhead migrate long distances during their typical 1 to 3 winters at sea, leading to a broad distribution across the NPO. Ocean age-0 steelhead migrate farther offshore than other salmonids in their first year at sea, and many immature steelhead from North America have been sampled west of 180° and off the Kuril Islands, Russia (Myers 2018). Steelhead in the open ocean are opportunistic foragers, but they specialize to some degree on a few species of micronekton, including cephalopods (especially *B. anonychus*) and small mesopelagic fishes, and zooplankton such as adult euphausiids, pelagic decapods, amphipods, and pteropods (Myers 2018).

Steelhead feed at a somewhat higher trophic level than pink salmon, but they also share many common prey, leading Atcheson et al. (2012a) to conclude that ocean age-0 and older steelhead may compete with maturing (ocean age-1) pink salmon. In the central NPO, consumption of highly energy-dense mesopelagic forage fishes and squids was negatively correlated with abundance of eastern Kamchatka pink salmon, whereas the percentage of empty stomachs increased with increasing pink salmon abundance

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(Atcheson et al. 2012b). These researchers recognized that pink salmon are less abundant in the central NPO than in the central BS, but suggested that large runs of adult pink salmon may deplete prey resources as they migrate through broad North Pacific regions from winter to spring (Myers 2018). They also hypothesized that the surface orientation of foraging steelhead may be a mechanism to reduce trophic interactions with pink salmon.

Steelhead survival indices in BC provide evidence that pink salmon may adversely affect their survival at sea. Adult recruit per spawner anomalies of critically endangered Thompson River summer-run steelhead in the interior of the Fraser River watershed were negatively correlated with the biomass of NPO pink salmon that overlapped their final 2 yr at sea during 1978–2012 (Fig. 12a; Text S1). Smolt-to-adult survival of Keogh River (northeast Vancouver Island) winter-run steelhead was negatively correlated with pink salmon biomass in 1977–2018 (Fig. 12b). Approximately 46 and 49%, respectively, of the annual variability in the Thompson River and Keogh River steelhead survival indices were explained by pink salmon abundance. In the Chilcotin River (interior Fraser River), steelhead recruit per spawner anomalies were negatively correlated with pink salmon abundance (r= –0.65), but autocorrelation was high and reduced the significance of the relationship (linear regression, df = 1, 38, p = 0.14). Predation by local populations of seals on adult and post-smolt steelhead is also considered a key factor in the decline of these steelhead populations (COSEWIC 2020, Wilson et al. 2022). We found that seal and NPO pink salmon abundances are highly correlated, so it is not possible to quantify their relative influence on the decline of steelhead. However, Friedland et al. (2014) reported that smolt-to-adult survival of Keogh River steelhead (1977–1999) was correlated with their scale growth during the first year at sea, especially during summer and fall when they overlap with abundant pink salmon in the north (Myers 2018; Text S1).

In the Columbia River Basin, we found that B-run summer steelhead exhibit a pronounced biennial pattern of abundance, suggesting strong interactions with pink salmon at sea (Fig. 12c). These fish are

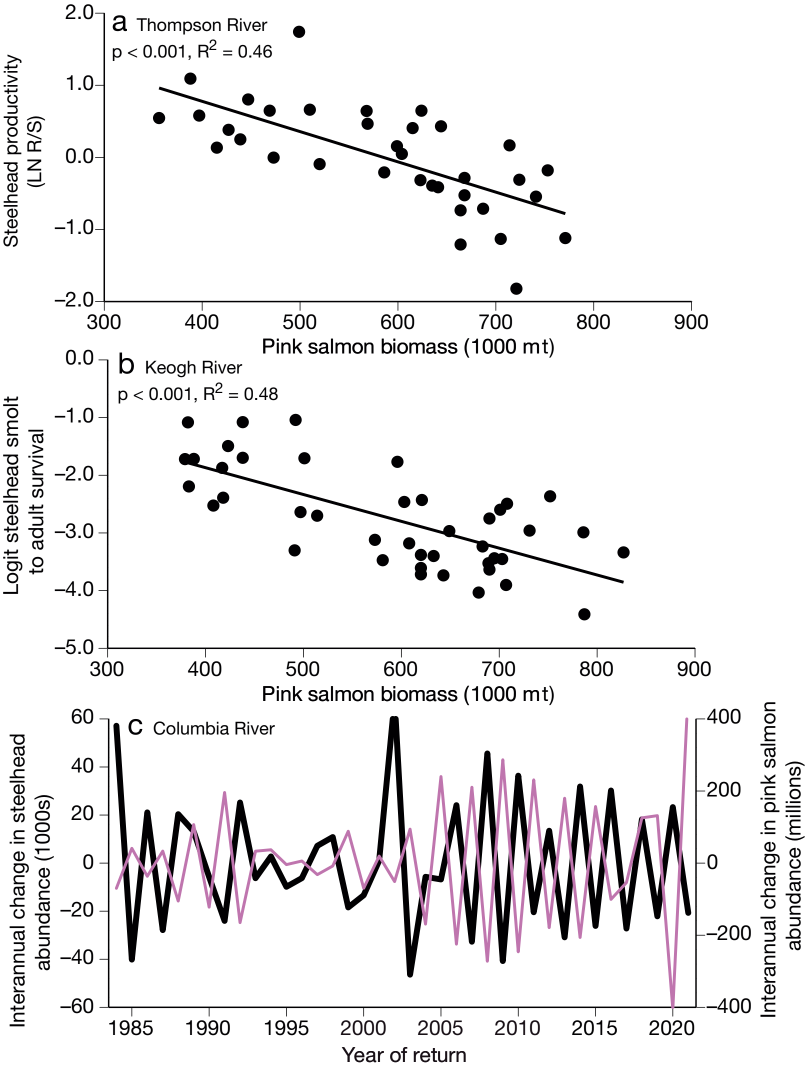

Fig. 12. Potential influence of North Pacific Ocean (NPO) pink salmon abundance on (a) the productivity (return per spawner, R/S) of Thompson River summer-run steelhead (Fraser River watershed, BC), brood years 1978–2012, and (b) smolt to adult survival of Keogh River winter-run steelhead (NE Vancouver Island), smolt years 1977–2018. (c) Interannual change in abundances of Columbia River B-run summer steelhead (black line) and North Pacific pink salmon (pink line) during 1984–2021, where interannual change in abundance (A) in year $i = A_i$ – avg. (A_{i-1}, A_{i+1}). Pink salmon biomass is the average biomass 3 and 4 yr after the brood year for Thompson steelhead (mostly 5 yr old fish that spend 2 winters at sea and the last winter in freshwater), and average biomass 1 to 3 yr after the smolt migration of Keogh River steelhead (up to 3 winters at sea), accounting for overlap at sea and different age composition of the 2 steelhead populations. Autocorrelation in the linear regressions was inconclusive (a) or non-significant (b). Data sources for our analyses: Ratzburg (2021), WDFW/ODFW (2022), R. Bison unpubl. data

listed as 'threatened' under the US Endangered Species Act. Returning B-run steelhead counted at Bonneville Dam were 38% less abundant in odd versus even years during 1984–2021 (*t*-test, $p = 0.014$, $n = 38$). Furthermore, odd-year pink salmon have become more dominant in recent years (Irvine et al. 2014), and this is reflected in the negative correlation between interannual change in abundances of B-run steelhead and NPO pink salmon over the past 38 yr (Fig. 12c; linear regression, $p = 0.014$ after accounting for autocorrelation).

In contrast to B-run steelhead, A-run summer steelhead abundance did not differ between odd and even years (*t*-test, $p = 0.24$, $n = 38$). B-run steelhead typically spend 2 yr at sea and migrate farther north and west and potentially interact with more abundant pink salmon than A-run steelhead, which spend only 1 yr at sea (Myers 2018). Importantly, the biennial abundance pattern shown by B-run, but not A-run, steelhead suggests substantial mortality after the first year at sea, consistent with late marine mortality observed in other salmon species described here.

3.4.6. Pink salmon

In comparison with other Pacific salmon, pink salmon appear to be well-adapted to foraging in a warming ocean given that the ocean supports more pink salmon now than at any other time since detailed record keeping began in 1925. Pink salmon stomachs are often much fuller than those of other salmon species, they typically consume higher caloric prey than chum and sockeye salmon, and they have high daily rations (Fig. 6; Davis 2003, Karpenko et al. 2007, Karpenko & Koval 2012, Shuntov et al. 2017, Radchenko et al. 2018). Bioenergetic analyses show that body growth declines less in pink salmon (−31%) than in chum (−52%), sockeye (−43%), and coho salmon (−33%) when ocean temperature increases from 5 to 9°C and daily ration is constant (Davis et al. 1998). Growth of smaller salmon is more efficient than growth of larger salmon as temperature rises (Beauchamp 2009). These studies suggest that the strength of density-dependence at sea among pink salmon may be weaker than within other salmon species.

Intraspecific studies of pink salmon at sea often examine interactions between hatchery and wild fish because approximately 1.35 billion juvenile pink salmon are released into the NPO each year, 1990–2021, of which 66% are released in Alaska, primarily in PWS (NPAFC 2022b). Multiple studies reported that adult run size and returns per spawner of PWS wild pink salmon declined in response to increased hatchery production (Hilborn & Eggers 2000, 2001, Amoroso et al. 2017). In contrast, abundances of wild pink salmon in adjacent regions of Alaska increased during this period, further indicating increased hatchery production of pink salmon influenced the decline of wild pink salmon in PWS.

Increased intraspecific competition for prey in PWS and at sea was identified as a key mechanism affecting wild PWS pink salmon. In support of the competition hypothesis, the food demand of juvenile pink salmon in PWS reportedly exceeded the standing stock of preferred prey during July when salmon densities were high (Cross et al. 2005), resulting in reduced growth, greater size-dependent predation, and higher mortality (Willette et al. 2001), although a bioenergetic model approach suggested prey availability may be adequate (Boldt & Haldorson 2002). Adult body size of wild PWS pink salmon also declined with greater releases of hatchery pink salmon, leading to reduced fecundity and a loss of approximately 1 million wild adult pink salmon per year (Wertheimer et al. 2004). More recently, using 60 yr of data on wild pink salmon abundances, hatchery releases, and ecological conditions in the ocean, Ohlberger et al. (2022) provided evidence that hatchery pink salmon releases into PWS (i.e. 700 million fish yr^{-1}) reduced productivity of wild pink salmon by 55%. That study also provided evidence that productivity of emigrating juvenile pink salmon declined with increasing numbers of returning pink salmon, thereby supporting the hypothesis that biennial patterns in adult pink salmon are partly related to brood interactions at sea (Ruggerone & Nielsen 2009, Krkosek et al. 2011, Irvine et al. 2014).

Analyses of scale growth of pink salmon sampled in the GOA and adult pink salmon returning to PWS hatcheries indicated significant size-selective mortality of juvenile pink salmon during and after the first growing season — slower-growing salmon experienced reduced survival (Cross et al. 2008, 2009). A potential bottleneck for growth during early to mid-July was observed, corresponding with fewer zooplankton. The authors concluded that the large influx of juvenile pink salmon into the GOA, in conjunction with the seasonal dynamics of zooplankton prey, could create localized prey depletions, density-dependent growth, and reduced survival (see Section 3.1).

Most, but not all, studies have observed density-dependent growth of pink salmon at sea. Body length and scale growth of pink salmon sampled in the central BS and in the western NPO during 1972–1998 were negatively correlated with catch per

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unit effort of pink salmon in the non-selective research gillnets (Ishida et al. 1995, Azumaya & Ishida 2000), consistent with a 23% decline in pink salmon stomach fullness in odd- compared with even-years, 1991–2000 (Davis 2003). Body weight of maturing Fraser River pink salmon declined as zooplankton availability declined at Ocean Station P, 1957–1977 (odd years only, r = −0.86, p < 0.001; Peterman 1987). In BC (1951–1993) and Puget Sound, Washington (1959–1999), weight of odd-year adult pink salmon declined up to 40% with increasing pink salmon abundance (Welch & Morris 1994, Ruggerone & Nielsen 2004, Jeffrey et al. 2017). In Russia, size of pink salmon migrating through the Kuril Islands and returning to the Sea of Okhotsk region was negatively correlated with pink salmon biomass, 1991–2003 (Shuntov & Temnykh 2005). Throughout Asia and North America overall, the combined average weight of adult pink salmon declined with increasing pink salmon abundance, 1925–2015 (Ruggerone & Irvine 2018).

Density-dependent growth was not observed in other studies. For example, second-year scale growth of pink salmon sampled south of the central Aleutian Islands was positively correlated with Asian pink salmon abundance after the 1977 regime shift (1983–1995), but negative prior to the 1977 shift (Walker et al. 1998). Size of pink salmon returning to eastern Kamchatka was not related to Kamchatka pink salmon abundance, 1971–2001 (Shuntov & Temnykh 2005).

3.5. Seabirds

Most species of seabirds in the subarctic NPO fall into a functional planktivore or omnivore trophic guild (Text S2). Overlap in diet between guilds does occur, and the guilds are separated by somewhat less than one trophic level. Diets in both guilds overlap extensively with diets of pink salmon, which prey on the same species and taxa of zooplankton and fishes (Text S2). Evidence of interactions between resident seabirds and pink salmon can be found across a broad region from the western Aleutian Islands to the eastern GOA, and in 1 migrant species from the southern hemisphere that spends the austral summer primarily in the BS and Chukchi Sea.

3.5.1. Southeastern Bering Sea and Aleutian Islands

Biennial patterns in numerous elements of the diets and breeding biology of several species of seabirds in both guilds were conspicuous in the Aleutian and Pribilof Islands in the BS in 1988–2012 (Springer & van Vliet 2014; Supplement 2). Although biennial patterns in all nesting parameters of all species were not found at all colonies, among omnivores, nesting phenology (indexed by hatch date) was later in odd years compared to even years for as many as 6 species nesting at as many as 4 colonies (e.g. Fig. 13). Clutch sizes of the 2 species that lay more than 1 egg were smaller in odd years. Laying success, hatching success, fledging success, and productivity (chicks per nest attempt) of 3 or more species at up to 3 colonies were lower in odd years. The biennial differences indicated that foraging conditions for those species in late spring through summer were better in even years than in odd years. A biennial pattern in the stress hormone corticosterone in thick-billed murres *Uria lomvia* at St. George Island, which is rel-

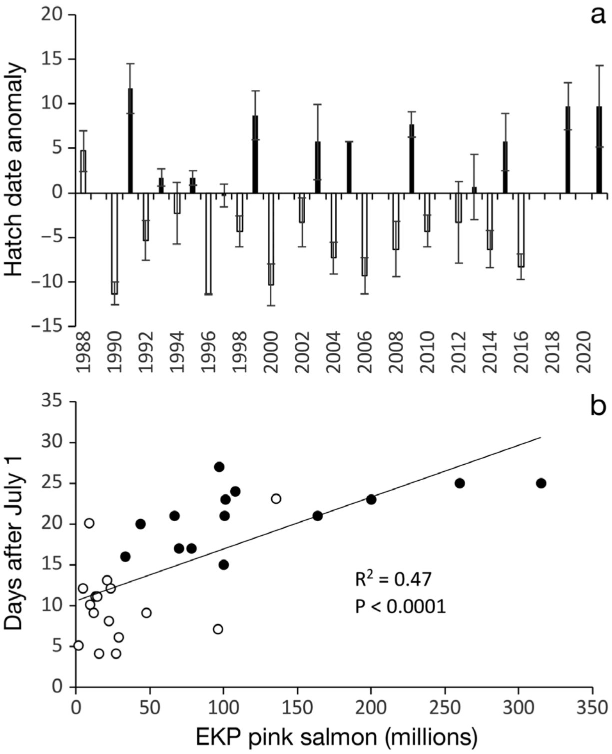

Fig. 13. (a) Phenology of tufted puffins at Buldir Island (Aleutian Islands) indexed as average hatch date each year relative to overall average hatch date across all years (no. of d relative to July 15). No data were acquired in 1989, 2017, or 2020; n = 1 nest in 2001, 2007, and 2018 and were excluded. (b) Relationship (linear regression) between eastern Kamchatka pink salmon abundance (EKP) and tufted puffin annual average hatch date (no of d after 1 July). Open bars and circles = even years; filled bars and circles = odd years. Tufted puffin data from Higgins et al. (2022); pink salmon data from Ruggerone & Irvine (2018) and Ruggerone et al. (2021)

atively high in odd years and low in even years, further supports a nutritional stress explanation for biennial variability in nesting characteristics of omnivores (Text S2).

Patterns in nesting parameters of planktivores were out of phase with those of the omnivores (Springer & van Vliet 2014). The hatching phenology of as many as 4 species at 2 locations in the Aleutian Islands and 1 species at the Pribilof Islands was earlier in odd years of higher pink salmon abundance than in even years of lower abundance. Additionally, the fledging success and productivity of 1 species at St. George Island (Pribilof Islands) were higher in odd years. Thus in contrast to omnivores, by these measures foraging conditions for planktivores apparently were better in odd years than in even years. We presently do not propose a mechanism for this observation.

In contrast, planktivorous least auklets *Aethia pusilla* at Buldir Island (western Aleutians) consumed *Neocalanus plumchrus/flemingeri*, a primary prey, in greater amounts in even years than in odd years, and consumed more of 4 out of 5 secondary prey in odd years (Springer & van Vliet 2014). Likewise, planktivorous whiskered auklets *A. pygmaea* at Buldir consumed more *N. cristatus*, a primary prey, in even years than in odd years. Those biennial dietary patterns are opposite patterns of breeding biology and suggest that even years are good relative to odd years, as in the case of the omnivorous species, and are consistent with evidence discussed above that pink salmon deplete stocks of large copepods in odd years.

Several nesting parameters of the omnivores were highly correlated with the abundance of eastern Kamchatka pink salmon (Springer & van Vliet 2014). For example, the phenology (mean hatch date of eggs) of tufted puffins *Fratercula cirrhata* at Buldir has been relatively late in odd years and early in even years since data were first acquired in 1988 (Fig. 13). In addition, annual hatch dates have been highly correlated with the abundance of eastern Kamchatka pink salmon, the dominant pink salmon population in this region. The relationship is very strong across all years, but differs between even and odd years — it is weaker in even years (linear regression, $p = 0.13$) and stronger in odd years ($p = 0.03$). As the mean abundance of pink salmon in even years since 1988 (30.4 ± 9.0 million [SE]) has been just 24 % as large as in odd years (124 ± 22 million), the implication is that for the most part, only in odd years and rare even years of uncommonly high returns are pink salmon sufficiently abundant to materially alter prey fields to the detriment of tufted puffins, and by extension other seabirds. Among prey important to both tufted puffins and pink salmon are squids (Davis et al. 2005, Higgins et al. 2022), which also have been implicated as an important variable in competition for prey between pink and other species of salmon as noted above. Nesting parameters of the planktivores in the Aleutian and Pribilof Islands were not correlated with eastern Kamchatka pink salmon. We do not understand the reason for a lack of correlation, but it may be related to the even-year bad, odd-year good pattern in breeding parameters, which is opposite that of the omnivores.

3.5.2. Prince William Sound

The productivity of black-legged kittiwakes *Rissa tridactyla* in PWS has been monitored systematically since 1985 (Irons 1996, D. B. Irons unpubl. data), and since 1990, it has been positively correlated with annual returns of PWS pink salmon (wild + hatchery, linear regression, $p = 0.032$). Overall during that time, pink salmon returns were nearly twice as large in odd years as in even years (55 ± 7.2 vs. 34 ± 3.9 [SE] million salmon; *t*-test, $p = 0.018$). Notably, the relationship to kittiwake productivity was driven primarily by hatchery stocks (linear regression, $p = 0.030$) and not wild stocks ($p = 0.31$).

That positive relationship to pink salmon is opposite the negative relationship at Chowiet Island in the western GOA (Text S2), and in the BS as discussed in Section 3.5.1 and in Text S2. For PWS, several sources of evidence lead to the hypothesis that predation on kittiwake eggs and chicks rather than competition is the primary driver of this pattern. First, a major factor in the nesting success of kittiwakes in many PWS colonies is the level of egg and chick loss to bald eagles *Haliaeetus leucocephalus*, peregrine falcons *Falco peregrinus*, common ravens *Corvus corax*, and glaucous-winged gulls *Larus glaucescens*; the presence of these aggressive predators also causes adult kittiwakes to stay away from nests for extended periods, which allows opportunistic predators such as northwestern crows *C. caurinus* and black-billed magpies *Pica pica* to prey upon nests (Suryan et al. 2006, Robbins 2009, McKnight et al. 2020). Second, kittiwakes in PWS typically lay eggs in early June on average, which hatch in early July, and chicks leave the nest in approximately mid- to late August (Suryan et al. 2006). The PWS pink salmon run begins in mid-June and extends through late July to mid-September (ADFG 2022), thus overlapping entirely with the kittiwake nesting season. Third, McKnight et al. (2020) found that kittiwake productivity at 1 colony in PWS was higher in years of earlier pink salmon runs than in years of later runs, i.e. more salmon throughout the full nesting season in early run years diverted avian predators. We hypothesize an analogous scenario: in odd years of high pink salmon returns, the attention of avian predators is focused more on them, which provide a much higher energetic return on investment than kittiwake eggs and chicks, and PWS kittiwakes thereby achieve higher reproductive output than in even years of low pink salmon returns.

3.5.3. Southern Hemisphere

Short-tailed shearwaters *Ardenna tenuirostris*, trans-hemispheric migrant seabirds that breed in Australia and Tasmania and spend the austral winter primarily in the BS and Chukchi Sea, also have been linked to pink salmon through diet overlap and competition for prey. They are very abundant, on the order of 25–30 million, and provide terrestrial ecosystem services by aerating soils and promoting vegetation growth in nesting colonies where they burrow. They further provide cultural and societal services to Indigenous peoples who have harvested chicks for millennia.

Short-tailed shearwaters in the BS were found to be in poorer physiological condition and to die in greater numbers in odd-year summers in 1981–1990 (Lobkov 1991); and in 2002–2008, their body mass and liver mass were negatively correlated with pink salmon biomass, which was 23 times higher in odd years than in even years (Toge et al. 2011). In the southern hemisphere beginning in 2007, major mortalities of adults occurred in every odd year (but none in even years) through at least 2013 as the birds arrived on their nesting grounds after returning from the NPO (Springer et al. 2018). Shearwaters depend upon fat reserves acquired on northern feeding grounds to carry them through their 15000 km non-stop southward migration, and because the birds in the die-offs were emaciated, it appeared that those reserves were insufficient in odd years. Mean and median abundance indices of nesting short-tailed shearwaters at 2 well-studied colonies were consistently greater in even years than in odd years during 1976–2016 at one colony and between 1997 and 2015 at the other colony. The biennial differential at both colonies was most pronounced in 2005–2016, when pink salmon abundance was exceptional, especially in odd years (Fig. 1) — in this interval, the median even:odd year ratio of nests was 1.49 at Montague Island and 1.16 at Furneaux Island (Springer et al. 2018).

3.6. Humpback whales

Humpback whales *Megaptera novaeangliae* migrate to northern SEAK to feed on forage fishes and euphausiids during spring through fall, returning south to Hawaii and Mexico in winter to breed while also fasting (Gabriele et al. 2017). Using data from Neilson et al. (2022) we calculated that from 1985 to 2013, the 'crude birth rate' was 33% lower in odd years (7.5 ± 0.7% [SE]) than even years (11.3 ± 1.1%; *t*-test, df = 27, p = 0.006; Fig. 14). In 14 of 19 odd years, the crude birth rate was lower than the mean birth rate in the adjacent even years (Fig. 14). The onset of marine heat waves in 2014 may have reduced the magnitude of the biennial pattern.

The mechanism leading to this previously unreported biennial pattern is uncertain, but we hypothesize it is related to pink salmon and their effect on the prey of humpback whales in SEAK. Humpback whales feed on forage fishes, such as herring and capelin, and euphausiids (Jurasz & Jurasz 1979, Krieger 1990), all of which may be influenced by pink salmon (see Section 3). Fewer calves were observed during summer in odd than even years, based on counts reported by Neilson et al. (2022). Those whales were born the previous winter following an even-year

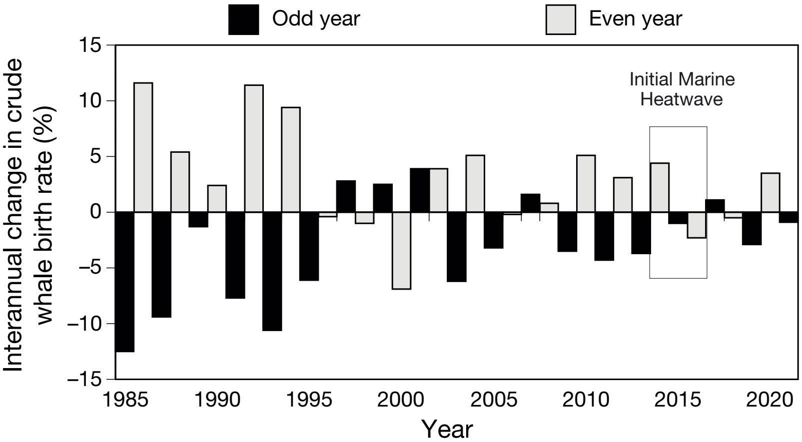

Fig. 14. Interannual change in crude birth rates of humpback whales in Southeast Alaska during even and odd years, 1985–2021. Crude birth rate is the number of unique calves divided by the total number of unique whales observed in Glacier Bay and Icy Strait from 1 June to 31 August (Gabriele et al. 2022, Neilson et al. 2022). Interannual change in birth rate (*BR*) in year i = $BR_i - \text{avg.}\ (BR_{i-1}, BR_{i+1})$

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summer in which pink salmon were less abundant (see Fig. 5a). However, the parent breeding season was during the previous winter, following an odd year in which pink salmon were more abundant. Thus, the feeding rate and nutritional state at the end of odd years may have affected the mating and/or gestation of the parents, leading to fewer calves observed in SEAK during the following odd year.

3.7. Southern Resident Killer Whales

Southern resident killer whales (SRKWs) rarely eat pink salmon (Ford et al. 2016), yet this critically endangered population, which ranges from central California to mid-Vancouver Island and into the Salish Sea, exhibited a highly unusual biennial pattern in both successful births and mortality. From 1998 to 2020, mortality of newborn and older SRKWs was 3.1 times higher (65 versus 21 deaths) and successful births 42 % lower (19 versus 33 calves) in even than in odd years as the population decreased from 92 to 74 animals (Fig. 15a; Ruggerone et al. 2019, CWR 2021). The biennial pattern was not apparent during the earlier period (1976–1997) when the population was stable or increasing, the primary prey (Chinook salmon) were more abundant, and pink salmon were less abundant. SRKWs feed primarily in the Salish Sea during spring through early fall on maturing Chinook salmon (Ford et al. 2016). Ruggerone et al. (2019) hypothesized that pink salmon, whose escapement to Salish Sea rivers increased 135 % during the period of SRKW decline, interfered with the foraging efficiency of the animals as they attempted to capture Chinook salmon. Both returning Chinook and pink salmon concentrate along the west side of San Juan Island and into Boundary Pass from late July through early September, but pink salmon are only abundant in odd years (avg. 18 million versus 0.4 million in even years). In odd years, pink salmon are approximately 50 times more abundant than co-migrating Chinook salmon. According to the hypothesis and support from available data (Fig. 15a), reduced foraging efficiency of SRKWs in odd years when pink salmon are abundant would lower their nutritional status, which would be expressed in the following even year (increased mortality and fewer successful births) because these large mammals have a strong physiological buffering capacity (Ford et al. 2010).

Body condition measurements also support the hypothesis that prey consumption by SRKWs was reduced in odd years, potentially in response to abundant pink salmon (Stewart et al. 2021). During 2008–2019, the body condition index of the L Pod of SRKWs, which was measured in September after most pink salmon have passed through the SRKW

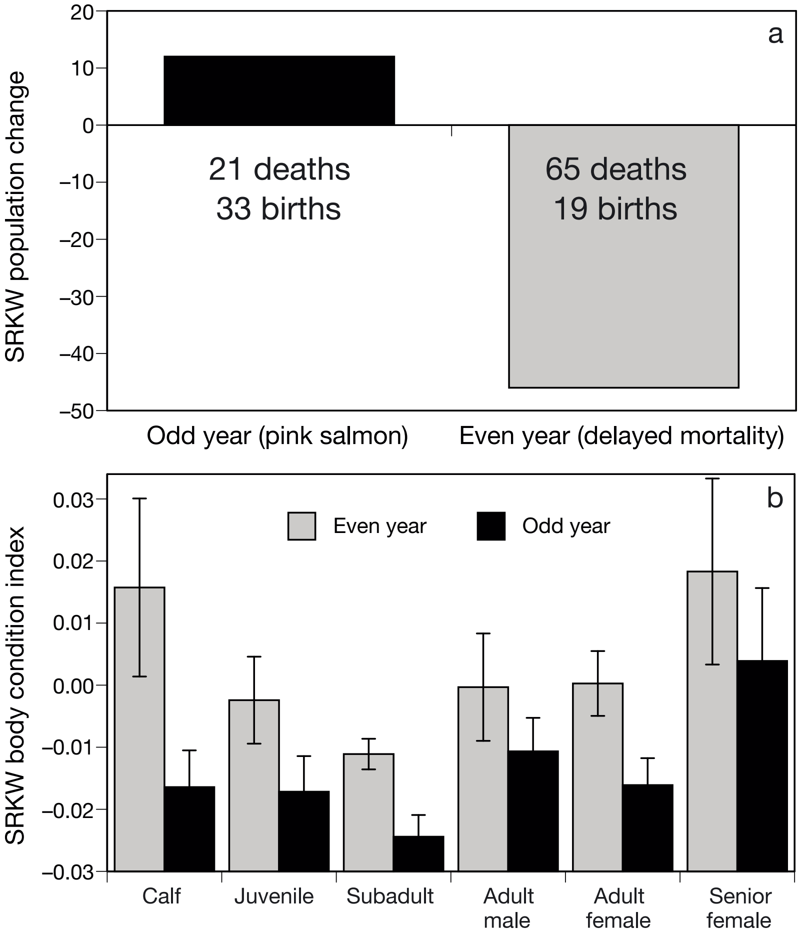

Fig. 15. (a) Southern resident killer whale (SRKW) population declined 20 % from 1998 to 2020, including 46 fewer individuals in even years (19–65 animals) after interacting with abundant pink salmon in the previous odd year but increased by 12 individuals in odd years (33–21 animals) due to more successful births and fewer deaths (Ruggerone et al. 2019, CWR 2021). (b) From 2008 to 2019, annual mean (±1 SE) body condition of each age class of L Pod (SRKW) in September was lower during odd years after numerous pink salmon had migrated through the Salish Sea, the primary feeding area of SRKWs during summer. Body condition measurements were taken from Fig. S6 of Stewart et al. (2021), who recognized the biennial pattern in relation to pink salmon

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foraging area, was markedly lower on average during odd versus even years in each of the 6 age categories (Fig. 15b). A biennial pattern in body condition was not readily apparent in J and K pods, populations that have declined less than the L pod since 1997. From 1998 to 2020, approximately 55 % of mortality and 90 % of the population decline was associated with the L Pod, which exhibited strong biennial patterns in body condition, mortality, and successful births.

Understanding the mechanism of this biennial pattern is critical to the recovery of the endangered SRKW population. For example, if births and mortality during even years had been similar to those during odd years, especially within the L Pod, then the SRKW population would have substantially increased rather than decreased during the past 20 yr (Fig. 15a). In recent years, however, SRKWs have reduced foraging time in the Salish Sea (Shields et al. 2018, Ettinger et al. 2022), a behavior that may influence the extent to which the biennial pattern holds into the future.

4. DISCUSSION

Our synthesis reveals compelling evidence for top-down effects of pink salmon on numerous pelagic species, food webs, and ecosystem function spanning broad regions of the western, central, and eastern NPO, the BS, and semi-enclosed waters including PWS and the Salish Sea (Table 1; Supplement 2). Those effects were largely, but not entirely, unknown until scientists began to notice and track biennial patterns in marine organisms that coincided with the biennial patterns of pink salmon abundance. For instance, regular large interannual differences in sockeye salmon diets were documented in the 1950s (Ito 1964), long before the spectacular rise in pink salmon abundance. Overall, pink salmon apparently have interacted strongly with other species in the NPO for many decades, playing important top-down roles in structuring pelagic ecosystems.

4.1. Conceptual model

We developed a conceptual model that synthesizes our hypotheses based on evidence discussed in Section 3 (Table 1; Supplement 2). It expands upon the 'Trophic Triangle' conceptual model presented by Aydin (2000) and Shaul & Geiger (2016), who emphasized the importance of predation by pink salmon on *Berryteuthis anonychus*. The following points highlight key dynamics implied by what we refer to as the 'Pink Salmon Impacts Model,' and are elaborated upon in Text S3 and Fig. 16.

(1) Warming in the north increases pink salmon abundance, especially odd-year adult returns (Fig. 1).

(2) Biennial variability in predation by pink salmon drives biennial fluctuations of squid abundance (*B. anonychus*), including adult squid, their progeny, and subsequent generations as a result of the 2 yr life cycle of squid (Section 3.3).

(3) Pink salmon can initiate pelagic trophic cascades through predation on large herbivorous zooplankton, lowering their abundance, which can lead to greater biomass of phytoplankton (Section 3.1).

(4) Abundant odd-year pink salmon efficiently exploit prey (zooplankton, small fishes, squid), thus reducing prey needed by other salmon species, forage fishes, and seabirds for growth, productivity, and survival, especially in odd years (Section 3). In a warming ocean, reduced prey availability, especially energy-rich squid and fishes, is particularly harmful for larger and older salmon such as Chinook salmon (Beauchamp 2009). Most salmon evidence involves interactions after their first year at sea, indicating the importance of late marine life to growth, survival, and abundance.

(5) Forage fishes, which are critical prey for many marine species, also exhibit biennial growth or abundance patterns in relation to biennial pink salmon abundance and their predation on common prey resources (Section 3.2).

(6) Humpback whales and SRKWs exhibit biennial demographic patterns that are related to pink salmon (Sections 3.6 and 3.7, respectively).

(7) The intensity of species interactions and regularity of biennial patterns varies across time and ecosystems. The strength of competition in the shared resource spaces is not expected to be equal across all species and locations, and the effects of pink salmon may interact with those of oceanographic conditions, weather, and climate. Thus, interrupted and emerging biennial patterns would not necessarily share common time frames.

Our conceptual model does not specifically address early life stages at sea of salmon in more southerly regions, such as in the Pacific Northwest or Japan, where climate warming generally leads to less favorable conditions for them during early life at sea compared with those in the north (e.g. Hare et al. 1999, Mueter et al. 2002, Mackas et al. 2007, Bi et al. 2011, Keister et al. 2011, Malick et al. 2017a). However, many southern populations of each species that migrate

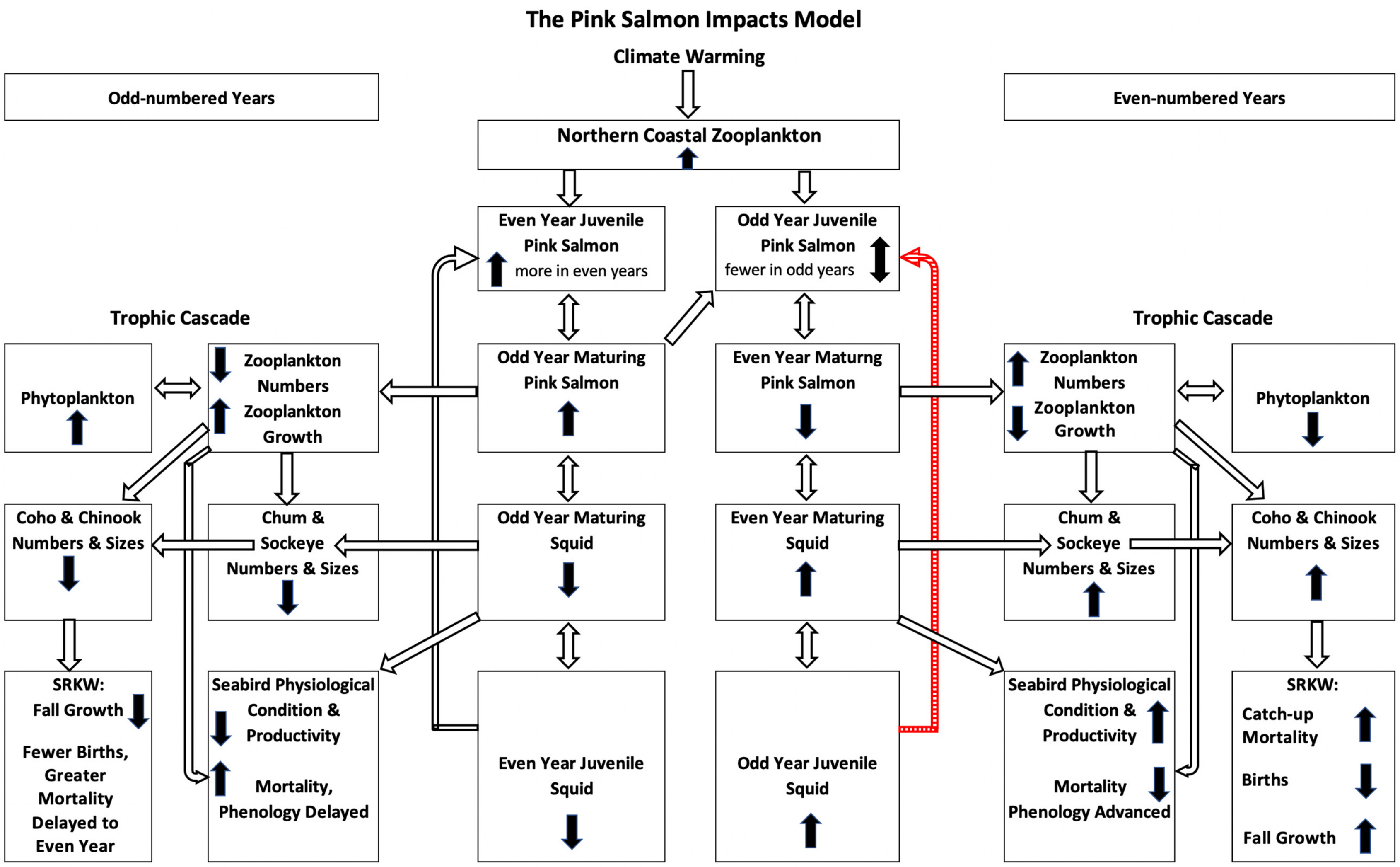

Fig. 16. The conceptual Pink Salmon Impacts Model showing how climate warming, biennial variation in pink salmon abundance, and biennial squid dynamics may influence offshore ecosystems in the North Pacific Ocean and Bering Sea. Solid arrows indicate an increase or decrease in either population abundance, growth or other variable. Hollow arrows indicate direction of influence. Red dashed arrow indicates negative competition effect of increasing juvenile squid. Although both odd and even calendar-year pink salmon abundances are currently increasing over time, odd years here reflect effects of higher pink salmon abundances relative to even years. See Section 3 for linkages to forage fishes and other species, and Text S3 for more details on the model

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north into the GOA, BS, and beyond, including Chinook salmon (Larson et al. 2013), have experienced substantial declines in size, survival, and abundance (Welch et al. 2021, Buckner et al. 2023). We hypothesize that those north-migrating salmonids from the Pacific Northwest and Japan have low marine survival due to less favorable conditions during early life at sea and to reduced foraging opportunities after the first winter at sea, especially for energy-rich squid and small fishes needed to sustain larger and older Chinook salmon in a warming ocean (Section 3).

4.2. Competition exacerbated by climate warming — the case of salmon

We hypothesize that pink salmon and the warming of the NPO and adjacent seas will synergistically enhance competition between pink salmon and other marine species until continued warming leads to declines of all salmon species. Pink salmon abundance has more than doubled in the NPO since the mid-1970s ocean climate regime shift, associated warming, and increased hatchery production (Fig. 1). Pink salmon appear to have initially benefitted from increased abundance of zooplankton in northern regions (e.g. Brodeur & Ware 1992, Brodeur et al. 1996), potentially leading to faster early marine growth and improved survival compared with that prior to the mid-1970s (Ruggerone et al. 2007, Cross et al. 2009). However, warming ocean temperatures also exacerbate competition, because greater consumption of high-calorie prey is needed to offset increasing physiological demands imposed by higher temperature, especially for larger Chinook salmon (Brett 1979, Hinch et al. 1995, Beauchamp 2009, Piatt et al. 2020). Pink salmon are smaller, tend to consume prey more effectively at low densities, and more efficiently utilize food at higher temperatures than other salmon species (Davis et al. 1998), likely factors contributing to their exceptional growth in abundance in recent decades. Thus, the combined effects of greater pink salmon abundance, reduced physiological efficiency in other species at higher temperatures, and apparently fewer high-calorie prey partly in response to increasing predation by pink salmon, in addition to other oceanographic conditions (e.g. Mueter et al. 2002, 2003, Wells et al. 2008, Stachura et al. 2013, Cunningham et al. 2018, Ohlberger et al. 2019, Howard & von Biela 2023), have likely contributed to the long-term and widespread declines in growth and size of all salmon species throughout most of their range (Bigler et al. 1996, Oke et al. 2020). Furthermore, continued warming is also projected to shrink the amount of thermally suitable marine habitat available to each species (Abdul-Aziz et al. 2011, Lindley et al. 2021) and force more salmon into an increasingly crowded BS (Larson et al. 2013, Kaeriyama 2023).

Frequent marine heat waves and high pink salmon abundance are hypothesized to have led to the largest single-year collapse in salmon abundance on record (Ruggerone et al. 2021). Heat waves in the NPO were unusually frequent during 2014–2019 (Litzow et al. 2020b). In 2018 and 2019, a combined 1.34 billion adult pink salmon returned from the NPO, the highest 2 yr abundance since at least 1925 (Fig. 1). In 2020, the combined commercial harvest of all salmon species in Asia and North America declined more relative to average catch in the previous 10 yr (187 million salmon decline) than in any previous 10 yr period since 1925; escapement information indicated that low abundance rather than the COVID-19 pandemic was responsible (Ruggerone et al. 2021). Harvests of Chinook salmon in 2020 were the lowest on record since 1925, declining 54% compared with the previous 10 yr. Chum salmon harvests in 2020 declined 42%, followed by pink (−40%), coho (−27%), and sockeye salmon (−10%). Sockeye salmon harvests beyond those in Bristol Bay declined 44%. In 2021, commercial harvests of pink salmon rebounded to a record level (527 million, or 81% of all salmon), but harvests of chum (−41%), Chinook (−33%), coho (−24%), and sockeye salmon beyond Bristol Bay (−26%) remained low relative to 2010–2019. Harvest of Chinook salmon was the fourth lowest on record (NPAFC 2022a). Thus, the combined effects of both pink salmon and ocean temperatures appear to have contributed to the sharp recent decline in Pacific salmon.

4.3. Implications for salmon hatcheries and ocean carrying capacity

Annual releases of Pacific salmon from hatcheries increased 6-fold from 1970 (0.9 billion juveniles) to 1990 (5.1 billion juveniles), producing approximately 25% of all adult salmon, or 40% of the total mature and immature salmon biomass at sea (Ruggerone & Irvine 2018). This steep rise in overall hatchery production in Asia and North America occurred in part because the primary bottleneck for increased salmon abundance was thought to be in freshwater, and managers believed hatcheries would enable a rapid return to the large harvests that occurred in the early

1900s (Larkin 1974). Also, simulation models and sampling of zooplankton at sea suggested the NPO could readily support more salmon (Sanger 1972, Favorite & Laevastu 1979, Honkalehto 1984, Shuntov et al. 2017). However, some scientists suggested that the ocean could not support large-scale hatchery production without some adverse effects on wild salmon growth and survival (Peterman 1978, 1984a,b), but evidence was somewhat limited at that time (Moberly 1983, Heard 1998, Cooney & Brodeur 1998, Pearcy et al. 1999). Furthermore, Cooney & Brodeur (1998, p. 460) warned 25 yr ago that '[t]o ignore the signals manifested in diminished size of Pacific salmon is to invite potential disaster for these and other resources.' Nevertheless, from 1990 to 2020, annual juvenile salmon released from hatcheries in relatively pristine regions of Alaska and Russia increased by 50 and 75%, respectively, or by approximately 555 million juvenile salmon per year in each region (NPAFC 2022b).

Although hatchery salmon may lead to net gains in commercial harvests in local fisheries, these gains can come at the expense of local wild populations (Amoroso et al. 2017, Ohlberger et al. 2022) and distant populations that co-mingle with them, including depleted and at-risk wild populations from the Pacific Northwest and Alaska (Ruggerone et al. 2012, Larson et al. 2013, Cunningham et al. 2018, Frost et al. 2021). Furthermore, large-scale hatchery production can undermine the natural compensatory density-dependent response that would otherwise benefit wild salmon growth, maturation rate, and reproductive potential during periods of low abundance. For example, in the absence of hatchery salmon, wild salmon would potentially grow faster and thereby have higher reproductive potential (egg mass is proportional to female body mass) at a given age, mature at an earlier age, and therefore have greater survival at sea. The unique biennial patterns shown by salmon interacting with pink salmon provide strong evidence that large-scale hatchery production has unintended consequences and can lead to a tragedy of the commons. The latter topic is expanded upon by Holt et al. (2008).

Some scientists have argued that competition among salmon for prey at sea is limited, and that hatchery fish have little effect on wild populations (Favorite & Laevastu 1979, Shuntov et al. 2017, 2019, Radchenko et al. 2018, Naydenko & Somov 2019). This view is based on calculations suggesting a surplus biomass of prey is available to salmon — that consumption by salmon is only about 1–15% of prey consumed by all epipelagic nekton — and because salmon do not form dense schools that might deplete local concentrations of prey. However, those studies did not consider the nutritional value for each prey species, capture efficiency, or predation risk while foraging. Moreover, they have yet to explain widespread observations of density-dependent growth and survival of salmon, especially the unique biennial patterns of pink salmon abundance that are expressed in the growth, age, survival, and abundance of competing salmon species. Furthermore, investigators such as Shuntov et al. (2017, 2019), who argued that competition among salmon is limited, have investigated the western BS and/or western North Pacific, whereas most studies reporting evidence for competition among salmon were in other regions. Consequently, neither group of scientists has a reason to generalize too widely and deny the validity of the observations and conclusions of the other group.

Salmon typically do not form dense schools while foraging at sea, but they are often found in aggregations or groupings (Hartt & Dell 1986). Evidence collected over multiple decades of sampling salmon on the high seas indicates a significant trade-off between predation risk and foraging success in relation to group size. For sockeye, chum, coho, and pink salmon, the probability of injury (predation risk) decreased with increasing total group size (all salmon species) and conspecific group size, but the probability of consuming prey also declined for each species except pink salmon (Polyakov et al. 2022). For example, the probability of consuming prey declined approximately 20% for sockeye salmon, 6% for chum salmon, and 45% for coho salmon as total group size increased (up to about 2500 salmon per seine net). These findings suggest that salmon groups can deplete local concentrations of prey (Section 3), and that competition is exacerbated by forming groups to reduce predation risk. The decline in prey consumption was greatest for the largest and oldest salmon, which is consistent with the growth decline in older salmon such as Chinook salmon in relation to pink salmon (Section 3). In contrast, pink salmon were not adversely affected by competition, and appeared to experience greater probability of consuming prey when in larger groups.

4.4. Implications of pink salmon on other marine species, ecosystem services, and society

Most of the relationships between pink salmon and other pelagic species reported here imply direct

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competition between them for common-pool prey resources or indirect food web responses to pink salmon forcing. Details of the actual mechanisms are not always known. Nonetheless, unique biennial effects have been seen in lower physiological condition, delayed nesting phenologies, lower breeding propensity, lower productivity, and higher mortality of seabirds; slower growth and lower recruitment in forage fishes; fewer births in humpback whales; and reduced body condition, higher death rate, and reduced birth rate of SRKWs (Table 1). In the case of black-legged kittiwakes in PWS, higher numbers of pink salmon appear to enhance the birds' nesting success as a result of avian predators switching from kittiwake eggs and chicks to pink salmon.

The negative effects of pink salmon on the growth, survival, and abundance of other salmon also impacts commercial, subsistence, recreational, and cultural values humans derive from them. Although climate warming has enhanced overall harvests of sockeye salmon in Bristol Bay, for example, approximately 59 million fewer sockeye salmon returned there during 1977–1997 (excluding the cyclic Kvichak population) after interacting with abundant pink salmon in odd-numbered years, and those fish would have had a value to fishermen of approximately US $310 million if they had survived (Fig. 8d; Ruggerone et al. 2003). In many regions of the Pacific Rim, especially in the Arctic–Yukon–Kuskokwim region of western Alaska, people depend on salmon for subsistence and cultural needs in addition to monetary income from commercial fisheries (Brown et al. 2022). Salmon subsistence harvests, particularly Chinook salmon, have declined over the past 25 yr, and this may partially reflect adverse interactions with pink salmon (e.g. Ruggerone et al. 2012, 2016b, Agler et al. 2013, Cunningham et al. 2018, Frost et al. 2021). Although declines in the abundance of salmon are the most obvious impact to humans, declining body size of salmon over time, which is partially linked to growing abundances of pink salmon, also has the potential to affect both humans and ecosystem services such as meals, price, eggs, and marine-derived nutrients per fish (Bigler et al. 1996, Oke et al. 2020).

Lastly, salmon are typically managed for the number of spawners or for harvest rates that rarely consider the size and fecundity of the spawning salmon and the ecosystem services they provide. Such management practices ignore the fact that decreasing body size, which is often related to increasing abundances of pink salmon, leads to fewer eggs being deposited in the spawning gravel for an equivalent number of fish (e.g. Shaul & Geiger 2016, Ohlberger et al. 2020). Declining body size and fecundity in relation to competition for prey can reduce future abundance of salmon, especially Chinook salmon, whose size, fecundity, and abundance has sharply declined over time (Section 3.4.4, Fig. 10).

5. CONCLUSIONS

The most parsimonious explanation for the many, widespread biennial patterns across the broad range of species and trophic levels in the NPO documented in this synthesis is the interaction with pink salmon. The evidence is consistent and strong that pink salmon can exert competitive dominance for common-pool prey resources shared by 4 forage fish species, all 5 species of Pacific salmon and steelhead trout, and 11 species of seabirds (Table 1; Supplement 2). It further indicates that pink salmon can have a strong influence on ecosystem structure and function by, for example, initiating pelagic trophic cascades. Whether or not it can be considered a keystone species sensu Power et al. (1996), pink salmon is clearly a very strongly interacting species in marine ecosystems of the NPO.

We cannot identify every link between pink salmon and other species. However, competing upper trophic level predators serve as proxies for the inferred direct effects pink salmon have on lower trophic level populations of food web species, including zooplankton, forage fishes, and squids. The present lack of abiotic explanations for the many biennial patterns in the natural histories of numerous species that interact with pink salmon should not be construed as evidence that physical forcing, or other biological factors, are not important to them directly or indirectly. Effects of the recent Pacific Marine Heatwave on ocean food webs and individual species are prime examples of such physical forcing (Piatt et al. 2020, Arimitsu et al. 2021).

Scientists should take advantage of the predictable biennial pattern in abundance of pink salmon, and their increasing numbers in response to ocean heating, to test these and other hypotheses about ecosystem function and species and food web interactions. Although the vast spatial scales of oceanic regions limit possibilities for true treatment–control manipulations, the biennial fluctuations fortunately create a unique natural 'experiment' that can illuminate the influence of pink salmon on their competitors and lower trophic levels. Future ecosystem models should include pink salmon as top-down drivers, in addition to the bottom-up drivers of climate and physical oceanographic forcing. Such information is necessary for effective ecosystem-based management, especially of species harvested by humans (Malick et al. 2017b).

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Pioneer Alaskan Fisheries
Nancy Hillstrand
[redacted]
Homer, Alaska [redacted]
[redacted]
9/29/23

RE: October 2023 Hatchery Committee considerations

Dear Chairman Carlson-Van Dort and members of Alaska's Board of Fisheries,

I own and operate a 58-year in business Alaskan Fisheries Corporation that for the past 32 years has operated as a commercial, sport, personal use and subsistence, value added custom seafood processor, seafood galley, cannery, smokery, direct marketer for local fishermen, and retail seafood market with internet sales at welovefish.com. We do business as Coal Point Trading Company on the Homer Harbor.

The BOF Hatchery Joint Protocol gives authority for ADFG Chief salmon scientist Templin's 2020 suggestion of an Academy of Sciences panel to help with hatchery issues *"so the department isn't caught flat footed"* .

> *"As appropriate, the board and department may agree to invite other state and federal agencies, professional societies, scientists, or industry spokespersons to attend and to contribute information on particular topics, or sponsor other discussions, such as marketing or intrastate effects."*

Hatchery industry already contributes information so to invite the wealth of information from "other state and federal agencies, professional societies, or scientists", provides a comprehensive "statewide perspective" of open discussion with broader knowledge while endorsing required conservation.

The legislatures Hatchery Act stated mandatory conditions for the privilege and responsibility of a private hatchery operation in Alaska's wild pastures:

> ***for the purpose of contributing, by artificial means, to the rehabilitation of the state's depleted and depressed salmon fishery.***

Twice in one sentence, natural fish of the state were stipulated:

> ***"The program shall be operated without adversely affecting natural stocks of fish in the state and under a policy of management which allows reasonable segregation of returning hatchery-reared salmon from naturally occurring stocks."***

Are pink salmon depleted and depressed?
As a fish Culturist with the state of Alaska for over 20 years in hatcheries, priority had no focus if ever on natural stocks of fish. Fish culture is animal husbandry, not science, so the focus is on commodity production, instead of natural wild production of wild living fish, the food web and ecosystems that self-perpetuate.

The Board and department are the only statutory authorities to ensure hatcheries "***would not jeopardize natural stocks, (***AS 16.10.400). and with Board of Fisheries authority using AS 16.10.440(b) may uphold natural fish wild priority with balance of the statewide perspective as the legislature intended.

It is clearly understood that The Board of Fisheries may not issue or deny any original hatchery permits issued. Issuing or denying original permits is the commissioners job after a lengthy public process of meetings and notices stated clearly in AS 16.10.400 - 16.10.470.

However, **ADFG nor the commissioner, have no statutory authority to alter original permits they themselves issued** with one exception given in AS 16.10.430 directs, the commissioner may alter, suspend or revoke the permit only when problems are perceived:

> ***" If the commissioner finds that the operation of the hatchery is not in the best interests of the public, the commissioner may alter the conditions of the permit to mitigate the adverse effects of the operation."***

The statutory authority to alter these original permits provides a needed balance of power in AS 16.10.440(b)

> ***(b) The Board of Fisheries may, after the issuance of a permit by the commissioner, amend by regulation adopted in accordance with AS 44.62 (Administrative Procedure Act), the terms of the permit relating to the source and number of salmon eggs, the harvest of fish by hatchery operators, and the specific locations designated by the department for harvest.***

Attached is a transcript of Aaron Petersons comments on Board authority at the 2020 Hatchery Committee meeting as well as two other attorney General opinions

Hatchery information is fractured and segregated without the cohesive framework of Board of Fisheries authority that adopts regulations in accordance with the Administrative Procedures Act, to organize and structure regulations.

Instead, altering originally issued permits has becomes isolated, in generally inaccessible remote towns by primarily self-appointed members heavily weighted by industry. Information can be vetted by RPT's like advisory committees but final decisions require a formal statewide perspective envisioned by the legislature. Without this added statewide open forum, consideration of all wild fish or wild fisheries interactions or their markets are lost by the narrow stroke of a self-serving pen.

To widen scientific scope that determines knowledge instead of whim will make certain, that hatchery operations are not adversely affecting natural stocks of fish and integration of hatchery fish with wild is not occurring.

Some solutions to consider to regain order of hatchery issues far-flung splinters of information, centralize information into a cohesive accessible structure for transparency and accessibility instead of obscurity.

1. First please **institute the BOF statutory mandate of AS 16.10.440(b)** to provide lost balance of power to alter original permits by regulation, using the Administrative Procedures Act. This allows examination of any further Permit Alteration Requests (PARs) by industry, to still be vetted by the Regional Planning Team just like a Fish and game advisory committees but from there, requests and considerations are elevated to allow the Board of Fisheries process to deliberate with other regional staff for a more comprehensive statewide perspective.

2. **ADFG anadromous waters Atlas Quadrangle Index mapping system** would create at a glance, interactive GIS layers to clearly depict hatchery stocking and release harvest and straying sites distinct from wild salmon streams.

   Presently hatchery SHA's; THA's; Remote Release Sites; and other stocking release sites and hatchery harvest areas are scattered without any centralized location. Access is almost impossible. Find and place them on the Anadromous Waters Map.

- 5 AAC Chapter 40
- Management Plans;
- SHA's and release or harvest sites embedded within original PNP permits;
- remote release sites and hatchery harvest areas embedded in past Permit Alteration Requests (PARs) and minutes
- mixed stock hatchery/ wild fisheries harvest area

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3. **GIS layer of Sensitive nursery areas where wild fish spawn** reproduce and rear have been obscured by misguided focus on hatchery fish rather than wild species. Bring the science to life.
    - Create a GIS layer using the baseline established in the ADFG Alaska Habitat Management Guide Map Atlas with upgrades using available bathymetry to prioritize these designated spawning, rearing and reproductive concentration areas of diverse wild fish species nearshore nurseries productive shelves Using these sensitive delicate nurseries as monoculture hatchery feed lots for 10s of millions of one species is counterproductive to diversity of wild fisheries priority.

4. **Overlay NOAA Shore Zone mapping showing food web** and wild fish habitat nursery attributes and shellfish stocks.

5. **Create a GIS layer using mark tag lab database** or any other data of past and ongoing hatchery salmon straying data to determine accuracy of wild salmon escapements.
    - Historic data of escapements before hatcheries
    - Historic data of escapements after hatchery implementation
    - Tag Lab Coded wire and thermal marked straying data
    - Reports

6. Identify a GIS layer of **wild salmon only systems uncontaminated by hatchery stray** homogenization in each region as a 2023 baseline.

    - Designate these uncontaminated wild only salmon systems as "sanctuary stocks"
    - Request a monitoring schedule to detect hatchery stray contamination.
    - Take action when contamination is detected.

7. Call for proposals in cycle to examine and **reassess all 5 AAC hatchery regulations**. Most of these are 40 + years old when an entire ADFG Division of 144 staff had oversight over hatchery programs. Ensure consistency with the best available science to ensure state regulations prioritize wild fish precaution and the much later created sustainable Salmon Policy.
    - Chapter 40. – PNP Hatchery Regulations
    - Chapter 41 – Transportation, Possession, and release of live fish; Aquatic Farming
    - Chapter 93 – Department programs – (Use or Waste of Hatchery Salmon)

8. Create a **GIS layer of where mixed stock fisheries occur** to determines where wild fish are masked unknown when harvested and lost in hatchery returns.

9. **Request otolith sampling monitoring** information of wild fish proportions in season be placed on this mixed stock layer.
    - Where is department sampling mixed stock hatchery/wild fisheries harvests.
    - Who is paying for this monitoring

10. Communicate and **standardize "size, scale and level of risk"** of releases and returns by "order of magnitude" as a gauge of permitted capacity and PAR Remote Releases discharged from a facility or remote release site and to minimize confusion from the misleading generic term "hatchery",
    - 10,000; Magnitude 1
    - 100,000; Magnitude 2
    - 1,000,000 Magnitude 3
    - 100,000,000 Magnitude 4

11. Standardize this Magnitude size of hatchery with ADEC that uses **"Concentrated Aquatic Animal Production (CAAP)** depending on the discharge of aquatic animals per year and pounds of feed, feces, carcasses, medications, fungicides, pesticides etc.
    a. DEC clarified that higher volume CAAP facilities pose higher levels of risk to water quality.
    b. This higher or lower level of risk to wild fish extends to magnitude of release or return.

12. **Reevaluate all Comprehensive Salmon Plans**
    - Are they comprehensive for wild fish production obligations?
    - Are” significant stocks”[1] based on genetic policy frameworks?
    - Are smaller portfolio stocks deemed “non-significant” sacrificed as insignificant without consideration for the power of the combined collectives to the biomass?
    - Are portfolio stocks sacrificed due to size as genetics policy warns against?
    - Are principles and recommendations followed or is Alaska off course.

13. Request Department **coordinate an in-depth monitoring** effort of hatchery marking programs paid for by PNP’s
    - Where is monitoring of otolith marking taking place in the State of Alaska?
    - What areas of Alaska are not monitored for straying into wild streams?
    - Otolith sampling must become routine annual monitoring protocol to detect and document how far and how much hatchery strays are expanding.
    - Do PNP hatcheries pay for sampling and these otoliths to be read?
    - If not why not
    - Do all Treaty involved fish have an adequate required marking program?
    - Which hatcheries have hard to read or failures confounding these marking programs?

14. Acquire List of all **statewide pathology reports** GIS hot spots on AWC
    - Release of diseased BKD fish
    - Medications
    - Transport of eggs or fry from diseased parents

15. **Fiscal Effects of Hatcheries to the State of Alaska Public Trust**
    - What does Alaska receive in hatchery revenue not including pass through enhancement taxes?
    - What does Alaskan agencies spend on hatcheries diverted from wild fish priority:

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[1] ADFG Genetics Policy

    - ADFG operations,
    - ADFG at RPT meetings
    - ADFG Reading and signing off on AMPS (Annual Management Plans)
    - ADFG reading and signing off on FTP (Fish Transport Plans)
    - ADFG otolith sampling
    - ADFG Mark tag lab reading otoliths
    - ADFG pathology lab
    - Facility capital expenditures with General funds $30 million in 2015)
    - Other state agency expenditures due to permitting or lawsuit conflicts
    - ADNR; ADPOR; DEC

16. **Cost analysis consideration of loss to wild fisheries**
    - From density dependency to wild fish weight loss to the state
    - smaller sockeye salmon documented when large pink hatchery returns and the poundage loss to the wild fish fisherman.

17. **Annual Enhancement Reports currently are misleading** to the Legislature because they lack comprehensive detailed information required by law. The complexity of the hatchery issue is simply happy talk This Report can be upgraded by inserting pertinent factual data of all aspects of the hatchery operations in relationship to wild stocks and wild stock harvest wild stock markets and updates on the Alaska Hatchery Research Program.

Thank you kindly for your consideration
Nancy Hillstrand

Submitted by: Nancy Hillstrand

Community of Residence: Homer, Alaska

Comment:

Attached is a transcript of Assistant Attorney General Aaron Petersons comments at the 2020 Hatchery Committee meeting on Board Authority.

2020 MARCH BOF HATCHERY COMMITTEE

ASSISTANT ATTORNEY GENERAL AARON PETERSON Transcript on
Board of Fisheries Hatchery Oversight Authority begins around 7:34 on video

https://www.youtube.com/watch?v=CE-Cl_-cFz8&feature=youtu.be

CHAIR MORISKI:
Seven board members present 3:43 pm. Next item on our agenda is Department of Law briefing on Board of Fish extent of authority and ADFG's extent of authority related to hatcheries

Mr. Peterson are you ready to give us some information
AARON PETERSON:

Yes, I am. Thank-you Mr. Chair. So first I will give a brief overview

I talked to the board a little bit at the Lower Cook Inlet meeting in Seward and much of the remarks that I made there, directly relate back to a memo that was authored by a couple of assistant attorneys general from 1997. That memo is on the website for today's meeting as well, and that information is still relevant, because there has been basically no change, in the past twenty three years.

There has been one case that talked about the primary statute 16.10.440b and I'll talk about that a little bit, but essentially that memo from the department of law has been the consistent guidance for the better part of the last three decades and it continues to be that, from the Department of Law.

So there are three primary points, that I concluded with, at the Lower Cook Inlet And I will start with them here.

1. The permitting and administration of hatcheries rests with the department of Fish and Game.
2. The board has some indirect control over hatchery production by virtue of its authority to amend hatchery permits with respect to Special Harvest Areas (SHA) and the harvest of broodstock and cost recovery fish.
   The boards authority to amend permits is limited to terms in the permit relating to the
   - The source and number of salmon eggs
   - the harvest of fish by hatchery operators and
   - the specific locations designated by the department for harvest

3. Though the board may affectively amend hatchery permits by regulation in a manner that may affect hatchery fish production, previous guidance by the department of law is that the board may not

   <u>one:</u> adopt regulations that effectively veto or override a fundamental policy decision regarding whether to authorize the operation of a particular hatchery or

   <u>two:</u> adopt regulations preventing the department from exercising its authority to permit a hatchery operation.

So, let me go through a little bit of how I get to that point.

So first the broad permitting authority detailed in Title 16 assigns primary responsibility for whether to authorize the operation of a PNP hatchery to the commissioner and the department of Fish and Game.

And, the board may exercise, as I said, indirect authority of hatchery production by:

- regulating the harvest of hatchery related hatchery released fish in the common use fishery,
- hatchery broodstock,
- cost recovery harvest and
- by amending hatchery permits related to the source and number of salmon eggs
- hatchery harvested and the designation of the special harvest areas

But board action that effectively revokes or prevents the issuance of a hatchery permit is probably not authorized

The board regulations over the authorities is governed primarily by

16.05.251
16.10.440
16.05.730
And of course 16.05.251 is the boards general rulemaking power of statute

And these powers include setting time, area, methods and means, and the limitations for the taking of fish, and of course setting quotas, bag limits, and harvest levels, the standard board authority.

The boards authority also extends to the regulations of harvest of hatchery fish and egg collection and existing regulation's such as

5AAC 40.005 which explains board authority over hatchery produced fish, reflect that principle as well.

AS 16.10.440 is the statute that relates to releasing fish and

subsection a., of that statute confirms that fish released by hatcheries are available for common use and subject to the regulations by the board until they return to the hatchery harvest area.

And Subsection b., is sort of the primary thing that this all turns on, I'll read that in the entirety

AS 16.10.440 subsection (b) Regulations Relating to Released Fish.

(b)The Board of Fisheries may, after the issuance of a permit by the commissioner, amend by regulation the terms of the permit relating to the source and number of salmon eggs, the harvest of fish by hatchery operators, and the specific locations designated by the department for harvest. The Board of Fisheries may not adopt regulations or take any action regarding the issuance or denial of any permits required in AS 16.10.400 - 16.10.470.

And I mentioned at the top that there has been one case that talked about that statute 16.10.440b in the past 20 years and that was a case called

O'Callaghan v Rue and that was in the year 2000 and in that case the supreme court said quote:

"The power to modify permit terms is shared. It lies with the commissioner in the first instance, but is subject to the ultimate control by the board. citing 16.10.440b

That was not, I should caution you, the central holding of that case. That is not precedent. It was dicta, but it's the only case where the supreme court talked about this statute so it is worth noting.

AS 16.05.730 Management of Wild and Enhanced Stocks of Fish, requires the Board of Fish to manage all stocks consistent with the sustained yield of wild stocks, and the statute requires the board to consider the need of enhancement projects to obtain broodstock when allocating enhanced fish stocks and authorizes the board to direct the departments management to achieve adequate return for broodstock.

The board may also consider the need for enhancement projects to harvest and sell fish to obtain funds for project operation and may direct the department to provide a reasonable harvest of fish to the hatchery for those purposes and may adopt management plans to provide fish to the hatchery to <u>obtain funds for the purposes allowed by statute.</u>

Than finally, I would point out that in 16 05.251 –(8)(9) the board is specifically authorized to adopt regulations.

Quote: "Prohibiting and regulating live capture possession transport or release of native or exotic fish or their eggs" Unquote:

> but that may not apply to hatchery fish. The more specific statute on point of 16.10.440b doesnt specifically authorize the board to adopt regulations that amend the terms of the permits that govern the release of hatchery fish. Those things that relate to hatchery fish
>
> And regardless the board is delegated that authority to the commissioner by adopting 5AAC 41.

But, so one of the things that I went back and looked at after the Lower Cook Inlet meeting was the legislative history related to specifically to 16.10.440b and I found a couple of things that I thought were notable there:

<u>First:</u> in April 24 of 1979, the legislative council wrote a a sectional analysis of the bill to a senator Kerttula, I might be mispronouncing that, but, it reads as follows:

"Section 2 of the bill amends 16.10.440b, the effect of the amendment would be to limit the regulatory power of the Board of Fisheries in relation to the provisions of AS 16 10.470, these sections of law relating to salmon hatchery permits. Currently the Board of Fisheries has the power, under this section to promulgate regulations necessary to implement these sections.

The proposed amendment would limit the boards regulatory power in this specific area by allowing the board to adopt regulations <u>amending the terms of permits issued under 16.10. 400-470</u> which relate to the harvest of broodstock, by hatchery operators and the specific locations designated by the department for harvest by the hatchery operators.

The amendment would specifically provide that the board may not adopt regulations or take any action regarding the issuance or denial of the permit.

So an amended 440b the legislature equivocally limited the boards authority over hatcheries there is no question about that.

But, it did not strip the board of all authority. It seems pretty clear from the legislative history, that if the legislature had wished to do that, they simply would have repealed 16.10.440b.

Further in March 15 of 1979, the House journal explained that one of the purposes of amending that section of 440b was to clarify that the board does not have the authority to promulgate regulations regarding the Department of Commerce and Economic Development. It was unclear from the history if that had been an issue but that was specifically noted in the house journal that that was part of the reason for the amendment.

And The final thing I want to point out from the House Journal is the following passage:

> "The amendment clarifies the role of the Board of Fisheries. The role of the Board of Fisheries as envisioned by the original legislation was to regulate the harvest of salmon returning to the waters of the state.
>
> That role extends to regulating those fish that are returning as a result of releases from natural systems and also from hatchery releases."
>
> There are provisions in other portions of the Non Profit hatchery act which allow the designation of specific locations for the harvest of salmon by the hatchery operator for sale, and use of the money from that sale, for the specific purposes stated in AS 16.10.450.
>
> The added language clarifies that the Board of Fisheries may adopt regulations relating to the harvest of the fish by hatchery operators at these specifically designated locations."

And the legislative history on this amendment was not very… there was not very much of it, there was a couple of recordings, a few hand written letters and then the house journal and the legislative sectional analysis from the legislative attorney. Then there was quite a bit of other material that didn't relate to the amendment subsection 440 b so these were the highlights that directly relates to the question that comes up now.

It doesn't do anything to undermine the consistent advice that the Department of Law has been giving the Board for the better part of the last three decades it generally affirms the advice that has been given as recently as the Lower Cook Inlet meeting and as far back at least as the 1990's.

So with that I'd answer any questions about this and I will certainly attempt to if there are any.

CHAIR MORISKI:

Thank-you Mr. Peterson. Mr. Wood

JOHN WOOD:

I am going to try to approach this systematically so we narrow down to where this question of what jurisdiction this body has or does not have.

Clearly the law is crystal clear that only the commissioner has the right to issue or revoke a permit correct?

AARON PETERSON:

That's correct That is in the statute

JOHN WOOD:

The only exception to where the board may have some jurisdiction falls within that 440b where it makes specific mention of the authority of the Board to amend a permit. Is that correct?

AARON PETERSON:

Through the chair, member wood, I think the most direct authority is in 16.10.440b. There is also some implied authority in 16.05.730 and there is general authority in 16.05.251 the general enacting statutory authority of the Board.

JOHN WOOD:

Okay, for my purposes of the Board, the question right now I want to focus on right now is 440b and looking at the memorandum and I don't know the PC number of it, but Ashburn and Mason maybe PC 31, legal opinion, went through what they conceived or perceived rather as the legislative intent, that the eggs being taken back then were from the wild stocks as opposed to hatchery eggs and that was the justification for doing what they did in implementing section b.

Looking at it in greater detail if that were the only purpose in mind, I don't understand what the necessity for the additional language they put in there saying the board of fisheries may not adopt any regulations nor take any action regarding the issuance or denial of the permit, and then they go forward and say or would have the effect of negating a permit.

So my question I guess to you is , It seems clear, there is nothing scientific about the terms used that this board does have the ability to amend a permit for the stated purposes in 440b. with relating to the source and number of salmon eggs of the fish by hatchery operations at specific locations designated by the department for harvest.

Under what authority would anybody claim otherwise?

AARON PETERSON:

Through the chair member Wood

I wouldn't presume to know why someone would argue other than or that that statute means something other than exactly what it says. I mean I could probably construct an argument that, well yes I could actually.

In Alaska there is a sort of general statutory construction theory that is relatively prevalent in most states and in the federal system, known as the plain language mean right?

But in Alaska our courts have said that the meaning behind the statute…the intent of the statute, can overcome that plain language I don't have the exact citation in front of me

JOHN WOOD:

Isn't that one of ambiguity in the interpretation in the language?

AARON PETERSON:

It's a sliding scale

JOHN WOOD:

mmhem

AARON PETERSON:

So if the language is very clear and takes very strong very overwhelming legislative authority to the contrary to overcome that plain language. If there is ambiguity, then the legislative history indicating alternative meaning doesn't have to be as strong.

JOHN WOOD:

Do you see any ambiguity in the wording of that subsection??

AARON PETERSON:

Do I?

JOHN WOOD:

Yes!

AARON PETERSON:

NO, and again I'll point out the consistent advice from the department of law has been that that statute means what it says. Um and so that has been the consistent advice from the Department for the better part of three decades.

JOHN WOOD:

Thank-you very much I have no other questions.

CHAIR MORISKI

Mr. Payton

ISRAEL PAYTON:

Thanks, I'm going to ask you the same questions in a different way I guess. In your opinion, does the statement the number of salmon eggs apply to both wild broodstock and returning hatchery broodstock?

AARON PETERSON:

Through the chair member Payton, um

The advice from the department of law has been yes that it does and that's as I said before been consistent through the memo and if you were to look at the house journal talking about 440b it specifically says the role extends to regulating those fish that result, which are returning as a result of natural systems and also from hatchery releases so that’s from the house journal from 1978 no I’m sorry 1979 talking about the purpose of that bill.

CHAIR MORISKI:

Further Board questions from Mr. Peterson
Hearing none thank-you Mr. Peterson

Submitted by: Nancy Hillstrand

Community of Residence: Homer, Alaska

Comment:

attached is a 1997 assistant attorney generals Robert C. Nauheim and Lance B. Nelson opinions on board authority to Board of Fisheries request

MEMORANDUM

State of Alaska
Department of Law

TO: Dr. John White
Chair
Alaska Board of fisheries

The Honorable Frank Rue
Commissioner
Department of Fish & Game

DATE: November 6, 1997

FILE NO.: 661-98-0127

TELEPHONE NO.: 269-5240

SUBJECT: Authority of the Board of Fisheries Over Private Nonprofit Hatchery Production

FROM: Robert C. Nauheim
Lance B. Nelson
Assistant Attorneys General
Natural Resources-Anchorage

I. Introduction

In your memorandum of June 24, 1997, and in discussions at the recent Board of Fisheries (Board) work session, you requested guidance regarding the authority of the Board over private, nonprofit salmon hatcheries and their operations. Specifically, you asked for a review of (1) statutes and regulations relating to the authority of the Board and the Commissioner of the Department of Fish and Game (commissioner) over hatchery salmon production and cost recovery, (2) the historical development of Board authority in this area, (3) the scope of the Board's authority over hatchery salmon production, and (4) the relationship between the Department of Commerce and Economic Development's hatchery loan program, the Board, and the Department of Fish and Game (department). We understand that you require an analysis of these issues to assist the Board in its discussions during its upcoming meetings.

II. Summary Answers

1. The legislative scheme for the regulation of private, nonprofit hatcheries vests the more detailed, comprehensive authority in the commissioner and department.

2. Although the board initially had broad rule-making authority over all aspects of the private, nonprofit hatchery program, the legislature significantly restricted that authority by an amendment to AS 16.10.440(b) in 1979.

3. The Board may exercise indirect authority over hatchery production by regulating the harvest of hatchery-released fish in the common use fishery, hatchery brood stock and cost-recovery harvests, and by amending those portions of hatchery permits relating to the source and number of salmon eggs, hatchery harvests, and the designation of special harvest areas by the adoption of appropriate regulations. However, Board action that effectively revokes, or prevents the issuance of, a hatchery permit is probably not authorized.

4. The Commissioner of the Department of Commerce and Economic Development is independently responsible for the implementation of the hatchery loan program under AS 16.10.500 - 16.10.560.

III. Discussion

This discussion focuses primarily upon an evaluation of existing Board authority over the operation of private, nonprofit salmon hatcheries. It opens with a review of the extensive statutory authority of the commissioner and the department over hatcheries.

Beginning in 1974, the legislature adopted various statutory provisions regulating the construction and operation of private, nonprofit salmon hatcheries in Alaska. The goal of the program was “the rehabilitation of the state's depleted and depressed salmon fishery.” Sec. 1, ch. 111, SLA 1974. Although the legislature initially granted both the department and the Board responsibility for the program, it limited what was initially a broad grant of rule-making authority to the Board over the implementation of the program by statutory amendment in 1979.

A. Commissioner/Department Authority over Hatcheries

The hatchery statutes place direct and nearly comprehensive responsibility for the private, nonprofit hatchery program in the hands of the commissioner and the department. The legislature has granted exclusive authority to the commissioner to issue permits for the construction and operation of salmon hatcheries. *Id.* at § 2; AS 16.10.400-16.10.430 (as amended). We believe this broad and detailed permitting authority was intended to assign responsibility for the fundamental policy determination of whether to authorize the operation of a private, nonprofit hatchery to the commissioner and department.

1. Pre-permit Responsibilities

Pursuant to AS 16.10.375 the commissioner must designate regions of the state for salmon production and develop a comprehensive salmon plan for each region through teams consisting of department personnel and nonprofit regional associations of user groups. The commissioner also has the task of classifying an anadromous fish stream as suitable for enhancement purposes before a permit for a hatchery on that stream may be issued. AS 16.10.400(f). AS 16.10.400(g) requires a determination by the commissioner that a hatchery would result in substantial public benefits and would not jeopardize natural stocks. The statutes also require the department to conduct public hearings near the proposed hatcheries, and to consider comments offered by the public at the hearings before issuance of a permit. AS 16.10.410.

2. Permit Issuance and Hatchery Operation Responsibilities

For issuing a private, nonprofit hatchery permit, the legislature delegated to the department the power to control the following:

(1) the specific location where eggs or fry may be placed in the waters of the state (AS 16.10.420(2));

(2) the source of salmon eggs procured by the hatchery (AS 16.10.420(1));

(3) the resale of salmon eggs procured by the hatchery (AS 16.10.420(3));

(4) the release of salmon by the hatchery (AS 16.10.420(4));

(5) the designation of the manner and place for the destruction of any diseased salmon (AS 16.10.420(5));

(6) the specific locations for the harvest of adult salmon (AS 16.10.420(6));

(7) the first option to purchase surplus eggs from a hatchery and inspection of eggs and the approval of sale of those eggs to other hatcheries (AS 16.10.420(7));

(8) the determination of reasonable segregation by location) of hatchery from natural stocks (AS 16.10.420(10));

(9) the source and number of salmon eggs to be used by the hatchery (AS 16.10.445(a)); and

(10) the inspection of hatchery facilities (AS 16.10.460).

3. Alteration, Suspension, or Revocation Authority

The commissioner may suspend or revoke a permit after determination of a failure to comply with conditions and terms of the permit. AS 16.10.430(a). Upon a finding "that the operation of the hatchery is not in the best interests of the public, the commissioner may alter the conditions of the permit to mitigate the adverse effects" and, in extreme cases, may "initiate termination of the operation under the permit over a reasonable period of time under the circumstances, not to exceed four years." AS 16.20.430(b).

The foregoing authorities demonstrate that the legislature granted detailed and broad authority to the commissioner and the department for the implementation and day-to-day regulation of salmon hatcheries. On the other hand, the specific authority given to the Board is more circumscribed.

B. Board of Fisheries' Authority over Hatcheries

Although the legislature placed primary administrative authority over the permitting and day-to-day operation of hatcheries within the department, it also vested considerable general and specific authority in the Board of Fisheries. The Board's regulatory authority over private, nonprofit hatcheries is governed primarily by AS 16.05.251, 16.10.440 and 16.10.730.

1. Board Authority under AS 16.05.251

The Board's general rule-making powers over fish and the taking of fish are set out in AS 16.05.251. These powers include setting time, area, and methods and means limitations on the taking of fish. AS 16.05.251(a)(2), (4). The Board also establishes quotas, bag limits and harvest levels. AS 16.05.251(a)(3).

The Board has broad authority to "adopt regulations it considers advisable . . . for regulating commercial, sport, guided sport, subsistence, and personal use fishing as needed for the conservation, development, and utilization of fisheries." AS 16.05.251(a)(12).

This authority includes the power to allocate fishing opportunities between competing user groups. *Meier v. State*, 739 P.2d 172, 174 (Alaska App. 1987); AS 16.05.251(e). The Board's authority extends to the regulation of the harvest of hatchery fish and egg collection. *See* 1990 Inf. Op. Att'y Gen. 41 (August 1; 663-90-0327) (Board's regulatory authority extends to management of hatchery brood stock and allocation of cost-recovery fishing). Existing regulations reflect this principle. *See* 5 AAC 40.005 (harvest of hatchery-produced fish governed by Board regulation). The Board also has general authority to adopt regulations for "prohibiting and regulating the live capture, possession, transport, or release of native or exotic fish or their eggs." AS 16.05.251(a)(9). This provision would include, but is not limited to, regulation of the capture, possession, transportation, and release of salmon and their eggs by hatcheries. *Id.*

2. Board Authority under AS 16.10.440

In former AS 16.10.440, the legislature initially vested broad rule-making authority in the Board of Fisheries and Game[1] over hatchery-produced fish and the implementation of the hatchery program in general. Sec. 2, ch. 111, SLA 1974. Former AS 16.10.440 provided:

> REGULATION: (a) Fish released into the natural waters of the state by a hatchery operated under secs. 400 - 470 of this chapter are available to the people for common use and are subject to regulation under applicable law in the same way as fish occurring in their natural state until they return to the specific location designated by the department for harvest by the hatchery operator.
>
> (b) The board may promulgate regulations necessary to implement secs. 400 - 470 of this chapter.

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[1] Prior to 1975, regulatory authority over the harvest of fish and game resources was vested in the Board of Fisheries and Game. In 1975 the legislature abolished the Board of Fisheries and Game and simultaneously created a separate Board of Game and Board of Fisheries, each having broad regulatory powers. Ch. 206, SLA 1975; *see also* AS 16.05.221, 16.05.241, 16.05.251, 16.05.255. The legislature also amended AS 16.10.440(b) to clarify that the authority over hatcheries formerly resting in the Board of Fisheries and Game was to be held by the newly created Board of Fisheries.

Alaska Statute 16.10.440 (a), which has remained unchanged since 1975, confirms that fish released by hatcheries into the natural waters of the state are, as are all wild fish and game within the state, available for common use and subject to lawful regulation. *See generally McDowell v. State*, 785 P.2d 1, 5-9 (Alaska 1989)(equal access clauses of art. VIII of Alaska Constitution are intended to provide the broadest possible public access to state's fish and game.)

Alaska Statutue 16.10.440(a) does purport to exempt the effect of at least some applicable law to hatchery-produced fish once the fish arrive at areas designated by the department for harvest by the hatchery operator. *See* AS 16.10.440(a) (fish subject to regulation "until they return to the specific location designated by the department for harvest by the hatchery operator"). For reasons discussed in greater detail below, AS 16.10.440(a) does not significantly limit the authority of the Board or the department to regulate hatchery-produced fish at these locations, since AS 16.10.440(b) goes on to grant specific authority for regulation at the point of return.

Former AS 16.10.440(b) vested in the Board of Fisheries and Game broad authority to "promulgate regulations necessary to implement sec. 400 - 470 of this chapter." This broad language purported to give the Board of Fisheries and Game expansive rule-making authority over all aspects of carrying out the hatchery program.

In 1979, the legislature amended AS 16.10.440(b), eliminating the broad authority "to promulgate regulations necessary to implement" the hatchery program, and replacing it with more specific, but limited responsibilities:

> (b) The Board of Fisheries may, after the issuance of a permit by the commissioner, amend by regulation adopted in accordance with the Administrative Procedures Act (AS 44.62), the terms of the permit relating to the source and number of salmon eggs, the harvest of fish by hatchery operators, and the specific locations designated by the department for harvest. The Board of Fisheries may not adopt any regulations nor take any action regarding the issuance or denial of any permits required in AS 16.10.400-16.10.470.

Sec. 3, ch. 59, SLA 1979.[2]

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[2] In 1979, the legislature also authorized the Commercial Fisheries Entry Commission to issue special harvest area limited entry permits to operators of private, nonprofit hatcheries. Sec. 1, ch. 64,

The legislative history of the 1979 amendment reveals the legislative intent behind the new, more restricted language:

> Section 2 of the bill [HB 359] amends AS 16.10.440(a)(b). The amendment clarifies the role of the Board of Fisheries. The role of the Board of Fisheries as envisioned by the original legislation was to *regulate the harvest of salmon returning to the waters of the state. That role extends to regulating those fish which are returning as a result of releases from natural systems and also from hatchery releases.* There are provisions in other portions of the non-profit hatchery Act which allow the designation of specific locations for the harvest of salmon by the hatchery operator for sale, and use of the money from that sale, for the specific purposes as stated in AS 16.10.450. *The added language clarifies that the Board of Fisheries may adopt regulations relating to the harvest of the fish by hatchery operators at the specifically designated locations*. The Board of Fisheries in the past year or two has enacted regulations relating to those harvests for several of the private non-profit hatcheries in the state.
>
> The intention of the original bill relating to the non-profit hatchery Act as amended in recent years was that the permits for the construction and operation of the private non-profit hatcheries were to be issued by the Commissioner of the Department of Fish and Game. Specific language in AS 16.10.400 lays out the grounds for the issuance of the permits and AS 16.10.420 lays out the statutory guidelines that must be included in such a permit. Those statutory provisions remain the same under this amendment.
>
> In this bill AS 16.10.440(b) is deleted and the necessary powers are substituted in the language which is added to (a).[[3]] That deletion helps

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SLA 1979; AS 16.43.400-16.43.440. Special harvest areas may be designated by the department in a hatchery permit, by emergency orders under AS 16.10.420, or by regulation adopted by the Board under AS 16.05.251 or AS 16.10.440(a). *See* 1993 Inf. Op. Att'y Gen. 273 (July 16; 663-93-522).

[3] In the final version of the bill passed by the legislature, the language referenced here was again divided into two subsections, leaving AS 16.10.440(a) intact and moving the new language into subsection (b).

> clarify a technical problem which has arisen because the original section (b) stated that the Board of Fisheries may promulgate regulations necessary to implement subsections 400 - 470 of this chapter. That in effect gave the Board of fisheries the power to enact regulations regarding a requirement by the Department of Commerce and Economic Development. In section .470(b) the Department of Commerce and Economic Development is instructed to provide a form to the permit holder for submission of an annual report regarding the financial aspects of the hatchery operation, if such a hatchery operator has obtained a loan from the State of Alaska.

House Journal, March 15, 1979 (remarks of Rep. Fred Zharoff, Chm. House Resources Committee regarding HB 359) (emphasis added).

3. Board Authority under AS 16.05.730

In 1992, the legislature enacted AS 16.05.730[4], which requires the department and Board to manage all fish stocks consistent with the sustained yield of wild fish stocks and authorizes, but does not require, management consistent with the sustained yield of enhanced stocks. AS 16.05.730(a). In addition, the statute mandates Board consideration of the need of enhancement projects to obtain brood stock when allocating enhanced fish stocks, and authorizes the Board to direct the department's management to achieve an adequate return for brood stock. AS 16.05.730(b). The Board may also consider the need for enhancement projects to harvest and sell fish to obtain funds for project operation, may direct the department to provide a reasonable harvest of fish to the hatchery for those purposes, and may adopt management plans to provide fish to a hatchery to obtain funds for the purposes allowed under AS 16.10.450 or AS 16.10.480(d). AS 16.05.730(c). Significantly, while the statute requires Board consideration of hatchery brood stock needs, it does not mandate any particular level of hatchery harvest of enhanced fish stocks. Consideration of harvest and sale of fish for project funding is authorized, but not required.

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[4] AS 16.05.730 provides:

> **Management of wild and enhanced stocks of fish.** (a) Fish stocks in the state shall be managed consistent with sustained yield of wild fish stocks and may be managed consistent with sustained yield of enhanced fish stocks.
>
> (b) In allocating enhanced fish stocks, the board shall consider the need of

C. The Balance between Department Commissioner and Board Authority over Private Nonprofit Hatchery Production

As the foregoing discussion suggests, the department and the Board share regulatory authority over private, nonprofit hatcheries. Although primary responsibility over permitting and the administration of the hatchery program rests with the department, the Board has substantial, indirect control over hatchery production by virtue of its regulatory authority to amend hatchery permits with respect to special harvest areas, the harvest of brood stock[5] and cost-recovery fish.[6]

> fish enhancement projects to obtain brood stock. The board may direct the department to manage fisheries in the state to achieve an adequate return of fish from enhanced stocks to enhancement projects for brood stock; however, management to achieve an adequate return of fish to enhancement projects for brood stock shall be consistent with sustained yield of wild fish stocks.
>
> (c) The board may consider the need of enhancement projects authorized under AS 16.10.400 and contractors who operate state-owned enhancement projects under AS 16.10.480 to harvest and sell fish produced by the enhancement project that are not needed for brood stock to obtain funds for the purposes allowed under AS 16.10.450 or 16.10.480(d). The board may exercise its authority under this title as it considers necessary to direct the department to provide a reasonable harvest of fish, in addition to the fish needed for brood stock, to an enhancement project to obtain funds for the enhancement project if the harvest is consistent with sustained yield of wild fish stocks. The board may adopt a fishery management plan to provide fish to an enhancement project to obtain funds for the purposes allowed under AS 16.10.450 or 16.10.480(d).
>
> (d) In this section, "enhancement project" means a project, facility, or hatchery for the enhancement of fishery resources of the state for which the department has issued a permit.

[5] In this memorandum, we use the term "brood stock" to designate fish returning to the hatchery as a result of hatchery operations that are harvested for the purpose of the biological reproduction of fish.

[6] In this memorandum, we use the term "cost-recovery" fish to designate those fish or eggs authorized to be harvested for purposes of sale under AS 16.10.450.

Though no statute expressly grants the Board regulatory authority over hatchery production *per se*, it may exercise considerable influence over hatchery production by virtue of its authority to directly amend hatchery permit terms relating to fish and egg harvesting.[7] We have previously advised that while the Board is authorized to do so, it is not required to allocate cost recovery fish to a hatchery. 1990 Inf. Op. Att'y Gen. 41 (Aug. 1; 663-90-0327); AS 16.05.730(c). Similarly, we have advised that the Board has authority to regulate brood stock harvest. *Id.*

The Board must *consider* hatchery brood stock needs in determining appropriate harvest levels. AS 16.05.730(b). The Board may also consider hatchery cost recovery needs. AS 16.05.730(c). However, it is not *required* to provide harvest opportunities that are inconsistent with what the Board reasonably determines to be appropriate. 1990 Inf. Op. Att'y Gen. 41 (August 1; 663-90-0327). For example, to the extent the Board believes that a hatchery permit issued by the department provides too liberal or restrictive an opportunity to harvest salmon or collect eggs,[8] it may amend the permit by adopting appropriate regulations.

As previously noted, AS 16.05.730 requires the Board to manage all stocks of fish consistent with the sustained yield of wild fish stocks and to consider the need of fish enhancement projects for brood stock. Accordingly, in evaluating whether to amend a hatchery permit or adopt regulations governing hatchery harvests, the Board must carefully consider the needs of fish enhancement projects to obtain brood stock and manage harvests so as to be consistent with the sustained yield of wild fish stocks. AS 16.05.730(a), (b).

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[7] It might be argued that the authority set out in AS 16.10.440(b) to amend hatchery permits, particularly as to the "source and number of salmon eggs," is express and direct authority to regulate hatchery production. Since the statute does not expressly address "hatchery production" or any similar concept, we have, in previous oral comments to the Board, characterized the authority over this area to be "indirect" and "implied." We continue to believe that this advice is correct.

[8] It has been suggested that the Board's authority to regulate the harvest of eggs from returning hatchery fish may be distinguishable from its authority to regulate the harvest of eggs from wild fish stocks. We see no reason to distinguish between these two. The Board has authority to amend hatchery permits as they relate to "the source and number of salmon eggs." AS 16.10.440(b). We believe this language covers the harvest of eggs from both wild and hatchery stocks.

The Board's authority over hatchery production is circumscribed by the 1979 amendment to AS 16.10.440(b) and, to a lesser extent, by AS 16.05.730. The Board's authority to amend permits is limited to terms in the permit "relating to the source and number of salmon eggs, the harvest of fish by hatchery operators, and the specific locations designated by the department for harvest."[9] Under AS 16.10.440(b) the Board "may not adopt any regulations or take any action regarding the issuance or denial of any permits required in AS 16.10.400-16.10.470." Although the meaning of this limitation is not completely clear, we conclude for the reasons set forth below that the limiting language contained in AS 16.10.440(b) was intended to clarify that the Board's specific regulatory authority over the amendment[10] of hatchery permits is to be limited to the authority set out in AS 16.10.440(b).[11]

The following principles would guide a court in interpreting AS 16.10.440(b). In interpreting a statute, a court's goal is to give effect to the intent of the legislature with due regard to the plain meaning of the statute. *Cook v. Botelho*, 921 P.2d 1126, 1129 (Alaska 1996). In addition, a court may consider the overall purpose of a statute and its legislative history. *Muller v. BP Exploration (Alaska), Inc.*, 923 P.2d 783, 789-91 (Alaska 1996). Whenever possible, each part or section of a statute must be interpreted to create a harmonious whole. *Rydwell v. Anchorage School District*, 864 P.2d 526, 528 (Alaska 1993).

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[9] AS 16.10.440(a) provides that hatchery-released fish are subject to Board regulation "until they return to the specific location designated by the department for harvest by the hatchery operator." However, given the Board's general authority over the allocation of fishery resources under AS 16.05.251 and its specific authority to amend hatchery permits by regulation under AS 16.05.440(b), it may, therefore, regulate the harvest of salmon or collection of eggs *after* salmon have returned to the location designated for harvest or egg collection in that manner.

[10] The legislature's use of the concept of "amending" permits by the adoption of Board regulation presents an unusual mixture of administrative law principles. We believe the legislature's use of the concept of amending a hatchery permit by regulation was not intended to vest the Board with administrative adjudicatory authority over permits. *See* AS 16.05.241 (the Board has rule-making authority, but does not have other administrative powers). Instead, we interpret the legislature's use of the term "amend" to allow the Board to adopt regulations that may *effectively* change or modify an existing permit by virtue of the change in regulatory setting created by appropriate Board regulation. *See also* AS 16.10.400(a) (commissioner-approved permits are "subject to the restrictions imposed by statute or regulation under AS 16.10.400-16.20.470").

[11] This view is supported by AS 16.10.400(a), which specifically provides that permits are subject to "restrictions imposed by . . . regulation under AS 16.20.400-16.10.470."

Finally, where a potential conflict or ambiguity exists, a statute that deals more specifically with a particular issue must govern over a more general statute. *Welch v. City of Valdez*, 821 P.2d 1354, 1363 (Alaska 1991).

Given (1) the detailed statutory scheme granting specific authority to the department over nearly every aspect of the permitting and operation of nonprofit hatcheries, (2) the more general statutory authority of the Board over the harvest of fishery resources, and (3) by contrast, the limitations imposed upon the specific statutory authority of the Board over hatchery permits by the amendment to AS 16.10.440(b) in 1979, we conclude the following. Though the Board may effectively amend hatchery permits by regulation in a manner that affects hatchery fish production, we do not believe the Board may either (1) adopt regulations that effectively veto or override a fundamental department policy decision regarding whether to authorize the operation of a particular hatchery or (2) adopt regulations preventing the department from exercising its authority to permit a hatchery operation. We believe that Board actions falling into either of these two categories would risk being viewed by a court as constructing an impermissible impediment to the department's role as the primary government agency responsible for the regulation of hatcheries. In particular, such actions would risk being deemed incompatible with the limitations imposed by the 1979 amendment to AS 16.05.440(b).

A recent decision by the Alaska Supreme Court supports this view. In *Peninsula Marketing Ass'n v. Rosier*, 890 P.2d 567, 573 (Alaska 1995), the court held that in absence of specific statutory authority for the commissioner to issue emergency orders concerning a question previously considered by the Board, the commissioner could not effectively veto a decision by the Board for which there was specific statutory authority. The court ruled that "[i]nferring a broad veto power would make superfluous the detailed provisions dividing power and authority within the Department" and effectively eviscerate the powers explicitly granted to the Board. *Id.* Similarly, to read the limited grant of authority to the Board over hatcheries set out in AS 16.10.440(b) to permit the Board to effectively veto fundamental policy decisions by the department for which there is specific statutory authority would upset the balance of the statutory scheme chosen by the legislature.

Additional reasons support that conclusion. As previously noted, the Board "may not adopt any regulations or take any action regarding the *issuance* or *denial* of any permits required under AS 16.10.400-16.10.470." AS 16.10.440(b) (emphasis added). We believe that a Board regulation that so drastically amends a hatchery permit to render the hatchery's operation impracticable might be viewed by a court to be an impermissible action by the Board "regarding the issuance or denial . . . of a permit." *See* AS 16.10.440(b). In other words, a Board amendment that puts a hatchery out of operation might be construed as an effective revocation or denial of a hatchery permit, an action that is expressly prohibited by AS 16.10.440(b). Similarly, Board regulations prohibiting the establishment of a hatchery in a particular area deemed by a court as an action by the Board regarding the issuance of a permit and, therefore, unlawful under AS 16.10.440(b).[12]

One additional aspect of Board and department authority merits some discussion. AS 16.05.251(a)(9) specifically authorizes the Board to adopt regulations "prohibiting and regulating the live capture, possession, transport, or *release* of native or exotic fish or their eggs" (emphasis added). This statute must be read, if possible, to be harmonized with AS 16.10.420, the statute governing the department's authority to issue hatchery permits, and the limitation on Board authority with respect to Board "amendment" of hatchery permits set out in AS 16.10.440(b). *See Borg-Warner v. Avco Corp.*, 850 P.2d 628 (Alaska 1993). Although AS 16.10.420 requires the department to issue hatchery permits specifying that a hatchery may not place or release salmon eggs or fry in the waters of the state other than those provided in the permit, the statute does not directly conflict with the Board's authority over the release of fish set out in AS 16.05.251(a)(9). However, AS 16.10.440(b) does not specifically authorize the Board to adopt regulations that amend the terms of the permit governing the release of hatchery fish.

Currently, the Board has delegated its authority over the release of fish to the department commissioner by the adoption of 5 AAC 41. These regulations establish a process for the issuance of permits by the commissioner according to regulatory criteria for the release of fish. Accordingly, absent a repeal by the Board of this delegation of authority, there may not be significant potential for conflict between the Board and the department.

D. Fisheries Enhancement Loan Program

In 1977, the legislature created the fisheries enhancement revolving loan fund within the Department of Commerce and Economic Development for making loans to private, nonprofit hatchery permit holders and to regional associations for long-term, low-interest loans for the planning, construction, and operation of salmon hatcheries, and the

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[12] We realize that without additional clarification from the legislature the parameters of permissible Board regulations remain somewhat murky. However, we believe that the more significantly a particular Board regulation restricts the effective functioning of a hatchery in a way that is incompatible with a departmental decision to permit the hatchery's operation, the greater is the risk that the Board regulation may be invalidated by a reviewing court.

rehabilitation and enhancement of salmon fisheries. Sec. 9, ch. 154, SLA 1977; AS 16.10.500-16.10.500. The Commissioner of the Department of Commerce and Economic Development independently administers this loan program.[13] *See* AS 16.10.500-16.10.560.

The Commissioner of the Department of Commerce is authorized to make loans from the fisheries enhancement revolving loan fund to holders of private, nonprofit salmon hatchery permits issued by the Department of Fish and Game under AS 16.10.400-16.10.470. AS 16.10.505, 16.10.510. The commissioner may also make grants to qualified regional associations for "organizational and planning purposes." AS 16.10.510(9).

While this loan and grant program is administered independently from the Department of Fish and Game and the Board, only qualified regional associations and private, nonprofit hatchery permit holders are eligible to receive them. *See* AS 16.10.510-16.10.520.

IV. Conclusion

We hope this discussion provides answers to your questions. Please do not hesitate to contact us if we can provide additional assistance.

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[13] As the legislative history set out previously in this memorandum suggests, the broad rule-making authority under former AS 16.10.440 created uncertainty regarding whether the Board could, by adopting appropriate regulations, affect the requirement of hatcheries to report to the Department of Commerce and Economic Development under AS 16.10.470. The 1979 amendment to AS 16.10.440 clarifies that the Board may not regulate in this area.

PC3

Submitted by: Nancy Hillstrand

Community of Residence: Homer, Alaska 99603

Comment:

attached is Assistant Attorney General Steven White to Commissioner Carl Rosier in 1993 opinion on board authority and hatchery funding of projects

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Hon. Carl L. Rosier
Commissioner
Alaska Dep't of Fish and Game

July 16, 1993

663-93-0522

465-3600

Special harvest areas and funding of hatchery evaluation projects

Stephen M. White
Assistant Attorney General
Natural Resources Section - Juneau

You have asked two questions about private nonprofit hatcheries.[1] These questions and our answers follow.

Question 1. How may the Department of Fish and Game ("Department") establish special harvest areas ("SHA's") or change the boundaries of SHA's for private nonprofit hatcheries ("PNP's")? In particular, is it necessary for the Board of Fisheries ("Board") or the Department to adopt regulations for this purpose?

Answer: Among other ways, SHA's may be established or changed by an emergency order issued by you or your authorized designee. The issuance of an emergency order does not require an associated regulation.

Discussion: An SHA may be designated by Board regulations, within the hatchery permit, or by emergency orders issued by you or your authorized designee. 5 AAC 40.005(c). Harvesting of salmon in SHA's may be opened and closed by regulation or emergency order. 5 AAC 40.005(d). SHA boundaries that are set out in regulations or in PNP permits may be altered by emergency order if necessary for the proper management of natural or hatchery stocks. 5 AAC 40.005(e). Thus, the "designation, opening, and closure" of SHA's may be achieved through emergency orders. Boundaries established by regulation or in a PNP permit may be altered by emergency order if the Department finds it necessary for proper stock management.

Emergency order authority is described in AS 16.05.060. This law authorizes you or your designee "when circumstances require" to summarily open or close seasons or areas or to change weekly closed periods on fish or game. AS 16.05.060(a). An emergency order has the force and effect of law after it has been announced, and, most important for your question, it is not

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[1] You also asked a question about the use of a fish trap by a federal fish hatchery. We will be answering this question in a separate memorandum.

subject to the Administrative Procedure Act, the law governing the adoption of administrative regulations. AS 16.05.060(c).

Thus, an emergency order may be issued without requiring or referring to a previously adopted regulation that deals with the subject matter of the order. In this particular situation, you may issue an emergency order that designates, opens, or closes an SHA for salmon harvest without need of, or reference to, any regulation. If it is necessary for proper stock management, you may issue an emergency order that amends an SHA boundary established in a PNP permit without there being a regulation that pertains to the SHA. Essentially, an emergency order is a "stand alone" provision that is neither derived from nor dependent on administrative regulations.[2]

Question 2. You have asked whether you may add a requirement that PNP's fund projects that evaluate fish tagging programs (a) to a new PNP permit, (b) unilaterally to an existing PNP permit, or (c) to an existing PNP permit as a condition for granting the PNP's request for altering its permit.

Answer: You have statutory authority to add such a requirement to a new permit, to an existing permit as a condition of granting a PNP's request for altering the permit, and, if certain findings are made, unilaterally to an existing permit. This authority, however, should not be exercised until you adopt regulations that set out the conditions and procedures for including this requirement in a permit.

Discussion: Concerning a new permit, you or your designee may issue a PNP permit "subject to the restrictions imposed by statute or regulation." AS 16.10.400(a). Although the law sets out conditions that must be included in a PNP permit (see AS 16.10.420), that list is not exclusive. These authorities lead us to conclude that you may include in a new permit a requirement that the PNP pay for fish tagging evaluation projects but only if the conditions and procedures under which it may be included are first established by regulation. The regulations, of course, must be consistent with your duty to manage, protect, maintain, improve, and extend the fish resources

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[2] We have noticed that nearly all emergency orders issued by the Department are expressed as "amendments" of regulations adopted by the Board. This is not only not necessary, but it is also incorrect. Absent a delegation of authority from the Board, the Department may not "amend" a Board regulation.

of the state. AS 16.05.020(2).

Concerning an existing permit, the law authorizes you to alter a PNP permit "to mitigate the adverse effects of the (hatchery) operation" if you find that the "operation of the hatchery is not in the best interests of the public." AS 16.10.430(b). Thus, before you may unilaterally add a project funding requirement to an existing permit, you must find that (1) the failure of the hatchery to fund such a project causes its operation to not be "in the best interests of the public" (for example, that its operation threatened the viability of wild salmon stocks), and (2) adding the funding requirement would mitigate the adverse effect caused by the hatchery's operation (for example, would serve to protect wild salmon stocks). We also believe, consistent with our advice above, that the conditions and procedures for including this requirement in a permit must first be established by regulation.

Finally, we note that a regulation allows a PNP to propose an alteration of its permit or its management plan. 5 AAC 40.850. You have indicated that most PNP proposals are to allow the hatchery to increase salmon production or to change release sites. We assume that the increased production or changed release sites create the need for a fish tagging evaluation project. In this event, you would have the opportunity to condition your approval on the added requirement that the PNP fund the project. Before doing this, however, we again urge you to adopt regulations that set out the procedures and conditions for adding this requirement.

Please contact us if we can be of further assistance.

SMW:lae

Submitted by: Donald Johnson

Community of Residence: Soldotna

Comment:

Dear Alaska Board of Fisheries, (Hatchery Committee)

I am contacting the Alaska Board of Fisheries (Hatchery Committee) regarding its directives within Title 16, Chapter 10, Section 400, G, where the ADF&G Commissioner is required to “only” grant hatchery permits if a permit will result in “substantial public benefit and not jeopardize a natural fisheries resource”.

I submit to the Board that its current Alaska hatchery program and permitting system is producing hatchery fish that are defective and inferior to wild fisheries resources and are therefore genetically destructive to all of Alaskas current pristine wild DNA natural fisheries resources. I claim destruction of Alaska’s wild fisheries DNA with hatchery stocks does not result in substantial public benefit. I am claiming that Alaska hatchery stocks are jeopardizing Alaska’s natural fisheries resource.

I am claiming that Alaska’s current hatchery stocking program, by design, produces genetically weaker and less aggressive fish which are then less likely to survive in a wild or natural environment. Those inferior hatchery fish then spawn with wild natural fisheries resources and produce less wild and less aggressive offspring.

Less aggressive fisheries offspring in Alaska eventually causes wild runs to fail because predators always take full advantage of those less aggressive fish. Once those less aggressive runs fail the same predators that took advantage of those fisheries also ends up starving to death because the fishery they depended on no longer exists.

I am claiming that adding hatchery contaminated stocks to wild fisheries resources eventually over time corrupts those resources and destroys them. Once those wild fisheries resources have collapsed it is just a matter of time before predatory sea gulls, eagles, bears, wolves and whales will also eventually starve to death.

At first hatchery stocks appear to support and strengthen wild stocks but the less aggressive hatchery genetics eventually cause the collapse of the wild resources along with all the wild resources that depends on those wild resources.

I am therefore claiming that adding hatchery stocks to wild fishery resources is counter productive and destructive.

It then naturally follows that destroying entire ecosystems is not a “substantial benefit” to the Alaska public and this practice therefore violates the beneficial public directive of Title 16, Chapter 10, Section 400, (G).

Alaska‘s hatchery stocks not only eventually destroy wild fisheries resources “genetically” but they also destroy them “environmentally”. Hatchery stocks end up acting like a a supreme feeding machine that sweeps the ocean thereby reducing and depleting marine ecosystems which other natural fishery and game resources depend on.

When enough hatchery stocks are present they end up cutting in front of natural fisheries resources, thus forcing wild stocks to forage longer and expel more energy to sustain themselves. Some of those wild resources eventually fail to acquire sufficient calories therefore causing them to starve to death. I claim that causing wild fisheries resources to starve to death does NOT comply with the beneficial public directives of Section 400, (G).

All of Alaska hatchery stocks are currently violating Title 16, Chapter 10, Section 400, G, which would automatically void their current Alaska hatchery permits.

The only way Alaska hatchery stocks could be theoretically safely mixed with wild or natural fisheries is for the State to conduct tests and evaluation procedures that fully address the potential conflicts and consequences of genetically weakening natural wild fisheries. Since Alaska has not created or implemented these tests or procedures it is currently completely impossible to safely mix hatchery and wild fisheries resources.

Since Alaska lacks real evidence that its hatchery stocking program does not pose a substantial threat to wild or natural fisheries resources, its hatchery programs should be immediately placed on an indefinite hold until such evidence is produced and verified.

I therefore conclude that it is absolutely self destructive to in the short term “hatchery endanger” wild and natural fisheries resources upon which everyone and everything depends.Those who wield the power to genetically manipulate our wild fisheries resources with artificial stocks ought to be the first to demand absolute evidence that those hatchery stocks cannot genetically compromise our wild fisheries resources, just to ensure their own survival.

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Alaska Salmon Hatcheries?

Alaska salmon hatchery promoters have a really nasty habit of attempting to use Other Peoples Data. Therefore in many cases they don’t always get the complete picture. I have found that in most cases they do not have a realistic wild fisheries resource prospective about fisheries sustainability.

They actually believe that if their hatchery stocks aren’t currently crashing today, that they are therefore sustainable. Nothing could be farther from the truth. All you have to do is miss a single bit of critical information and suddenly all your hatchery fish are gone and it may take you decades to bring them back. If your depending on other people’s data you had better be real sure you haven’t missed any of their data.

The people who built the Titanic spent massive resources launching an “unsinkable ship” only to have it destroyed by a single hunk of ice floating around the Atlantic. There’s a lesson there right?That may sound pretty crazy but If you actually review all the evidence out there you will find there are zero sustainable hatchery salmon fisheries resources off Alaska or the west coast of Canada and the US. The same goes for wild crab and herring resources in these areas.

Alaska’s Bristol Bay illustration is a prime example of a hatchery salmon resource pumping away with all the appearances of a sustainable fisheries resource. Unfortunately all of it is built on artificial hatchery production which was mixed with wild salmon genetics. Forget about the defective food hatchery salmon are forced to consume, it is a proven scientific fact that hatchery salmons DNA is permanently altered from wild DNA just because of the hatchery environment itself. That damaged hatchery DNA was then mixed with “pristine wild DNA” and now we have alleged “wild salmon” with damaged DNA and a questionable sustainability claim. This is the “wild DNA reality” that most hatchery supporters either ignore or will not tell you about.

Bristol Bay hatchery fisheries may claim a salmon count sustainability but does that account for the bays salmon DNA degradation from its historic wild salmon DNA? No it doesn’t. Nobody cares about the DNA changes to the bays wild salmon. If in the future a new virus invades Bristol Bay and wipes out 100% of the bays salmon, everyone will then suddenly discover that “we should have known better” than to allow the wild DNA degradation and hatchery cloning.

The Bristol Bay salmon count may project theoretical sustainability but who is tracking the decreasing weight of these salmon? Has anyone plugged that into their sustainability equation? The same is happening to Cook Inlet salmon. If they did factor in those weight reductions would it change those sustainability claims? It sure would but nobody is going to do that. Does anyone know why the average weight is decreasing? Alaska does not have “sustainability reality” until it has DNA and weight stabilization but these issues are completely disregarded and “sustainable” is stamped on all these fisheries anyway.

The Titanic’s owners actually thought they built an “unsinkable ship” but that fantasy ran head-on into reality on April 12th, 1912. They were deceived by the appearance of previous success and “the lack of disaster”. The appearance of hatchery success and the lack of fisheries disaster is not proof of hatchery sustainability.

The State of Alaska and the ADF&G think they have built sustainable hatchery supported fisheries but they are dealing with a “fisheries house of cards” that can be instantly crash down or remain in place for years because of their disregard for wild salmon genetics. That is not sustainable.

All they need to do is miss a single hidden resource variable or get hit with a single deadly virus and billions of dollars worth of “sustainable” fisheries can crash over night and not be able to restore itself for 50 years. Does a 50 year repair plan actually meet your definition of the word sustainable?

The Titanic’s owners believed in their success because they lacked evidence of disaster. Alaska currently believes in hatchery success because it lacks evidence of hatchery disaster. I therefore believe that if you actually dig deep enough, you will discover the absolutely lethal nature of Alaska’s salmon hatcheries.

Donald Johnson

[redacted]

Soldotna Alaska 99669

[redacted]

Submitted by: Donald Johnson

Community of Residence: Soldotna

Comment:

Dear Alaska Board of Fisheries (Hatchery Committee),

I have a correction to the letter I sent to you on 09/23/23 regarding “How Hatchery Salmon Damage Wild Salmon”. The corrected version is listed below. Please accept the below version as my correct version. Thank you.

Donald Johnson

Dear Alaska Board of Fisheries (Hatchery Committee), (correction)

Below is a summary description of how I see hatchery salmon damaging wild salmon. I claim that hatchery salmon are significantly different from wild salmon in some really critical ways.

Wild salmon populations are genetically diverse because genetic diversity increases survival and survival is natures ultimate goal. Wild genetic diversity is the result of centuries of natural selection that tunes wild salmon for a maximum survival response within a constantly changing environment. Genetic variation is the best way to prevent inbreeding depression or loss of adaptive potential which ends up pushing salmon populations towards extinction. Wild salmon populations are naturally genetically predisposed to rapidly adapting to the environmental watershed conditions that they are born into. Wild salmon are therefore very resilient to any climate change that may come their way. (c).

Hatchery salmon stocks on the other hand are not genetically diverse because they have done a “short-cut” around natural selection and achieved “artificial selection” which provides them with clone genetics, which lacks genetic diversity. That lack of genetic diversity then predisposes hatchery salmon to an insufficient survival response to constantly changing environmental watershed conditions. Hatchery salmon stocks are therefore not resilient to climate changes that come their way.

Hatchery salmon stocks are raised by artificial selection, which means they are genetically less fit for survival in the wild, which means they genetically are more likely to die from viruses, predation or even climate change. Hatchery salmon are raised industrially to maximize their survival regardless of their health or fitness. Wild salmon are raised by natural selection which matches their survival with their health or fitness.

Hatchery salmon actually get their DNA modified while living in their insulated and protected environment. The lack of chasing down prey to survive while being fed processed pellets actually gets encoded within their DNA and ends up producing genetics and hormone levels that do not exist within wild salmon. (a).

Juvenile salmon hormone levels generate hatching, imprinting, smolting, feeding, size and spawning. Abnormal hormone levels reset many of those natural instincts and conditions. Normal hormone levels result from an intact wild DNA genome. Hatchery environments directly cause DNA genome degradation (damage) which then can cause abnormal hormone levels. Abnormal hormone levels degrade salmon feeding, migratory and spawning instincts and can cause migratory runs to get lost and drop off the map into oblivion. (a).

Wild salmon natural selection pressures force salmon to adapt to an ever-changing environment, which automatically ends up producing increased fitness and resilient salmon with genetic traits that cause a salmon to adapt to local conditions to survive and pass on their survival genes, even within dramatic climate changes.

Hatchery fish are usually rapidly released from a limited number of locations. These unnatural release conditions then increase predator impacts causing an unnatural distribution of fish and predators within an ecosystem. Hatchery releases can account for a tremendous influx of predators within an ecosystem which then prey on hatchery salmon, wild salmon and trout while at the same time consuming forage food that wild salmon historically depend on.

Unfortunately many people believe hatcheries are some kind of "techno cure-all solution" that can supply "wild salmon" despite overfishing, pollution, invasive species and even habitat degradation. All of these assumptions have resulted in a general failure to collect sufficient hatchery data to realistically assess hatcheries true impacts on wild salmon.

Scientists have just recently concluded that hatcheries are one of the primary factors that have contributed to the decline of wild salmon, along with overfishing and loss of habitat. In 1996, the National Academy of Sciences published a report that concluded that "In retrospect, it is clear that hatcheries have caused biological and social damage." (b).

For example, hatcheries have contributed to the more than 90% reduction in spawning densities of wild coho salmon in the lower Columbia River over the past 30 years."(b).

Hatcheries damage wild salmon populations in a variety of ways; within genetic, ecological, fisheries and facility impacts. The following damages result when hatchery salmon spawn with wild salmon and decrease the genetic fitness, adaptability, and diversity of wild salmon populations;

1.) Hatchery salmon damage wild salmon while spawning with wild salmon because there is a net loss of genetic "wild salmon productive capacity" within each spawning interaction.

2.) Hatchery salmon damage wild salmon when an influx of hatchery salmon overloads the carrying capacity of an ecosystem causing hatchery salmon to compete with wild salmon for scarce habitat and food resources.

3.) Hatchery salmon damage wild salmon when hatcheries artificially boost salmon populations in an area, which then attracts more predators that then prey on both hatchery and wild salmon.

4.) Hatchery salmon damage wild salmon when

hatchery salmon actually chase down and prey on juvenile wild salmon.

5.) Hatchery salmon damage wild salmon because when hatchery production increases, so does fishing effort and catch by commercial and recreational user groups, which then naturally causes increased mortality for both hatchery and wild salmon.

6.) Hatchery salmon damage wild salmon when hatchery facilities directly damage the surrounding environment by blocking wild salmon passage to upstream spawning habitats.

7.) Hatchery salmon damage wild salmon when hatchery salmon discharge contaminated bacteria, pathogenic fungi, parasites, and medical or chemical treatments into their environment.

8.) Hatchery salmon damage wild salmon when hatcheries intentionally kill wild salmon for hatchery broodstock.

9.) Hatchery salmon damage wild salmon by increasing the risk to wild salmon when hatchery diseases and pathogens are amplified and spread throughout the environment along with the release of hatchery contaminated water.

In many cases hatchery environmental damage is cumulative and proportional to the amount of hatchery salmon relative to wild salmon. The bottom line here becomes one of watching wild salmon populations continue to decline while seeing hatchery production dramatically increase. That increased hatchery production then impacts the few remaining wild salmon populations even more in a never-ending and increasing cycle of wild salmon destruction.

I claimthere is overwhelming evidence that hatchery salmon are NOT beneficial to the Alaska public because they definitely jeopardize natural or wild fisheries resources.

Title 16, Chapter 10 Section 400, G specifically states that the ADF&G Commissioner is required to ONLY grant hatchery permits "if a permit will result in substantial public benefit and not jeopardize a natural fisheries resource."

I find that many Alaska salmon hatcheries are currently jeopardizing Alaska's wild or natural fisheries resources and should never of had permits issued to them.

I claim that these hatchery salmon are destroying Alaska's wild salmon fisheries DNA with hatchery salmon DNA.

The above issues are evidence that current Alaska salmon hatcheries are not in compliance with (Title 16, Chapter 10 Section 400, G) requirement for the ADF&G Commissioner to only issue hatchery permits "if a permit will result in substantial public benefit and not jeopardize a natural fisheries resource." I find that Alaska's current and permitted salmon hatcheries do NOT benefit public fisheries in anyway because they actually work to eventually destroy those public fisheries.

I therefore request that all of these current or future Alaska salmon hatchery permits be immediately revoked and not reissued.

Reference (a) Involvement of Hormones In Olfactory Imprinting and Homing In Chum Salmon.

https://www.nature.com/articles/srep21102

Reference (b) National Research Council, Committee on Protection and Management of Pacific Northwest Anadromous Salmonids, Upstream: Salmon and Society in the Pacific Northwest 304 (National Academies Press 1996).

https://nap.nationalacademies.org/read/4976/chapter/14

Reference (c) The Crucial Role of Genome-Wide Genetic Variation In Conservation

https://www.pnas.org/doi/10.1073/pnas.2104642118.

Donald Johnson

[redacted]

Soldotna Alaska [redacted]

[redacted]

[redacted]

Submitted by: Penelope Haas, Kachemak Bay Conservation Society

Community of Residence: Homer

Comment:

Hatchery Committee:

Thank you all for your service to the State of Alaska and our proud fisheries.

Please consider the attached science regarding wide-ranging impact of large-scale hatchery production. We are only able to attach one document here, but will try to send additional scientific papers via email.

The data on the effects of competition and predation of hatchery fish on wild species of salmon, and other wild fishes in the nearshore and marine environment indicate that our fisheries are not being managed for maximum sustained yield or in a precautionary manner, as mandated by statute and policy. There is a real likelihood that our hatchery permits are hurting other species, such as shrimp, crab, and herring, as well as our wild salmon stocks (not to mention wild salmon prices). This is unacceptable. We encourage you to take meaningful steps to protect our rich coastal ecosystem and the rich and diverse fisheries it supports. Alaska must fulfill its promise to manage fisheries in a precautionary manner, prioritizing and protecting wild stocks, and for managing for maximum sustained yield.

Steps that could be taken include requiring both use of existing research and new research on impacts to species in the near-shore environment near hatchery releases, selecting genetics for hatchery production that are either earlier or later than most wild runs, reducing permitted releases to a number that is roughly proportional to wild runs--as was the original intent of Alaska's hatchery program, requiring at least two biologists with a background in hatchery-wild interactions to sit on all Regional Planning Teams, stopping all out-of-region straying (eg straying of PWS fish into LCI).

Thank you again for your service.

Penelope Haas

Vice-President,

Kachemak Bay Conservation Society

Effects of Hatchery-Origin Pink Salmon On Ecosystems and Other Pacific Salmon:

An Annotated Bibliography

Prepared by

CM Hersh

Consulting Aquatic Biologist Portland, OR waterhersh@gmail.com

For Cook Inletkeeper Homer, AK

www.inletkeeper.org

July 2018

Agler, B.A., G.T. Ruggerone, L.I. Wilson, and F.J. Mueter. 2013. Historical growth of Bristol Bay Agler, B.A., G.T. Ruggerone, L.I. Wilson, and F.J. Mueter. 2013. Historical growth of Bristol Bay and Yukon River, Alaska chum salmon (*Oncorhynchus keta*) in relation to climate and inter-and intraspecific competition. Deep-Sea Res II 94, 165-177.

This study of Bristol Bay and Yukon River adult chum salmon scales from 1965 through 2006 showed that increased growth was associated with higher regional ocean temperatures but slower growth associated with wind mixing and ice cover. Lower third-year growth was associated with high abundance of Asian chum and warmer sea surface temperatures (SST) in the Gulf of Alaska. High abundances of Russian pink salmon was also associated with lower third-year growth but the effects were smaller than those shown for high abundance of Asian chum and warmer GOA SST.

Amoroso, R. O., M. D. Tillotson, and R. Hilborn. 2017. Measuring the net biological impact of fisheries enhancement: Pink Salmon hatcheries can increase yield, but with apparent costs to wild populations. Canadian Journal of Fisheries and Aquatic Sciences 74:1233–1242.

This research estimated the net effect of the largest hatchery program in North America, the Prince William Sound pink salmon. Using other Alaska regions as reference sites (Kodiak, SE Alaska, and southern Alaska Peninsula), the authors used catch data from before establishment of hatchery programs (1960-1976) and after (1988-2011). The reference sites all had smaller programs than PWS (with no southern Alaska Peninsula pink hatchery program). Post late1970s climate regime shift, all regions had higher catches, with PWS having the greatest increase. Changes in wild salmon abundance were estimated for each region. Hatchery releases did not appear to decrease year-to-year variability in catches. No net positive effects (that is, taking into account the cost of the hatchery programs and reduced wild abundance) from the hatchery programs were detected for in Kodiak or SEAK. In PWS, the net effect was an increase in catch by 28%, lower than that estimated by other studies. This does not take into account other negative effects (e.g., other ecosystem effects, smaller size of returning fish), so any increases in hatchery programs should be done with a full accounting of risks and benefits.

Armstrong, J.L., Myers, K.W., Beauchamp, D.A., Davis, N.D., Walker, R.V., Boldt, J.L., Piccolo, J.J., Haldorson, L.J. and J.H. Moss. 2008. Interannual and spatial feeding patterns of hatchery and wild juvenile pink salmon in the Gulf of Alaska in years of low and high survival. Transactions of the American Fisheries Society, 137(5), pp.1299-1316.

This research compared hatchery and wild pinks in PWS and the northern coastal Gulf of Alaska (CGOA) with regard to their summer diets and feeding patterns (e.g., prey composition) in 1999-2004 (encompassing both high- and low-survival years). Hatchery and wild pink salmon had similar diets both during their residence in PWS and after they initially migrate to the CGOA. This lack in difference means that PWS hatchery pink can compete with wild fish for the available prey. Also, it appears that faster-growing fish can migrate from PWS earlier in summer and take advantage of better feeding opportunities in the CGOA.

Atcheson, M. E., K. W. Myers, N. D. Davis, and N. J. Mantua. 2012. (abs) Potential trophodynamic and environmental drivers of steelhead (*Oncorhynchus mykiss*) productivity in the North Pacific Ocean. Fisheries Oceanography 21:321–335.

“Information on prey availability, diets, and trophic levels of fish predators and their prey provides a link between physical and biological changes in the ecosystem and subsequent productivity (growth and survival) of fish populations. In this study two long- term data sets on summer diets of steelhead (*Oncorhynchus mykiss*) in international waters of the central North Pacific Ocean (CNP; 1991–2009) and Gulf of Alaska (GOA; 1993–2002) were evaluated to identify potential drivers of steelhead productivity in the North Pacific. Stable isotopes of steelhead muscle tissue were assessed to corroborate the results of stomach content analysis. We found the composition of steelhead diets varied by ocean age group, region, and year. In both the GOA and CNP, gonatid squid (*Berryteuthis anonychus*) were the most influential component of steelhead diets, leading to higher prey energy densities and stomach fullness. Stomach contents during an exceptionally warm year in the GOA and CNP (1997) were characterized by high diversity of prey with low energy density, few squid, and a large amount of potentially toxic debris (e.g., plastic). Indicators of good diets (high proportions of squid and high prey energy density) were negatively correlated with abundance of wild populations of eastern Kamchatka pink salmon (*O. gorbuscha*) in the CNP. In conclusion, interannual variations in climate, abundance of squid, and density- dependent interactions with highly- abundant stocks of pink salmon were identified as potential key drivers of steelhead productivity in these ecosystems. Additional research in genetic stock identification is needed to link these potential drivers of productivity to individual populations.”

Azumaya, T., and Y. Ishida. 2000. Density interactions between Pink Salmon (*Oncorhynchus gorbuscha*) and Chum Salmon (*O. keta*) and their possible effects on distribution and growth in the North Pacific Ocean and Bering Sea. North Pacific Anadromous Fish Commission Bulletin 2:165–174.

Data from Japanese salmon research vessels from 1972-1998 were analyzed to evaluate the long-term spatial and temporal distribution of chum and pink salmon. Chum salmon distribution varied out-of-phase with the odd-even differences in pink salmon abundance (pinks having higher abundance in odd years). Chum salmon growth was not directly affected by pink salmon abundance but was affected by chum salmon abundance (higher abundance = slower growth), indicating that intra-species competition was more important than inter-species competition. Dietary (stomach content) research would shed more light onto the importance of inter-specific competition.

Batten, S. D., G. T. Ruggerone, and I. Ortiz. In press. Pink Salmon induce a trophic cascade in plankton populations in the southern Bering Sea and around the Aleutian Islands. Fisheries Oceanography. DOI: 10.1111/fog.12276.

This study examined time series (2000-2014) of phytoplankton and copepod abundances around the Aleutian Islands and the southern Bering Sea and compared those numbers with pink salmon abundances, which were eight times higher in odd years than in even (2000-2012). In 2013 (odd year), the abundance was 73% lower than previous odd years and the next year, pink abundance was relatively high (although lower than the average odd year abundance). There are opposing biennial patterns in abundances of large phytoplankters and copepods relative to pink salmon abundances: in odd years, pink salmon abundance and large diatom abundance is high, while copepod (prey of pink salmon and grazer of diatoms) abundance is low. These associations were stronger than comparisons to "stanzas", the 4-6 year cycle of warm or cold temperatures found in the Bering Sea.

Beamish, R. J., R.M. Sweeting, T.D. Beacham, K.L. Lange, and C.M. Neville. 2010. A late ocean entry life history strategy improves the marine survival of Chinook salmon in the Strait of Georgia. NPAFC Doc. 1282. 14 pp. (Available at www.npafc.org).

One aggregated population of Georgia Strait Chinook salmon (South Thompson drainage of the Fraser River) has increased in recent years while most other Georgia Strait Chinook populations have declined. The South Thompson Chinook juveniles are not abundant in Georgia Strait in July but are by September, and by November are moving to sea, probably through the Strait of Juan de Fuca. Harrison River sockeye salmon are also a "late-entry" juvenile and doing better than others. It is theorized that high populations of pink and chum salmon present in Georgia Strait at the same time as earlier-entry populations of Chinook and sockeye are the reason why these populations of Chinook and sockeye are not doing as well as late-entry populations. Focused research is needed.

Brenner, R. E., S. D. Moffitt, and W. S. Grant. 2012. Straying of hatchery salmon in Prince William Sound, Alaska. Environmental Biology of Fishes 94:179–195.

The authors (all ADFG employees) sampled streams in PWS to determine stray rates using data gathered in two time periods, 1997-1999 and 2008-2010. Percentages of hatchery pink salmon in spawning areas varied from 0 to 98%. Most (77%) of spawning locations had pink salmon from three or more hatcheries, and the escapement at 51% of locations consisted of more than 10% hatchery pink salmon during at least one year surveyed. Application of an exponential decay model indicates that many streams would have over 10% hatchery pinks, even if distant from a hatchery. Besides the implication of genetic effects on wild populations, the authors express concern that estimates of wild escapement may be inflated by the assumption that all fish seen in weirs or in aerial surveys are assumed to be wild.

Debertin, D. J., J. R. Irvine, C. A. Holt, G. Oka, and M. Trudel. 2017. Marine growth patterns of southern British Columbia Chum Salmon explained by interactions between density-dependent competition and changing climate. Canadian Journal of Fisheries and Aquatic Sciences 74:1077–1087.

The authors report the results of a study of 39 years of scale growth measurements of chum salmon from Big Qualicum River (BC) in regard to climate variation and competition with other

North American salmon (chum, sockeye, and pink). When the North Pacific Gyre Oscillation was positive, growth increased (attributed to higher primary production). Growth at all ages was negative when the combined biomass of NA salmon was high. Competition effects increased when the NPGO was more positive and the Pacific Decadal Oscillation was more negative. The authors recommend the use of biomass estimates over abundance estimates to take into account inter-species variations and the observed trend of smaller returning salmon. The authors believe this study is the first to use a longitudinal model to examine growth versus the interactions of climate and density dependent competition. If their results are typical of wild salmon populations, reductions in hatchery releases should be considered.

Grant, W.S., 2012. Understanding the adaptive consequences of hatchery-wild interactions in Alaska salmon. Environmental Biology of Fishes, 94(1), pp.325-342.

This is a review of hatchery-wild interactions with an emphasis on genetic effects to wild populations. While the author acknowledges that some may argue that studies conducted elsewhere may not be applicable to Alaskan salmon populations for a variety of reasons, the near-universal result that introgression between hatchery fish and wild fish leads to reduced fitness in wild populations is a fact that must be considered when evaluating hatchery programs. The adaptive potential of wild populations must be preserved as a buffer against climate change and diseases.

Gritsenko A.V. and E.N. Kharenko. 2015 (abs). Relation between biological parameters of Pacific salmons of the genus Oncorhynchus and their population dynamics off the northeastern Kamchatka Peninsula. J Ichthyol 55:430–441.

“Results are provided of a 7-year study of biological parameters in females of three Pacific salmons of the genus *Oncorhynchus* (pink salmon *O. gorbuscha*, chum salmon *O. keta*, and sockeye salmon *O. nerka*) in the Olyutorsky and Karaginsky gulfs, Bering Sea. Abundance of the pink salmon is identified as the main determining factor of the interannual dynamics of maturity index in female Pacific salmon in coastal waters. Maturity index rises at high levels of abundance as a result of differently directed changes in two parameters: decreasing body weight and increasing ovary weight. In female chum salmon, maturity index depends on the age structure of the population and body weight dynamics of different age groups, factors influenced by high abundance of some pink salmon generations, and does not depend on the abundance of spawning chum salmon. The revealed association between pink salmon and sockeye salmon in dynamics of their biological parameters may result from the similarity of their diets; during the last year of fattening in the sea, the sockeye salmon is affected by the pink salmon, the most abundant of the three species. The interannual variation of biological parameters in pink salmon and chum salmon is more pronounced in Olyutorsky Gulf than in Karaginsky Gulf.”

Heard, W.R., 2012. Overview of salmon stock enhancement in southeast Alaska and compatibility with maintenance of hatchery and wild stocks. Environmental Biology of Fishes, 94(1), 273-283. PC022 5 of 24

This review of the hatchery programs of SEAK, as well as some relevant studies of wild-hatchery interactions, acknowledges that some interactions between hatchery salmon and of wild salmon are unavoidable, but concludes that “obvious adverse impacts from the current levels of hatchery releases and population trends in Alaska’s wild salmon populations are not readily evident.” The author believes that SEAK hatchery chum programs have been successful in increasing numbers for fisheries, but says that additional increases (which have been requested) should be limited to “gradual incremental steps” given concern over straying in some streams, until better information is generated on the possible impacts of hatchery programs on wild populations.

Hilborn, R. and D. Eggers. 2000. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. Transactions of the American Fisheries Society 129:333-350.

Wertheimer, A. C., W. W. Smoker, T. L. Joyce, and W. R. Heard. 2001. Comment: A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. Transactions of the American Fisheries Society 130:712–720.

Hilborn, R. and D. Eggers, 2001. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska: Response to Comment. Transactions of the American Fisheries Society 130:720–724.

Hilborn and Eggers used ADF&G catch data from four Alaska regions. The initial paper concluded that while the PWS hatchery program was successful in producing fish to be harvested, the overall increase in harvest wasn’t necessarily due to the PWS pink salmon hatchery programs, because other AK regions (with no, or geographically separated hatchery programs) experienced an increase in wild pink production. In fact, increases in pink salmon harvest in PWS occurred before large-scale hatchery programs there. Therefore, the hatchery-produced pink salmon replaced rather than augmented the wild fish. A decline in wild production in PWS was attributed to lower wild escapements and hatchery releases (the authors claim no evidence has been produced to show that the Exxon Valdez oil spill was detrimental to longterm pink salmon production).

Wertheimer et al. (2001) commented that Hilborn and Eggers vastly over-estimated wild pink production and therefore underestimated the proportion of the PWS pink harvest that could be attributed to hatchery production. They also used a longer time-series of catch data, along with other approaches to the data. Hilborn and Eggers (2001), in a response, stand by their conclusions and point out that in this case a longer time-series is not appropriate (positive changes in pink salmon habitat after the 1964 earthquake). They maintain that an increase in PWS pink production was evident before large-scale hatchery releases took place, and that hatchery releases replaced rather than augmented wild production.

Holt, C.A., Rutherford, M.B, and R.M. Peterman. 2008 (abs). International cooperation among nation-states of the North Pacific Ocean on the problem of competition among salmon for a common pool of prey resources. Marine Policy 32, 607–617.

“A common-pool problem in the North Pacific Ocean that remains largely ignored in international policy is competition for prey resources among salmon populations (*Oncorhynchus* spp.) from different countries. Hatcheries release large abundances of juvenile salmon into the North Pacific and the resulting decrease in mean body size of adult wild and hatchery salmon may lead to reductions in benefits. We examine incentives and disincentives for cooperation among nation-states on this issue. We recommend that either a new international organization be created or that amendments be made to the mandate and powers of an existing organization. The resulting organization could encourage collective action to reduce competition among salmon from different nations by using side-payments to change the incentive structure, by establishing a multi-national scientific assessment team to create a common frame of reference for the problem, and by implementing policy prescriptions."

Irvine, J. R., and M. Fukuwaka. 2011. Pacific salmon abundance trends and climate change. ICES Journal of Marine Science 68:1122–1130.

This study compared abundance of five species of salmon (represented by commercial catch data) in both Asia and North America with five climate regimes (1925-1946, 1946-1976, 19771988, 1989-1998, and 1999-2009). Higher catches in the western north Pacific are attributed to hatchery programs (both releases and better hatchery technology resulting in healthier fry). The results confirm earlier studies indicating regime "shifts" in 1947, 1977, and 1989. Higher catches of pink and chum since 1990 in all regions have occurred and can be attributed to hatchery releases in only the northwestern Pacific region because only Russia has significantly increased hatchery releases.

Jeffrey, K. M., I. M. Coté, J. R. Irvine, and J. D. Reynolds. 2016. Changes in body size of Canadian Pacific salmon over six decades. Canadian Journal of Fisheries and Aquatic Sciences 74:191–201.

Commercial catch data for five salmonid species from 1951-2012 were analyzed along with climatic variables (four Pacific Ocean indices), latitude of catch, and total salmonid biomass to determine if size of caught fish has changed, and if so, what variables are associated with the changes. Catch data from the least-selective method were used to minimize any size-selective gear bias. Analyses from the earlier part of the catch dataset agree with the results of previous research. The results from this study indicate changes in body size over time from oceanic changes as well as density-dependent effects. Pink salmon size declined initially but has changed relatively little over the last 20 years. Body size of Chinook, chum, and coho was most influenced by the total biomass of sockeye, chum, and pink salmon in the Gulf of Alaska. Inclusion of Asian chum salmon did not improve model performance. Pink salmon size was reduced as total biomass increased, with odd-years (higher abundances of pinks) showing a more pronounced effect. Chinook and coho body size increased with total salmon biomass,possibly reflecting better overall environmental conditions, given the lack of overlap in diet preferences between Chinook and coho vs. the other three species.

Jenkins, E.S., Trudel, M., Dower, J.F., El-Sabaawi, R.W. and A. Mazumder. 2013. Density-dependent trophic interactions between juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) in coastal marine ecosystems of British Columbia and Southeast Alaska. North Pacific Anadromous Fish Commission Technical Report 9:136-138.

This study employed stable isotopes to determine the degree of dietary overlap between juvenile chum and juvenile pink salmon (the southern end of SEAK to the northern end of Vancouver Island), and how that is affected by temperature, abundance (juvenile salmon), and prey availability. Juveniles were collected 2000-1 and 2004-5. The niches of pink and chum overlapped more when abundance was high and prey availability was low. The size difference between the species was not significantly correlated with overlap. It appears that when competition was greater (fewer prey items) both species became less selective and therefore they overlapped more. Hatchery releases resulting in greater numbers of juveniles may thus increase competition.

Kaev, A. M. 2012 (abs). Wild and hatchery reproduction of Pink and Chum salmon and their catches in the Sakhalin-Kuril region, Russia. Environmental Biology of Fishes 94:207–218.

“In the Sakhalin-Kuril region hatchery culture of pink and chum salmon is of great importance compared to other regions of the Russian Far East. During the last 30 years the number of hatcheries increased two-fold, and significant advances were made in hatchery technologies. As a result, chum salmon capture in regions where hatcheries operate (southwestern and eastern Sakhalin coasts, and Iturup Island) was 9 times as high during 2006–2010 than during 1986–1990, whereas wild chum salmon harvest markedly declined. Recent dynamics in pink salmon catch appear to track trends in natural spawning in monitored index rivers, suggesting natural-origin pink salmon play a dominant role in supporting the commercial fishery. It remains uncertain as to whether hatcheries have substantially supplemented commercial catch of pink salmon in this region, and I recommend continued research (including implementing mass marking and recovery programs) before decisions are made regarding increasing pink salmon hatchery production. Location of hatcheries in spawning river basins poses problems for structuring a management system that treats hatchery and wild populations separately. Debate continues regarding the existence and importance of density-dependent processes operating in the ocean environment and the role hatcheries play in these processes. Loss of critical spawning habitat for chum salmon in the Sakhalin-Kuril region has lead to significant declines in their abundance. I conclude by recommending increases in releases of hatchery chum salmon numbers in the region to help recover depressed wild populations and provide greater commercial fishing benefits in the region.”

Kaev, A. M., and J. R. Irvine. 2016. Population dynamics of Pink Salmon in the Sakhalin-Kuril region, Russia. North Pacific Anadromous Fish Commission Bulletin 6:297–305. PC022 8 of 24 I the central Bering Sea. Mar Ecol Prog Ser 478:211–221.

Run size (catch plus escapement) data and numbers of hatchery and wild fry were estimated for eight areas around Sakhalin Island and the southern Kuril islands over the 1975-2015 period. Marine survival was also indexed by dividing run size by the number of fry for each area. Odd-year runs are greater than even-year runs, with the difference increasing over time. The recent increase in pink salmon catch does not appear to be the result of hatchery releases (greater numbers of fry) but instead is the result of environmental conditions in early life stages. Increasing size of adults is attributed to conditions in the common area where pinks (from a number of investigated areas) mingle later in life.

Kaga T., Sato S., Azumaya T., Davis N.D., and M-a. Fukuwaka. 2013. (abs) Lipid content of chum salmon Oncorhynchus keta affected by pink salmon *O. gorbuscha* abundance in the central Bering Sea. Mar Ecol Prog Ser 478:211–221.

"To assess effects of intra- and inter-specific interactions on chum salmon in the central Bering Sea, chum salmon lipid content was analyzed as a proxy for body condition. We measured the lipid contents of 466 immature individuals collected during summer from 2002 to 2007. Individual variation in log-transformed lipid content was tested using multiple regression analysis with biological and environmental variables. A regression model that included chum salmon fork length and pink salmon CPUE (number of fish caught per 1500 m of gillnet) was the most effective in describing variation in lipid content. Path analysis showed that the negative effect of pink salmon CPUE was stronger than the effect of chum salmon CPUE on chum salmon lipid content. Stomach content analysis of 283 chum salmon indicated non-crustacean zooplankton (appendicularian, chaetognath, cnidarian, ctenophore, polychaete, and pteropod) was higher under conditions of high pink salmon CPUE. Increased consumption of non-crustacean zooplankton containing a low lipid level could lower the lipid content of chum salmon. Thus, chum salmon lipid content could be affected directly by their shift in prey items and indirectly by interspecific competition with pink salmon."

Malick, M.J. and S.P. Cox. 2016. Regional-scale declines in productivity of pink and chum salmon stocks in western North America. PloS one, 11(1), p.e0146009.

Historical population data from 99 wild chum and pink stocks in WA, BC, and AK were assessed, and trends in productivity noted. While productivity of some pink stocks in Alaska declined over time, others increased. The authors believe that the productivity of pink and chum stocks in western North America is driven by common processes "operating at the regional or multi-regional spatial scales." The effects are not constant but can change over time. While some environmental factors operating at the regional scale (and thus, are potential drivers of productivity) were identified, they were not investigated. "Mechanisms that operate over these spatial scales may include freshwater or marine processes such as disease or pathogens, changes in stream flow and stream temperature, competition with abundant hatchery salmon, or shifts in oceanographic condition such as the timing of the spring phytoplankton bloom or sea surface temperature." They found that most chum and some pink salmon stocks declined, in contrast to Stachura et al. (2014) and other reports. PC022 9 of 24

Malick, M.J. 2017. Multi-scale environmental forcing of Pacific salmon population dynamics. PhD thesis, Simon Fraser University, School of Resource and Environmental Management, Burnaby, BC. http://summit.sfu.ca/system/files/iritems1/17425/etd10171_MMalick.pdf

This researcher considered variable environmental factors (e.g., phytoplankton phenology, horizontal and vertical transport patterns) and their influence on salmon productivity (*see* Malick and Cox 2016). The thesis also contains a section on policy analysis where the author outlines the problems that arise from management of migratory anadromous fish species, e.g., multiple national and sub-national polities, the fact that management decisions of one entity can impact the resources of another, and incomplete use of real-time data to make management decisions.

The author believes that an “international ecosystem synthesis group” could integrate information from various managers and provide “strategic management advice” based on their synthesis of the various information they receive. Because of the complexity of managing Pacific salmon, a multi-faceted approach is warranted.

Manhard, C.V., Joyce, J.E., Smoker, W.W. and A.J. Gharrett. 2017. Ecological factors influencing lifetime productivity of pink salmon (*Oncorhynchus gorbuscha*) in an Alaskan stream. Can. J. Fish. Aquatic Sci. 74(9), 1325-1336.

A study of the pink salmon populations (both even- and odd-years) of a short (323 m) lake-outlet stream indicated that early marine survival was the primary determinant of overall productivity. An overall downward trend in productivity was associated with an observed decline in freshwater spawning habitat quality. A nearby hatchery released large numbers of pink fry 1988-2002 but no difference in marine survival was noted between that time period and afterwards (with no hatchery releases). “[W]hile commercial harvest and hatchery straying do occur, the effects of these processes on adult recruitment are more likely to be stochastic than deterministic.”

Morita, K. 2014. Japanese wild salmon research: toward a reconciliation between hatchery and wild salmon management. North Pacific Anadromous Fish Commission Newsletter 35:4–14.

This English-language article summarizes some Japanese-language literature on wild and hatchery salmon management in Japan. The author believes that wild salmon productivity is higher and more important than many people believe. Most large rivers in Japan have hatchery programs, and protecting wild populations is a way to guarantee continued success of the hatchery programs (e.g., genetic reserve, source of broodstock in integrated programs). Integrated hatchery programs are probably the best management option in highly-developed, hatchery-dominated Japanese watersheds.

Morita, K., S. H. Morita, and M. Fukuwaka. 2006. (abs) Population dynamics of Japanese Pink Salmon (*Oncorhynchus gorbuscha*): are recent increases explained by hatchery programs or climatic variations? Canadian Journal of Fisheries and Aquatic Sciences 63:55–62.

“Hatchery programs involving the mass release of artificially propagated fishes have been implemented worldwide. However, few studies have assessed whether hatchery programs actually increase the net population growth of the target species after accounting for the effects of density dependence and climatic variation. We examined the combined effects of density dependence, climatic variation, and hatchery release on the population dynamics of Japanese pink salmon (*Oncorhynchus gorbuscha*) from 1969 to 2003. The population trends were more closely linked to climatic factors than to the intensity of the hatchery programs. The estimated contributions of hatchery-released fry to catches during the past decade are small. We concluded that the recent catch increases of Japanese pink salmon could be largely explained by climate change, with increased hatchery releases having little effect."

Moss, J.H., Beauchamp, D.A., Cross, A.D., Myers, K.W., Farley Jr, E.V., Murphy, J.M. and Helle, J.H., 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Transactions of the American Fisheries Society 134(5)1313 1322.

Juvenile pink salmon originating from PWS hatcheries were sampled in PWS and the Gulf of Alaska in 2001 to identify the hatchery of origin and determine if larger, faster-growing pink salmon had higher survival rates. Adult pink salmon were also sampled in PWS (at cost-recovery fishing sites) in 2002 for scale analysis to determine if size-selective mortality was occurring after the juvenile sampling (through scale analyses). Both juveniles and adults showed high growth rates in June but lower in July. In July 2001, far fewer juveniles were caught in the Gulf of Alaska than in PWS, although catch rates were similar in August and September, a time when elevated growth rates were also seen. This indicates a bottleneck in growth for PWS pink salmon in July and possible density-dependent effects. The results also indicate that juveniles must attain a critical size in order to survive over the winter and bottlenecks in growth could prevent juveniles from attaining that size.

Myers, K.W., R.V. Walker, N.D. Davis, and J.L. Armstrong. 2004. Diet overlap and potential feeding competition between Yukon River chum salmon and hatchery salmon in the Gulf of Alaska in summer. Final Report to the Yukon River Drainage Fisheries Association. SAFS-UW-0407. School of Aquatic and Fisheries Sciences, University of Washington, Seattle. 63 p.

The overlap in diets and the potential for feeding competition distribution between Yukon River chum salmon and hatchery chum, pink, and sockeye from Asia and Alaska were investigated in summers in the Gulf of Alaska from 1993 through 2003 by examining almost 5000 salmon stomach contents. Inter-specific overlap in salmon diets was low to moderate, however the quality of chum salmon diets was lower than the diets of all sizes of pink salmon and large-sized sockeye salmon. There was a higher potential for competition between Yukon River chum and Alaska hatchery pink salmon in the northeast region of the GOA than in the southeast region. Stomach contents analyses were consistent with previous studies that showed that chum salmon switch their diets to lower-calorie prey when pink salmon abundance is high. The results lead to hypotheses that competition with hatchery salmon in the GOA may reduce the growth of immature Yukon River chum, especially when adverse ocean and climate conditions limit prey abundance, and that the reduction in growth may reduce survival by various mechanisms such as increased predation, decreased lipid storage, and increases in disease and parasites.

Ohnuki, T., K. Morita, H. Tokuda, Y. Oksutaka, and K. Ohkuma. 2015. (abs) Numerical and economic contributions of wild and hatchery Pink Salmon to commercial catches in Japan estimated from mass otolith markings. North American Journal of Fisheries Management 35:598–604.

"Evaluating the contribution of wild and hatchery fish to a fishery is essential to understand economic feasibility as well as the impact of hatchery fish on the ecosystem. However, a precise estimate of this contribution is often difficult to obtain, particularly when hatchery and wild fish are mixed in the catch. In this study, we quantified the contribution of hatchery and wild Pink Salmon *Oncorhynchus gorbuscha* to the mixed- stock commercial fishery in Japan by identifying the ratio of otolith- marked hatchery fish to unmarked and presumably wild fish. The contribution of hatchery fish to the total coastal catch of Pink Salmon in Japan was estimated to be 16.6% and 26.4% in 2011 and 2012, respectively. Thus, the majority of the commercial salmon catch originated from naturally spawned wild fish. Economic yield per release by Japanese hatcheries was 2.2 yen (¥2.2) (≈US$0.022) and ¥1.5 in 2011 and 2012."

Pearson, W.H., Deriso, R.B., Elston, R.A., Hook, S.E., Parker, K.R. and J.W. Anderson. 2012. Hypotheses concerning the decline and poor recovery of Pacific herring in Prince William Sound, Alaska. Reviews in Fish Biology and Fisheries *22*(1), pp.95-135.

In 1993, the Pacific herring stock of Prince William Sound dramatically declined: the stock was about 20% of the predicted record-breaking biomass. The authors examine a number of studies advancing a number of different hypotheses on the reason(s) for the observed decline, and could find no evidence that any of the following have led to either the decline or the poor recovery of PWS herring: oil exposure from the *Exxon Valdez* oil spill; harvest effects; spawning habitat loss; the spawn-on-kelp fishery; disease. Instead, the authors attribute the decline to poor nutrition that began in the mid-1980s and reached a low in 1993. Disease was a secondary response. The fact that the recovery of PWS Pacific herring has been poor despite fishery restrictions is attributed to oceanic conditions outside of PWS and juvenile pink salmon releases (pink salmon predation on age-0 herring and food competition between pink salmon and age-1 herring). Multi-species or ecosystem-based management, rather than single-species management is recommended.

Peterman, R. M., C. A. Holt, and M. R. Rutherford. 2012. The need for international cooperation to reduce competition among salmon for a common pool of prey resources in the North Pacific Ocean. North Pacific Anadromous Fish Commission Technical Report 8:99–101.

These researchers accept that density-dependent competition is occurring in the north Pacific and is caused by hatchery programs. Increasing hatchery releases may result in a diminishing return on the costs of hatchery programs, but if competition increases sufficiently wild populations will also be affected as well. The situation is that the "common-pool" resource that is the north Pacific is subject to the classic "Tragedy of the Commons". The North Pacific Anadromous Fish Commission, after amendments to its mandate, is the body best equipped to deal with the situation. The NPAFC should "identify and implement collective actions to prevent further increases in competition among salmon from different nations or even reduce it" as "[a]ction on this problem of multinational grazing of salmon food is long overdue." Action needs to be taken before a crisis occurs, such as climatic changes that may limit overall salmon productivity, and will likely lead to a knee-jerk call for more (ultimately counter-productive) hatchery releases.

Prince William Sound Science Center studies on hatchery-wild interaction:

Gorman, K., McMahon, J., Rand, P., Knudsen, E., and D.R. Bernard. 2018. Interactions of wild and hatchery pink salmon and chum salmon in Prince William Sound and Southeast Alaska. Final report for 2017. Prince William Sound Science Center, Cordova, AK.

Gorman, K., McMahon, J., Rand, P., Knudsen, E., and D.R. Bernard. 2016. Interactions of wild and hatchery pink salmon and chum salmon in Prince William Sound and Southeast Alaska. Progress Report for 2016. Prince William Sound Science Center, Cordova, AK.

Knudsen, E., Buckhorn, M., Gorman, K., Rand, P., Roberts, M., Adams, B., O'Connell, V. and D.R. Bernard. 2015. Interactions of wild and hatchery pink salmon and chum salmon in Prince William Sound and Southeast Alaska. Final Progress Report for 2014. Prince William Sound Science Center, Cordova, AK; Sitka Sound Science Center, Sitka, AK.

Knudsen, E., Buckhorn, M., Gorman, K., Crowther, D., Froning, K., Roberts, M., Marcello, L., Adams, B., O'Connell, V. and D.R. Bernard. 2015. Interactions of wild and hatchery pink salmon and chum salmon in Prince William Sound and Southeast Alaska. Final Progress Report for 2013. Prince William Sound Science Center, Cordova, AK; Sitka Sound Science Center, Sitka, AK.

Knudsen, E., Rand, P., Gorman, K., McMahon, J., Adams, B., O'Connell, V. and D.R. Bernard. 2016. Interactions of wild and hatchery pink salmon and chum salmon in Prince William Sound and Southeast Alaska. Progress Report for 2015. Volume 1. Prince William Sound Science Center, Cordova, AK; Sitka Sound Science Center, Sitka, AK.

Prince William Sound Science Center. 2013. Interactions of Wild and Hatchery Pink and Chum Salmon in Prince William Sound and Southeast Alaska. Annual Report 2012. For Alaska Department of Fish and Game Contract IHP-13-013

These reports were generated as part of a research effort sponsored by ADF&G. The purposes are to: "1) further document the degree to which hatchery pink and chum salmon straying is occurring; 2) assess the range of interannual variability in the straying rates; and, 3) determine the effects of hatchery fish spawning with wild populations on the fitness of wild populations." Ocean sampling was conducted in 2013-2015 in nine locations near the entrances to PWS to determine wild or hatchery origins of pink and chum in PWS (via examination of otoliths). Stream studies were also conducted to determine the proportion of hatchery-origin fish on the spawning grounds and an investigation into the relative survival of the offspring of naturally spawned fish (wild and hatchery-origin). These reports have reported basic data with no advanced statistical or biological analyses. Proportions of hatchery-origin pink salmon on spawning grounds range from zero to over 80% in some PWS streams.

Riddell, B., M. Bradford, R. Carmichael, D. Hankin, R. Peterman, and A. Wertheimer. 2013. Assessment of Status and Factors for Decline of Southern BC Chinook Salmon: Independent Panel's Report. Prepared with the assistance of D.R. Marmorek and A.W. Hall, ESSA Technologies Ltd., Vancouver, B.C. for Fisheries and Oceans Canada (Vancouver. BC) and Fraser River Aboriginal Fisheries Secretariat (Merritt, BC). xxix + 165 pp. + Appendices. Available at www.psc.org/publications/ workshop-reports/southern-bc-chinook-expert-panel-workshop. Accessed June 5, 2018

Evidence presented at a workshop discussing the decline of southern BC chinook did not support the hypothesis that pink salmon abundance had a role in the decline of southern BC Chinook. There was no apparent odd- and even-year pattern in Chinook survival (which would thought to be present if pinks were having an effect), although some recent literature (referenced in this report) indicated that there may be an effect.

Ruggerone, G.T., and J.R. Irvine. 2018. Number and biomass of natural- and hatchery-origin pink, chum, and sockeye salmon in the North Pacific Ocean, 1925-2015. Mar Coast Fish 10:152-168.

Abundance and biomass data are presented for pink, chum, and sockeye for the time period 1925-2015; this is the most comprehensive tally to date. These species are at an all-time high, as the late 1970s regime shift benefited these species. If immature salmon are included, the north Pacific contains 5×10^6 metric tons of these species. Pink salmon were the most abundant adult fish of the three (67%) and were 48% of the total biomass (chum 20% and 35%; sockeye 13% and 17%, respectively). Alaska produced 39% of the pink salmon with Japan and Russia producing most of the remainder. Hatcheries accounted for 15% of the pink salmon production (Alaska produced 68% of hatchery pink salmon) although hatchery fish dominated in some regions, such as PWS and SEAK. In the period 1990-2015, hatchery fish composed 40% of the total biomass in the north Pacific, which may be at its carrying capacity. Density-dependent effects are occurring although hatchery-wild interaction effects are difficult to quantify. Management agencies should mark hatchery fish and estimate hatchery- and natural-origin fish in their catch and escapement data to aid focused research efforts.

Ruggerone, G.T., Agler, B.A., Connors, B.M., Farley Jr., E.V., Irvine, J.R., Wilson, L.I. and E.M. Yasumiishi. 2016. Pink and sockeye salmon interactions at sea and their influence on forecast error of Bristol Bay sockeye salmon. North Pacific Anadromous Fish Commission Bulletin 6:349–361. doi:10.23849/npafcb6/349.361 (Available at http://www.npafc.org).

Ruggerone et al. (2010) showed that abundance of sockeye salmon in western and central Alaska tended to be positively correlated with pink salmon abundance, in contrast to more southern regions where sockeye abundance was negatively correlated with pink salmon abundance. Ocean conditions may be an overriding factor, so this research was focused on evaluation of the evidence of competition between Bristol Bay sockeye and pink salmon from Russia and central Alaska. Sockeye scales from 1965 through 2009 were evaluated for growth patterns; abundance of adult pink salmon was available in previously published literature. Growth patterns from all five BB sockeye stocks indicated a strong alternating-year growth pattern, consistent with the hypothesis that sockeye and pinks compete for food on the high seas. Sockeye growth at sea during odd-years was low; other referenced research indicated that pink and sockeye have a high diet overlap. Also, in odd-years sockeye stomach fullness was reduced. Examination of the ADF&G's sockeye salmon abundance forecasts from 19682010 indicated errors in an alternating-year pattern; a tendency for a too-high forecast in even-years, and too low in odd-years, consistent with a hypothesis that competition at sea between sockeye and pink (in the year previous to the sockeye return year) was indeed a factor but was not considered in the forecasts.

Ruggerone, G.T. and B.M. Connors. 2015. Productivity and life history of sockeye salmon in relation to competition with pink and sockeye salmon in the North Pacific Ocean. Can. J. Fish. Aquat. Sci. 72, 818–833.

The Fraser River (BC) sockeye salmon return in 2009 was the lowest in over 60 years, capping a decline that had started in the 1980s. Scientists indicated that declining productivity at sea was responsible rather than factors like spawner abundance or freshwater factors. Pink salmon abundance was identified as a possible factor due to overlapping spatial distribution in the north Pacific and diets. This research uses stock-recruitment dynamics and data from 36 sockeye salmon populations ranging from Washington State north to SEAK (18 were Fraser River drainage populations). Sea-surface temperature (SST) and farmed salmon were also considered as possible confounding factors. Results indicated that 1) during odd-years (high pink abundance), sockeye survival rates and length-at-age of returning sockeye were lower, as well as a higher proportion showing delayed maturation; 2) for all but one population (with a unique "ocean-type" life history) sockeye growth in the second year was negatively correlated with pink salmon abundance and led to lower sockeye productivity; 3) inclusion of environmental factors did not improve performance; and 4) there did not seem to be evidence that returning pink salmon preyed on out-migrating sockeye salmon. The 1970s regime shift saw an actual increase in pink salmon abundance from 200 million to 400 million; a model of pink salmon abundance and Fraser River sockeye returns predicted a reduction in Fraser River sockeye returns of approximately 5.5 million.

Ruggerone, G. T., B. A. Agler, and J. L. Nielsen. 2012. Evidence for competition at sea between Norton Sound chum salmon and Asian hatchery chum salmon. Environmental Biology of Fishes 94:149–163.

An important chum salmon population in Norton Sound, Alaska (Kwiniuk chum) has experienced reduced adult length-at-age, age-at-maturation, productivity, and abundance, corresponding with increased hatchery Asian chum salmon abundance. Analyses of the relevant data indeed show that hatchery Asian chum salmon abundance is negatively correlated with the size and age parameters, productivity, and abundance of the Kwiniuk chum. Inclusion of Asian and western Alaska wild chum salmon abundance did not improve the model. Lower productivity of Kwiniuk chum was correlated with high abundance of wild eastern Kamchatka Island pink salmon during odd-years; the effect was less than that of hatchery chum. This evidence for density-dependent effects points out the need for international cooperation on hatchery releases.

Ruggerone, G.T., Peterman, R.M., Dorner, B. and K.W. Myers. 2010. Magnitude and trends in abundance of hatchery and wild pink, chum, and sockeye salmon in the North Pacific Ocean. Mar Coast Fish 2, 306–328.

Total abundance numbers for both Asia and North America populations of chum, pink, and sockeye salmon were reconstructed from catch and spawner abundance data from 1952–2005. Pink salmon were the most abundant (70%), followed by sockeye (17%) and chum (13%). After the mid-1970s regime shift, pink and sockeye became more abundant while chum numbers decreased. Asian salmon numbers did not increase until the 1990s. Hatchery releases increased during the 1990s and early 2000s, reaching 4.5 x 10^9 juveniles/yr. Hatcheries were responsible large numbers of adult fish returning: 62% of the chum, 13% of the pink, and 4% of the sockeye in 1990-2005. Combined, wild and hatchery salmon in the same time period averaged 634 million fish, twice as many as during 1952-1975. Better data gathering and management are needed, as well as international cooperation to better manage the common waters, especially in light of possible increases in hatchery releases in the face of evidence of changing climate and density-dependent effects.

Ruggerone, G.T. and J.L. Nielsen. 2004. Evidence for competitive dominance of pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. Rev Fish Bio Fish 14, 371–390.

The alternating yearly cycle of pink salmon abundance lends itself to studies of competition with other Pacific salmon. This review article examined studies to date indicating that competition between pink salmon and other salmon is an important process negatively influencing other salmon species because pink salmon are efficient predators of the (common) prey. The authors are not aware of any studies of pink salmon being negatively affected by other Pacific salmon. Their abundance (pink salmon are the most common Pacific salmon), rapid growth, high feeding rates, and early entry combine to make pink salmon a dominant competitor. It also appears that pink salmon have been the dominant competitor in the north Pacific across multiple climate regimes.

Ruggerone, G.T., Zimmermann, M., Myers, K.W., Nielsen, J.L. and D.E. Rogers. 2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. Fish Oceanogr 12, 209–219.

The researchers hypothesized that competition between Bristol Bay sockeye and Asian pink salmon would be greater in odd-years when pink salmon abundance was generally greater. BB sockeye scale samples from 1955 to the 1990s (from variously aged fish) and fish length (from adult returns in each river system) from 1958-2000 were used to determine growth estimates. Scale growth estimates showed a distinctive alternating-year pattern as growth was typically below average in odd-years and above average in even-years for both ocean age-2 and age-3 sockeye. Lengths of adult BB sockeye were inversely related to Asian pink salmon abundance (of the previous year) for years other than the year of homeward migration. Sockeye survival also was negatively influenced by pink salmon abundance. In the years after the mid-1970's, when pink salmon abundance greatly increased, BB sockeye returns averaged a 22% reduction in the alternating years the when higher pink salmon abundance would exert greater influence. The alternating-years phenomenon is due to Asian, primarily the eastern Kamchatka pink salmon population. In the (smolt) years 1977 to 1997, the researchers estimate 59 million fewer sockeye salmon returned to BB due to the high Asian pink salmon abundance in alternating years.

Saito, T., Hirabayashi, Y., Suzuki, K., Watanabe, K. and H. Saito. 2016. Recent decline of pink salmon (O*ncorhynchus gorbuscha*) abundance in Japan. North Pacific Anadromous Fish Commission Bulletin, 6:279-296.

In-river catch data from twenty-two pink stocks from the coast of the Sea of Okhotsk were analyzed (separated into five regional groups) along with sea surface temperatures (SST). The long-term decline in pink salmon abundance is related to higher coastal SSTs which can cause decreased juvenile survival, preliminary adult mortality, and increased straying. The higher coastal SSTs can also cause a shift in migration timing, although pink salmon hatchery programs have been consciously selecting for earlier migration. No data were available to determine the proportion of wild fish in the escapement.

Schindler, D., C. Krueger, P. Bisson, M. Bradford, B. Clark, J. Conitz, K. Howard, M. Jones, J. Murphy, K. Myers, M. Scheuerell, E. Volk, and J. Winton. 2013. Arctic-Yukon-Kuskokwim Chinook salmon research action plan: Evidence of decline of Chinook salmon populations and recommendations for future research. Prepared for the AYK Sustainable Salmon Initiative (Anchorage, AK). v + 70 pp. Available at www.aykssi.org/wp-content/uploads/AYK-SSI-ChinookSalmon-Action-Plan-83013.pdf. Accessed June 5, 2018 PC022 17 of 24

The decline in AYK Chinook populations since the 1990s is discussed. All evidence (for and against) various hypotheses is summarized and research recommendations are made. The authors are careful not to be conclusive in their summary, instead stating that the hypotheses are not “statement of facts” but instead represent how the “salmon system” “may work”. One hypothesis, on anthropogenic changes to ocean conditions, includes a discussion of the evidence that hatchery releases of chum, pink, and sockeye are affecting (or not) the survival of AYK Chinook.

Shiomoto, A., Tadokoro, K., Nagasawa, K., and Y. Ishida. 1997. Trophic relations in the subarctic North Pacific ecosystem: possible feeding effect from pink salmon. Marine Ecology Progress Series, 150, 75-85.

Biomass of phytoplankton and macrozooplankton were sampled from 1985 to 1994 in the north Pacific Ocean and year-to-year variations noted. After comparing these data to pink salmon abundance data, the researchers noted that years in which the biomass of macrozooplankton was low corresponded with years when pink salmon were more abundant and phytoplankton biomass was higher. In years when pink salmon were less abundant, macrozooplankton biomass was higher and phytoplankton biomass was lower. Temperatures and surface nutrient concentrations did not show any year-to-year variation, ruling out phytoplankton blooms; also, phytoplankton productivity was higher in even-years than in odd-years. This indicates that the variation in phytoplankton biomass was not regulated by the chemical or physical environment, nor by the productivity of the phytoplankton. Similarly, the macrozooplankton biomass variation did not seem to be influenced by their own productivity. Instead (post-1989), the variations were regulated by predation by pink salmon.

Shaul, L.D. and H.J. Geiger. 2016. Effects of climate and competition for offshore prey on growth, survival, and reproductive potential of coho salmon in Southeast Alaska. North Pacific Anadromous Fish Commission Bulletin 6:329–347. doi:10.23849/npafcb6/329.347. (Available at http://www.npafc.org).

The relationship between Gulf of Alaska and their prey can be described as a “trophic triangle” where both pink and sockeye salmon prey upon minimal armhook squid and also compete with the squid for zooplankton prey. The squid is also the primary prey of coho; this research explored relationships between adult coho weight, environmental conditions, and top-down control on squid by pink and sockeye salmon, using data from 1970-2014 (for some variables, 1990-2014). Most of the variation in the size of coho salmon was equally explained by pink salmon biomass, and a PDO index corresponding with squid emergence and development. The late-marine period may be crucial for coho survival. Pink salmon is a keystone predator that controls the trophic structure of salmon food and directs energy flow in the offshore GOA. Sea ranching of chum salmon may offer an alternative to pinks as a way to lessen effects on higher trophic level species.

Springer, A., van Vliet, G.B., Bool, N., Crowley, M., Fullagar, P., Lea, M.A., Monash, R., Price, C., Vertigan, C., and E.J. Woehler. 2018. Transhemispheric ecosystem disservices of pink salmon in a Pacific Ocean macrosystem, PNAS 2018 115 (22) 5038-5045.

Short-tailed shearwaters make annual 30,000 km, non-stop round-trip migrations from their breeding grounds in southeastern Australia, the Bass Strait, and Tasmania to the north Pacific Ocean and Bering Sea (NP/BS). Other research has noted dietary overlap between pink salmon and shearwaters in the NP/BS and greater numbers of shearwaters (more than an order-ofmagnitude greater) dying in the Pribilof Islands in odd years (high pink salmon abundance) than even years. This research used proxies to estimate shearwater abundance at their breeding grounds and compared those data to pink salmon abundance data (catch plus escapement). There are strong correlations between low bird abundance and high pink abundance in all five examined time intervals. In recent odd-years, there have been increasing numbers of “wrecks”: massive bird mortality upon reaching their breeding grounds due to malnutrition during their time in NP/BS (the non-stop migration means that the birds rely on their reserves established in the NP/BS). Greater numbers of birds nest in even years than in odd years. Reduced numbers of shearwaters on the breeding grounds are thought to be responsible for changes in local (breeding ground) ecology, and forced reductions in commercial harvest of shearwaters by Aboriginal residents. These results suggest that pink salmon--and the hatchery releases of pink salmon--are “altering the distribution of wealth stored in this macrosystem.”

Springer, A.M. and G.B. van Vliet. 2014. Climate change, pink salmon, and the nexus between bottom-up and top-down control in the subarctic Pacific Ocean and Bering Sea. PNAS

2014 111 (18) E1880-E1888.

Monitoring data from four major seabird colonies (four islands) in the southern Bering Sea and Aleutian Islands were examined and indexed, such as “mean hatch date” and any anomalies noted (e.g., days before [“early”] or after [“late”] the mean). Thirteen of twenty omnivorous species/island samples had later hatch dates in even years, and this result was seen on all four islands. Clutch size was smaller in odd-years than in even-years for one bird species on all three islands where that species is found. Other significant effects were found for some species for parameters such as laying success, hatching success, fledgling success, and productivity, consistent with a hypothesis that in odd-years (high pink abundance) bird reproductive success was reduced. Some species build nests and in all cases where sufficient nests were counted to make comparisons, more nests were built in even-years than in odd-years. Many of these same nesting parameters were negatively correlated with a more specific parameter, the run size of eastern Kamchatka pink salmon. There were no consistent geographic patterns in the strength of the relationships (i.e, no island showed significantly more or fewer significant differences). As might be expected given these results, planktivorous seabirds showed an opposite response (or there was no relationship). The abundance of pink salmon in the northern Pacific and the results here that indicate top-down forcing call for a re-examination of fishing and hatchery practices and an ecosystem-based management.

Stachura, M. M., Mantua N. J., and M.D. Scheuerell. 2014. Oceanographic influences on patterns in North Pacific salmon abundance. Can. J. Fish. Aquatic Sci. 71(2), 226-235.

Authors took the 34 time series of regional salmon (wild North American and Asian, pink, chum, and sockeye) abundance used by Ruggerone et al. (2010) and applied three separate ordination techniques to identify patterns of abundance (as represented by the salmon abundance time-series) vs atmospheric and oceanographic variability (data from 10 environmental indices/datasets previously identified in the literature). Three dominant patterns were identified, accounting for 47% of the variability seen. Asian and North American populations had opposite trends for on pattern, indicating that large-scale climatic events may have different regional effects (e.g., NW Pacific vs. NE Pacific), or that density-dependent relationships become more important during these particular climatic events. Other factors “[f]or example, changes in harvest, hatchery practices, or freshwater habitat may contribute to abundance trends unrelated to climate and ocean variability” but were not investigated.

Sturdevant, M.V., R. Brenner, E.A. Fergusson, J.A. Orsi, and W.R. Heard. 2013. Does predation by returning adult pink salmon regulate pink salmon or herring abundance? North Pacific Anadromous. Fish Commission Technical Report 9: 153–164. (Available at www.npafc.org).

This study investigated predation by returning adult pink salmon on 1) juvenile pink salmon (cannibalism) and 2) Pacific herring in SEAK and PWS through 1) diet comparisons, 2) contrasting adult pinks with more piscivorous but less abundant coho and immature Chinook, and 3) examining climate mechanisms’ influence on predator-prey relationships. In the SEAK straits, herring and salmon were uncommon in adult pink salmon diets, unlike coho salmon diets; Chinook consumed herring but not salmon. In alongshore areas, pinks consumed greater numbers of fish. In PWS alongshore areas, pink diets varied monthly and between years. Pink salmon cannibalism was uncommon in either PWS or SEAK. No evidence was found to support that pink salmon cannibalism was a factor in the alternating-year nature of pink returns, although some results indicate that retuning pinks may locally affect herring in PWS. Environmental factors such as annual temperature variations can affect adult return timing as well as out-migration by juveniles and migration routes, and therefore shift temporal and spatial overlaps of prey and predators.

Sydeman, W.J., Thompson, S.A., Piatt, J.F., Garcia-Reyes, M., Zador, S., Williams, J.C., Romano, M. and H.M. Renner. 2017. Regionalizing indicators for marine ecosystems: Bering Sea - Aleutian Island seabirds, climate, and competitors. Ecological Indicators 78, 458-469.

Marine predators occupying upper-trophic levels, like birds, mammals, and piscivorous fish, are more affected by ocean climate variability than ones in mid-trophic levels. Seabirds are secondary and tertiary consumers and multivariate seabird indicators can be used as indicators of marine ecosystem health. This study used data from 1989 to 2012 on birds' breeding and diet (collected in the Alaska Maritime National Wildlife Refuge), pink salmon abundance, and environmental factors to investigate food webs and developed multivariate indices (principal components or PCs). Besides significant correlations between some PCs representing breeding success with some environmental PCs, there was a strong negative correlation for one breeding PC with pink salmon abundance. This is interpreted as regional kittiwake breeding success is negatively related to pink salmon abundance. Regional murre breeding success is unrelated to pink salmon abundance. The authors recommend keeping bird data separated by genera when developing PCs. Negative and positive relationships between environmental factors and breeding success show the importance of "early season" conditions and how those conditions affect food webs. For kittiwakes, the abundance of pink salmon is another such factor.

Toge, K., R. Yamashita, K. Kazama, M. Fukuwaka, O. Yamamura, and Y. Watanuki. 2011. The relationship between Pink Salmon biomass and the body condition of short-tailed shearwaters in the Bering Sea: can fish compete with seabirds? Proceedings of the Royal Society B: Biological Sciences 278:2584–2590.

From October to March, short-tailed shearwaters (*Puffinus tenuirostris*) breed mainly in Tasmania but spend May to September in the North Pacific Ocean. About 16 million can be found in the Bering Sea in summer, feeding on upper water-column krill, fishes, and small squid; thus they possibly compete with pink salmon for prey. Birds were sampled 2002-2008 for stomach contents and various condition factors, along with pink salmon to estimate pink salmon biomass. Body mass and liver mass were similar among the birds sampled in the central Bering Sea and the birds sampled in the northern Pacific Ocean, suggesting that the birds had in fact recovered their body condition after migration. Bird body mass and bird liver mass were found to be negatively influenced by pink salmon biomass (as represented by pink salmon catch per unit-effort or CPUE). Pink salmon CPUE was higher in odd-years. No significant relationship between stomach contents and pink salmon biomass was found, possibly because of the daytime feeding habits of the birds did not lend itself well to the nighttime sampling of birds.

Ward, E. J., M. Adkison, J. Couture, S. C. Dressel, M. A. Litzow, S. Moffitt, T. Hoem-Neher, J. T. Trochta, and R. Brenner. 2017. Evaluating signals of oil spill impacts, climate, and species interactions in Pacific Herring and Pacific salmon populations in Prince William Sound and Copper River, Alaska. PLoS ONE [online serial] 12(3): e0172898.

Pre- and post-oil spill (the 1989 *Exxon Valdez* oil spill, or EVOS) were used to determine what has driven changes in productivity of Pacific salmon (wild PWS pink, two PWS-lake sockeye populations, as well as Copper River Chinook and Copper River sockeye) and PWS Pacific herring. Five possible drivers were evaluated: 1) intraspecific density dependence; 2) EVOS, 3) changing environmental conditions, 4) interspecific competition, and 5) competition with and predation by adult fish (for salmon)/predation by humpback whales (for herring). Support was found for the first hypothesis for all evaluated fish stocks except wild PWS pink salmon. No support was found that the EVOS event negatively affected long-term productivity. The strongest environmental factor was that freshwater discharge negatively affected herring productivity. Little support was found for effects of juvenile-juvenile competition. A negative relationship was found between adult pink salmon hatchery returns and sockeye salmon productivity but was not shared with herring, Chinook, or PWS wild pink salmon. The lack of support seen in this study for so many of the drivers suggests that other factors may be important and operating on these fish stocks (e.g., disease).

Wertheimer, A. and E.V. Farley Jr. 2012. Do Asian Pink Salmon Affect the Survival of Bristol Bay Sockeye Salmon? North Pacific Anadromous Fish Commission Technical Report No. 8: 102-107.

Ruggerone, G.T., Myers, K.W., Agler, B.A. and J.L. Nielsen. 2012. Evidence for bottom-up effects on pink and chum salmon abundance and the consequences for other salmon species. North Pacific Anadromous Fish Commission Technical Report No. 8: 94-98.

Using the data analyzed by Ruggerone et al. (2003), Wertheimer and Farley conclude there is no evident effect on Asian pink salmon numbers on Bristol Bay sockeye. Using correlation analyses, they found no consistent response in the three BB sockeye stocks with pink numbers (separated into odd-even years). They reject the contentions of Ruggerone et al. (2012) that correlation analyses are not sufficiently robust to detect effects and stand by their conclusion that Asian pinks did not have a detrimental effect on BB sockeye.

Ruggerone et al. stand by the conclusions in Ruggerone et al. (2003) and later manuscripts (linking declines in Bristol Bay sockeye growth and survival to increased Asian pink salmon abundance), thus offering a rebuttal to Wertheimer and Farley (2012). They list a number of reasons why the use of correlation analyses by Wertheimer and Farley (2012) is incorrect, while acknowledging that use of correlation would lead to a conclusion that there is not a significant relationship between Asian pink abundance and BB sockeye survival. Ruggerone et al. also review a number of other papers offered as evidence of density-dependent relationships (while respecting changes in oceanographic conditions).

Wertheimer, A.C., Heard, W.R., Maselko, J.M. and W.W. Smoker. 2004. Relationship of size at return with environmental variation, hatchery production, and productivity of wild pink salmon in Prince William Sound, Alaska: does size matter? Reviews in Fish Biology and Fisheries, 14(3), pp.321-334.

Historically high returns of PWS pink salmon has been accompanied by decreasing body size. This research considered body size at return of PWS pink salmon against ten biophysical factors including hatchery inputs. Body size was also evaluated against wild pink salmon productivity. Two measures of temperature conditions were positively correlated to body size while three measures of pink salmon abundance (hatchery releases, hatchery returns, and overall GOA catch) were negatively correlated with body size. This is evidence that the growth of salmon in the ocean is density dependent and is also affected by environmental factors operating on the basin- and regional-scale. Body size significantly affected wild stock productivity, although marine environmental conditions explained most of the variability. Productivity of PWS pink salmon was affected more by regional environmental indices (e.g., GOA SST) than by basin-scale conditions (e.g., PDO) during their first year in ocean. Overall, density-independent factors affect wild pink salmon productivity more than do than density-dependent ones. While wild stocks may be affected by hatchery programs, the overall net benefit of hatcheries is much greater than the reduction in wild production. Continued evaluation of the efficacy of the hatchery programs is essential to give managers and policy-makers the data they need for informed decision-making.

Wertheimer, A.C., Heard, W.R. and W.W. Smoker. 2004. Effects of hatchery releases and environmental variation on wild-stock productivity: consequences for sea ranching of pink salmon in Prince William Sound, Alaska. Pages 307-326 *in*: K.M. Leber, S. Kitada, H. L. Blankenship, and T. Svasand, eds. *Stock Enhancement and Sea Ranching: Developments, Pitfalls and Opportunities*, Blackwell Publishing, Oxford, UK.

This study is a follow-up to the Wertheimer et al. (2001) comment on the Hilborn and Eggers (2000) study. Wertheimer et al. (2001) believed that the Hilborn and Eggers population model over-estimated wild production and did not consider other factors. Here, the researchers evaluate wild stocks (returns per spawner) against a number of parameters, including hatchery releases. Wild stock data (derived from ADFG harvest data and spawner surveys) from 19601998 were used. Environmental variables included winter air temperature; spring air temperature; spring zooplankton abundance; herring biomass; Gulf of Alaska (GOA) summer sea surface temperature (SST); GOA summer wind stress; Pacific decadal oscillation (PDO); PDO-1 (variable using the annual winter PDO index in pink brood year y -1; evaluates conditions during the adult ocean life-history phase of pinks); GOA pink salmon abundance; marine survival index (MSI); and hatchery releases. Three separate time series were used (1980-1998; 1975-1998; and 1960-1998) because data on all the variables were available only in 1960-1998. For all three time series, indices/variables of environmental conditions better explained variability in wild stock productivity than did hatchery releases. In the 1975-1998 time period, while hatchery releases were significant, MSI explained more variability. The authors believe that the assertions made in Wertheimer et al. (2001) are validated and that wild stocks in PWS have only been marginally negatively affected by hatchery releases, and that the net benefits of pink salmon hatchery programs are substantially greater (an increase in total runs 3x to 6x).

Yasumiishi, E.M., Criddle, K.R., Helle, J.H., Hillgruber, N. and F.J. Mueter. 2016. Effect of population abundance and climate on the growth of 2 populations of chum salmon (*Oncorhynchus keta*) in the eastern North Pacific Ocean. Fishery Bulletin, 114(2).

The seasonal and annual marine growth of chum salmon from an Alaskan creek and a Washington river were compared to abundances of pink and chum salmon and climate indices. Data from the early 1970s through 2004 were used. Pink salmon abundance negatively affected immature growth of chum salmon, except in the case of the first immature year of WA river chum. The exception may be due to the marine distribution of WA river chum; they were not as far west or as far north as the AK creek chum and thus did not overlap with pinks to be affected. Growth of both populations (except mature growth) was positively related to surface sea temperatures after accounting for density-dependent effects.

Zador, S., Hunt Jr., G.L., TenBrink, T., and K. Aydin. 2013. Combined seabird indices show lagged relationships between environmental conditions and breeding activity. Mar Ecol Prog Ser (485), 245-258.

Seventeen data sets related to the reproductive effort of five predacious seabirds were integrated into two indices using principal components analysis and then compared to environmental variables in the eastern Bering Sea. The two principal components (PC1 and PC2) accounted for 65% of the variability. Pink salmon abundance was not one of the environmental variables evaluated, but a “sawtooth” pattern in PC2 values was noted that corresponds to the odd/even year pattern in pink salmon abundance, reflecting lower kittiwake reproductive success in the odd-years (high pink abundance). The authors hypothesize that increased competition for prey between kittiwakes and pink salmon lead to lower kittiwake reproductive success in odd-years.

Zavolokin, A. V., V. V. Kulik, and L. O. Zavarina. 2014. The food supply of the Pacific salmon of the genus *Oncorhynchus* in the Northwestern Pacific Ocean 2: comparative characterization and general state. Russian Journal of Marine Biology 40:199–207.

The intent of the study was to determine how diet, growth, and survival interacted at various levels of salmon abundance and food abundance for salmon species in the northwestern Pacific, based on a hypothesis that salmon consume only a small portion of the prey available to them, even in periods of high salmon abundance. Periods of low food supply were identified for the western Bering Sea, the southern Sea of Okhotsk, and the northwestern Pacific Ocean, and most of these periods coincided with strong shoreward salmon migration. This evidence for a density-dependent effect included a shift in the diet composition and the feeding patterns of salmon. Because there was no reduction in growth or survival of salmon, the effect is thought to be small. The increase in salmon abundance in the 2000s was sufficiently supported by the available food.

Submitted by: Patrick McCormick

Community of Residence: Eagle River Alaska

Comment:

I am an area E drift gillnet holder, sport fishing guide, and have extensively studied fisheries management, hatchery/wild interactions and fisheries economics in both formal and informal settings.

It is clear to me that the current hatchery system in Alaska is causing great harm to wild fish and wild fish fisheries. For example in Prince William Sound the primary management driver during the month of August is PWSAC pink salmon, which has had a very unstable abundance and have produced generally small unusable fish, depressing prices of pink salmon, while allowing surplus wild salmon to go unharvested. This was the primary cause of the "disaster" in 2020, while wild stocks in the SW district were massively over escaped hatchery stocked failed completely.

Pink salmon are the most successful and numerous salmon in the North Pacific, and drive a bulk of the catch in Alaska. Pink salmon are favored by the seine fleet because of their abundance and the effectiveness of seine gear on pink salmon, they are favored by hatchery programs because of the low time period required to rear pink salmon.

Hatchery pink salmon cause a number of problems however, first and foremost, because they are the most likely salmon to stray, hatchery salmon are very likely to interbreed with, and lower the genetic fitness of wild pink salmon. Second it is becoming increasingly clear that pink salmon abundance greatly impacts the abundance of other salmon. While this research is in it's infancy, these interactions should be noted when creating hatchery policy in Alaska.

While the boards authority to regulate hatchery policy in Alaska is murky, I suggest that the board, if called up advocate for the following policies:

-Prioritizing steady abundance of pink salmon in Alaska.

Pink salmon abundance is much higher on odd years, therefor hatchery production should be greatly reduced on odd years. Having a steady supply, rather than very large swings will help stabilize markets.

-Managing pink salmon on biomass rather than abundance.

1 million 2 pound pink salmon are worth less than 500,000 4 pound pink salmon. The larger the fish, the more it is worth on the market. Currently hatchery pink salmon are averaging 2-3 pounds while wild pink salmon are averaging 4-5 pounds. By managing these fish based on abundance we are prioritizing number of fish rather than value of fish. Personally I would rather catch fewer fish for more money. I imagine most fishermen feel the same.

-Promoting equality among all user groups.

Currently in area E a bulk of hatchery fish are caught by one user group (seiners). There is an entire hatchery system that is purely for seiners (VDA). This is a symptom of the reliance of hatchery pink salmon. By decreasing pink salmon and increasing production or coho, sockeye and chinook salmon all user groups, seine, gillnet, subsistence, and sport will benefit. Thus bringing more prosperity to our state!

-Manage for wild fish.

The driver of management of wild fish should be the top priority in all fisheries. Period.

Thank you,

Patrick McCormick

F/V Sportsman, Chugach View Outfitters.

Submitted by: Chris Sergeant

Community of Residence: Seattle, Washington

Comment:

Comments to the Alaska Board of Fisheries Hatchery Committee regarding the impacts of stray hatchery salmon on dissolved oxygen and aquatic life in natural streams

Submitted by Dr. Chris Sergeant

University of Montana, Flathead Lake Biological Station

University of Washington, School and Marine and Environmental Affairs

Dear Board of Fisheries Hatchery Committee:

Thank you for the opportunity to comment on hatchery practices. My name is Chris Sergeant, and I am a Research Scientist with the University of Montana's Flathead Lake Biological Station and an Affiliate Instructor with the University of Washington's School of Marine and Environmental Affairs. While I currently live in Seattle, Washington, I was a resident of Juneau, Alaska from 2011-2020 and remain actively involved in salmon- and river-related research in the watersheds of southern Alaska and British Columbia. The intent of my comments here, along with the two attached research papers, are to help broaden the discussion around the impacts of hatchery salmon on wild salmon populations and freshwater ecosystems.

Attached are two papers in peer-reviewed scientific journals that I led in 2017 and 2023. They demonstrate the impacts and potentially widespread issue of adult hatchery salmon straying to rivers and creating low dissolved oxygen conditions. These low oxygen conditions, also known as hypoxia, can be lethal to natural-origin adult salmon and other organisms living in the river such as juvenile salmon, Dolly Varden, salmon embryos, and aquatic insects. While a larger amount of research attention has gone toward the genetic impacts of straying hatchery salmon on natural salmon populations, our papers bring attention to the additional concern that stray hatchery salmon can create a number of immediate ecological impacts, including: 1) mortality of spawning salmon and other resident fishes, 2) mortality or reduced diversity of benthic macroinvertebrates (e.g., aquatic insects that provide food for juvenile salmon), 3) inhibited salmon embryo growth, and 4) sublethal physiological stress on fish and other aquatic organisms. Essentially, stray hatchery salmon can become so dense in natural streams that they use up oxygen faster than it can be reaerated back into the stream through natural processes. In the attached papers, we corroborate our findings with a large number of peer-reviewed citations of academic literature and previous technical reports from Alaska Department of Fish and Game that discuss hatchery salmon straying rates.

Considering these known impacts to freshwater ecosystems and salmon populations caused, in part, by hatchery salmon, I see an opportunity to integrate research on hatchery-salmon-induced hypoxia with existing long-term monitoring programs. Government agencies such as the Alaska Department of Fish and Game and National Oceanic and Atmospheric Administration have research infrastructure in place throughout Southeast Alaska that could be leveraged to support monitoring programs aimed to answer three key questions: 1) where and in how many places do straying salmon increase the frequency and intensity of hypoxia events? 2) Do hypoxia events result in observable ecosystem responses such as decreased natural spawning productivity or decreased diversity of aquatic macroinvertebrates? 3) Are climate change and associated extreme events such as drought creating low-flow conditions that decrease the ability of streams to reaerate efficiently? As drought becomes more common in Alaska, low streamflow during salmon spawning season can contribute to the risk of hypoxia in addition to crowding by hatchery salmon.

I welcome the opportunity to follow-up on these comments at any time and would be happy to continue the conversation. Thank you for your work, time, and consideration.

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esa ECOSPHERE

High salmon density and low discharge create periodic hypoxia in coastal rivers

Christopher J. Sergeant,[1],† J. Ryan Bellmore,[2] Casey McConnell,[3] and Jonathan W. Moore[4]

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[3]*College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 17101 Point Lena Loop Road, Juneau, Alaska 99801 USA*
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Abstract. Dissolved oxygen (DO) is essential to the survival of almost all aquatic organisms. Here, we examine the possibility that abundant Pacific salmon (*Oncorhynchus* spp.) and low streamflow combine to create hypoxic events in coastal rivers. Using high-frequency DO time series from two similar watersheds in southeastern Alaska, we summarize DO regimes and the frequency of hypoxia in relationship to salmon density and stream discharge. We also employ a simulation model that links salmon oxygen respiration to DO dynamics and predicts combinations of salmon abundance, discharge, and water temperature that may result in hypoxia. In the Indian River, where DO was monitored hourly during the ice-free season from 2010 to 2015, DO levels decreased when salmon were present. In 2013, a year with extremely high spawning salmon densities, DO dropped to 1.7 mg/L and 16% saturation, well below lethal limits. In Sawmill Creek, where DO was monitored every six minutes across an upstream–downstream gradient during the 2015 spawning season, DO remained fully saturated upstream of spawning reaches, but declined markedly downstream to 2.9 mg/L and 26% saturation during spawning. Modeled DO dynamics in the Indian River closely tracked field observations. Model sensitivity analysis illustrates that low summertime river discharge is a precursor to salmon-induced oxygen depletion in our study systems. Our results provide compelling evidence that dense salmon populations and low discharge can trigger hypoxia, even in rivers with relatively cold thermal regimes. Although climate change modeling for southeastern Alaska predicts an increase in annual precipitation, snowfall in the winter and rainfall in the summer are likely to decrease, which would in turn decrease summertime discharge in rain- and snow-fed streams and potentially increase the frequency of hypoxia. Our model template can be adapted by resource managers and watershed stakeholders to create real-time predictive models of DO trends for individual streams. While preserving thermally suitable stream habitat for cold-water taxa facing climate change has become a land management priority, managers should also consider that some protected watersheds may still be at risk of increasingly frequent hypoxia due to human impacts such as water diversion and artificially abundant salmon populations caused by hatchery straying.

Key words: Alaska; bioenergetics; dissolved oxygen; ecosystem engineer; hatcheries; hypoxia; Pacific salmon; strays; subsidy–stress gradient; thermal regime.

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INTRODUCTION

Dissolved oxygen (DO) is essential to the survival of almost all aquatic organisms. Reports of oxygen depletion events (hypoxia) in nearshore marine environments have increased exponentially since the mid-20th century (Diaz and Rosenberg 2008, Vaquer-Sunyer and Duarte 2008). Freshwaters are also vulnerable to hypoxia (Mallin et al. 2006), and these events have contributed to documented fish kills across the globe (La and Cooke 2011). Natural events such as deep water entrainment at fjord sills (Arneborg et al. 2004) and prolonged ice cover in lakes (Wetzel 2001) often lead to hypoxia, but human-induced changes to aquatic systems such as nutrient overloading and flow regime modification commonly contribute to oxygen depletion, as well (USEPA 2007). There is also the growing appreciation that other aquatic species can strongly influence DO levels; for example, large beds of invasive plants can decrease DO levels in lowland rivers (Caraco and Cole 2002). Here, we examine the possibility that abundant Pacific salmon (*Oncorhynchus* spp.) and low streamflow can combine to create hypoxic events in coastal rivers.

Large sections of coastline along British Columbia and Alaska encompass watersheds with some of the most abundant populations of Pacific salmon in the world. As mature semelparous salmon return from the sea to spawn and subsequently die in their natal rivers, they require cool water that is high in oxygen, low in excess nutrients, and relatively free of pollution. These oligotrophic waters receive an influx of salmon-derived nutrients that subsidize terrestrial and aquatic food webs (Gende et al. 2002). While these subsidies are generally viewed as a benefit to stream food webs, the ecological consequences of spawning salmon can vary depending on the habitat characteristics of individual watersheds and reaches (Janetski et al. 2009, Holtgrieve et al. 2010*b*, Campbell et al. 2011, Bellmore et al. 2014, Benjamin et al. 2016).

In small watersheds (<30 km^2), dense spawning salmon can significantly modify the physical and chemical characteristics of rivers through processes such as respiration, nest building, and carcass decomposition (Montgomery et al. 1996, Peterson and Foote 2000, Moore et al. 2004, Holtgrieve and Schindler 2011, Levi et al. 2013, Fellman et al. 2015). Salmon nest building, for instance, has been shown to increase air–water gas exchange (Holtgrieve and Schindler 2011) and reduce the abundance of benthic organisms (Moore and Schindler 2008, Collins et al. 2011, Campbell et al. 2012). It is also possible that the metabolic demands of high densities of salmon spawners could reduce DO to levels that are harmful or lethal to salmon themselves and other sensitive aquatic life.

For over sixty years, biologists in southeastern Alaska have observed salmon die-offs in small watersheds (Murphy 1985, Chaloner et al. 2004). Most recently, Tillotson and Quinn (2017) demonstrated that high pre-spawn mortality rates of sockeye salmon (*Oncorhynchus nerka*) in a small southwestern Alaska creek were strongly correlated with low DO levels caused by dense salmon populations, warm water, and low discharge. To date, most studies touching on this issue provide point estimates or ranges of DO measurements within an individual year. Relatively little is known about how often low DO events occur, how long they persist, and importantly, how often salmon contribute to hypoxic events in concert with other environmental conditions.

Dissolved oxygen regimes vary not only with fluctuations in salmon density and water temperature, but also with discharge, which is a function of watershed size and water source (Hauer and Lamberti 2007). Even during times of high salmon abundance, water quality in medium (30–200 km^2) to large watersheds (>200 km^2) with high annual average discharge (>10 m^3/s) is likely to be controlled by abiotic factors such as bedrock geology or glacial coverage. Thus, small watersheds with relatively low discharge should be more vulnerable to observable DO depletion due to dense salmon aggregations than larger watersheds. Even in regions with high precipitation rates, these smaller watersheds can experience extremely low flows between rainfall events. Interacting human impacts such as artificially high abundance of straying hatchery salmon (salmon intended to return to a hatchery that instead migrate to other streams; Brenner et al. 2012, Piston and Heinl 2012) and water diversion in these watersheds would likely intensify DO depletion by decreasing available water volume in stream channels and increasing salmon density. But, across the geographic range of salmon, little long-term data exist describing the

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inter-annual patterns of DO regimes and seasonal magnitude and duration of hypoxia events.

The Northern Pacific Coastal Temperate Rainforest (NPCTR), defined by O'Neel et al. (2015) as, "the perhumid and subpolar region extending from the Skeena River watershed in British Columbia, to Kodiak Island, Alaska (total area = 448,550 km^2)," encompasses thousands of small to large watersheds that are ideal for examining the impact of dense salmon populations on DO regimes. Watersheds in the NPCTR range from small rain- and snow-fed streams to large glacially influenced rivers. Within the sub-region of southeastern Alaska alone, there are nearly 3000 coastal watersheds with drainage areas >1.2 km^2 that empty directly into saltwater (D'Amore et al. 2016). Although climate change modeling in this region predicts an overall increase in future annual precipitation, snowfall in the winter and rainfall in the summer are likely to decrease (Shanley and Albert 2014, Shanley et al. 2015), especially during warm phases of the Pacific Decadal Oscillation (PDO; Neal et al. 2002), which would in turn decrease summertime discharge in rain- and snow-fed streams and potentially increase the magnitude, duration, and frequency of hypoxia events.

We present high-frequency time series of DO from two similar watersheds dominated by rainfall and snowmelt in southeastern Alaska to summarize the inter- and intra-annual DO regimes and frequency of riverine hypoxia in relationship to spawning salmon density and stream discharge. In addition, we use an existing bioenergetics model of salmon respiration (Trudel et al. 2004, Holtgrieve and Schindler 2011) linked to an oxygen reaeration model to assess the extent to which observed decreases in DO can be attributed to spawning salmon. We extend this model to explore combinations of salmon abundance, discharge, and water temperature that may result in hypoxic conditions. Using this combination of field observation and modeling, we provide compelling evidence that dense salmon populations and low discharge can trigger hypoxia, even in rivers with relatively cold thermal regimes.

METHODS

Study sites

Coastal southeastern Alaska is dominated by steep topography, a wet maritime climate, glacially formed valleys, and temperate rainforest lowlands (Gallant et al. 1995). The Indian River and Sawmill Creek (Fig. 1) were chosen as complementary datasets for exploring potential mechanisms leading to low riverine DO in similar watersheds: The Indian River dataset provides water quality data at high temporal resolution over multiple years (2010–2015), while the Sawmill Creek dataset provides high temporal resolution across an upstream–downstream longitudinal gradient over one season (2015).

The Indian River watershed is located in Sitka, Alaska (Fig. 1), and has moderate human development from the mouth upstream to approximately river km 2.4. Annual precipitation in this area averages 217 cm (Western Regional Climate Center Data: http://www.wrcc.dri.edu/summary/Climsmak.html). The lowest 0.8 km flows through Sitka National Historical Park. In this lower floodplain reach, approximately half or less of substrates are finer than 64 mm, which is somewhat coarser than other streams in southeastern Alaska (Paustian and Hardy 1995). Several entities hold legal water rights to the river, including the National Park Service, Alaska Department of Fish and Game (ADFG), Sheldon Jackson Salmon Hatchery, and City and Borough of Sitka (CBS). While the CBS has infrequently diverted up to 0.11 m^3/s of river discharge for emergency drinking water, the only year-round water diversion occurs at river km 1.3 for use at the Sheldon Jackson Salmon Hatchery. From 1 December 2012 to 11 October 2016, diversion rates averaged 0.20 m^3/s and reached a maximum of 0.45 m^3/s (T. Schwarz, Alaska Department of Natural Resources, *personal communication*, 10 November 2016). This diversion is upstream from the water quality monitoring site in this study (river km 0.8). The majority of the upper Indian River watershed remains undeveloped and within the Tongass National Forest. Pink salmon (*Oncorhynchus gorbuscha*) comprise >95% of annual salmon spawning activity in the river (Stark et al. 2012), with the remainder consisting of chum (*Oncorhynchus keta*) and coho salmon (*Oncorhynchus kisutch*). From 2013 to 2015, 0–62% of sampled pink salmon carcasses were strays from the nearby Sheldon Jackson Salmon Hatchery (S. Gende, National Park Service, *unpublished data*), which has released approximately 700,000–3,000,000 pink salmon fry every year since 2008 (Stopha 2015). During the years of our study,

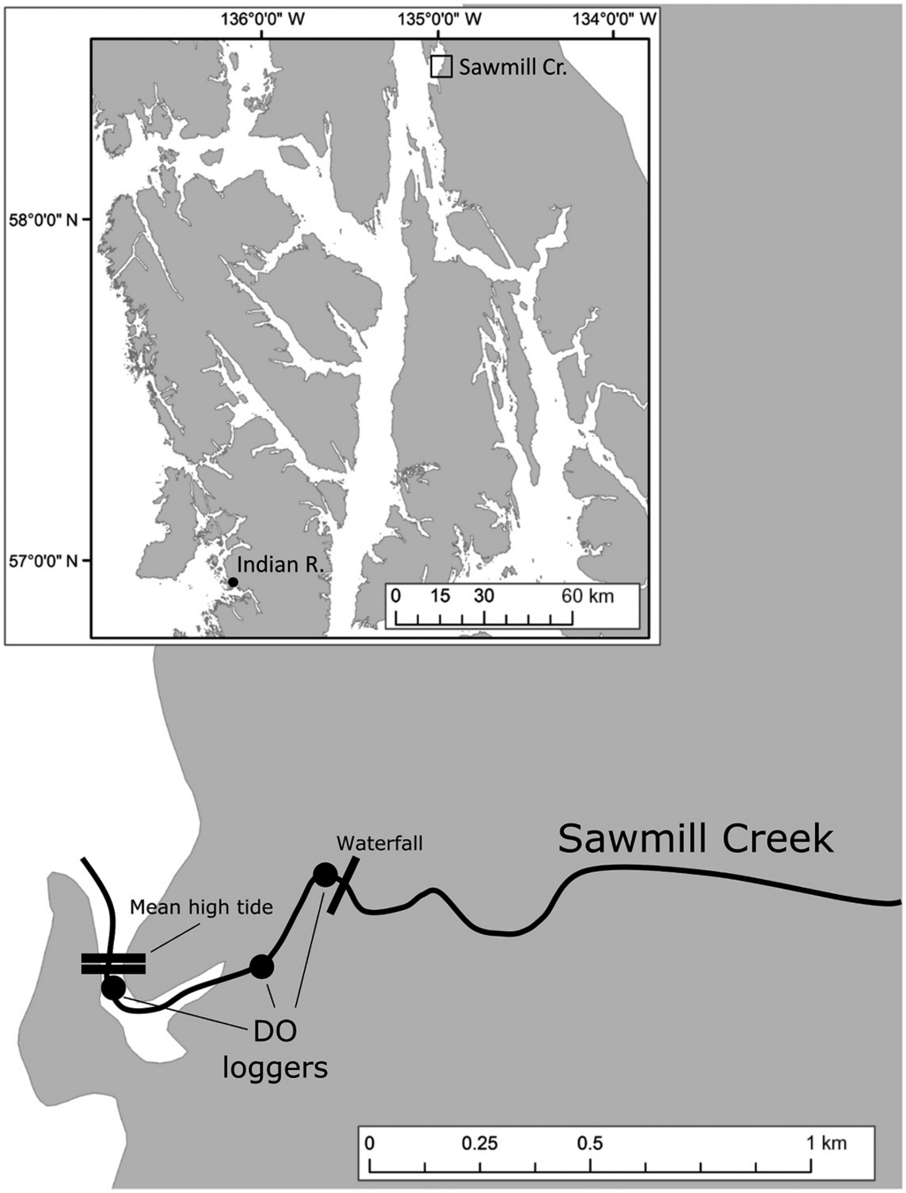

Fig. 1. Map of study area and Sawmill Creek dissolved oxygen (DO) logger locations in relation to anadromous barrier (waterfall) and mean high tide.

peak aerial counts of spawning pink salmon summed over the intertidal delta, river mouth, and main river channel ranged from 80,000 to 295,000 during August (Stopha 2015; ADFG, *unpublished data*).

Sawmill Creek drains a steep and undeveloped watershed located 45 km north of Juneau, Alaska (Fig. 1). Annual precipitation at the Juneau International Airport, the nearest long-term climate station, averages 147 cm (Western Regional Climate Center Data: http://www.wrcc.dri.edu/summary/Climsmak.html). Approximately 600 m above the mean high tide line, a 15-m waterfall blocks upstream anadromous migration and creates a plunge pool with constantly saturated DO levels. Extreme low tides expose an additional 700 m of intertidal spawning area used for spawning by pink salmon. From June to August 2015,

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chum and pink salmon were the predominant spawners in Sawmill Creek (see *Results*). During the study period, hatchery strays comprised 51% of total chum salmon returning to spawn (i.e., escapement; C. McConnell, *unpublished data*).

While the Indian River has a longer channel than Sawmill Creek, both study systems are similar in other general watershed characteristics (Table 1). Both rivers have specific conductance and discharge characteristics representative of southeastern Alaska watersheds fed primarily by rain and snow runoff. From 2010 to 2015, specific conductance in the Indian River was inversely proportional to relative river stage (i.e., river height or elevation) and ranged from 10 to 80 μS/cm during the ice-free season (Sergeant and Johnson 2016). The relative river stages of the Indian River and Sawmill Creek increase quickly in response to precipitation (See Neal et al. 2004 and Fig. 2 for Indian River; Fig. 3 for Sawmill Creek).

Water quality and discharge measurements

In the Indian River, from 2010 to 2015, DO concentration (mg/L), DO saturation (%), and water temperature (°C) were measured hourly at river km 0.8 from approximately mid-April to early November using a YSI 6920-V2 multiparameter sonde equipped with YSI 6150 optical DO sensor and YSI 6560 conductivity/temperature probe (YSI Incorporated, Yellow Springs, Ohio, USA). Sensors were checked, cleaned, and calibrated approximately monthly to confirm and sustain measurement accuracy. Data quality was assessed according to consistently applied long-term monitoring protocols (See Standard Operating Procedures 1–3 in Sergeant et al. 2013). Data collected using methods deviating from monitoring protocol standards (e.g., incorrect sensor calibration procedures) or data collected during periods when instruments were damaged or malfunctioning were removed from all analyses. Relative river stage (m) was recorded at the same location every 15–60 min during the study period using either a Druck 1830 (GE Druck, Boston, Massachusetts, USA) or In-Situ Level TROLL 500 vented pressure sensor (In-Situ, Fort Collins, Colorado, USA) housed within a small metal shelter mounted to the top of a bedrock-bolted steel pipe. From December 2013 to July 2014, seven wading discharge measurements ranging from 0.14 to 3.56 m^3/s were collected using a SonTek FlowTracker Handheld Acoustic Doppler Velocimeter (SonTek, San Diego, California, USA) to develop a stream stage–discharge relationship for DO modeling purposes described in the *DO modeling* subsection below.

In Sawmill Creek, from 1 June to 21 August 2015, DO concentration (mg/L), saturation (%), and water temperature (°C) were measured every six minutes at three stations (river km 0.6, 0.4, and 0.0) using miniDOT loggers manufactured by Precision Measurement Engineering (Precision Measurement Engineering, Vista, California, USA). To decrease the potential for sensor biofouling, each logger was shaded from sunlight by being mounted inside a section of polyvinyl chloride (PVC) pipe. Surveyors cleared any particulate matter build-up in the pipe approximately every two days during the study period. Relative river stage (m) was recorded during spawning salmon surveys by visually inspecting a staff plate installed in the channel at river km 0.5. Precipitation data were derived from the Federal Aviation Administration weather station at Juneau International Airport.

We defined hypoxic conditions as periods when DO concentrations were <7 mg/L and/or saturation <70% for water temperatures ranging from 5° to 15°C. Above these DO levels, freshwater fish species are unlikely to exhibit negative physiological effects caused by low DO (Davis 1975). Below these levels, biologists have observed decreased swimming performance and delayed upstream migration in sockeye (*O. nerka*), Chinook (*O. tshawytscha*), and coho

Table 1. Watershed characteristics for each study site.

Watershed	Watershed area (km^2)	Length (km)	Max. elevation (m)	Glacier (%)	Wetland (%)	Forest (%)
Indian R.	31	19.8	1158	1	18	55
Sawmill Cr.	23	7.0	1525	<0.5	2	50

Notes: Indian River characteristics were calculated for the watershed area above the fixed water quality sampling site at river km 0.8, while Sawmill Creek characteristics were described for the entire watershed. Data were derived from the National Hydrography Dataset and National Land Cover Database (http://viewer.nationalmap.gov/viewer/nhd.html).

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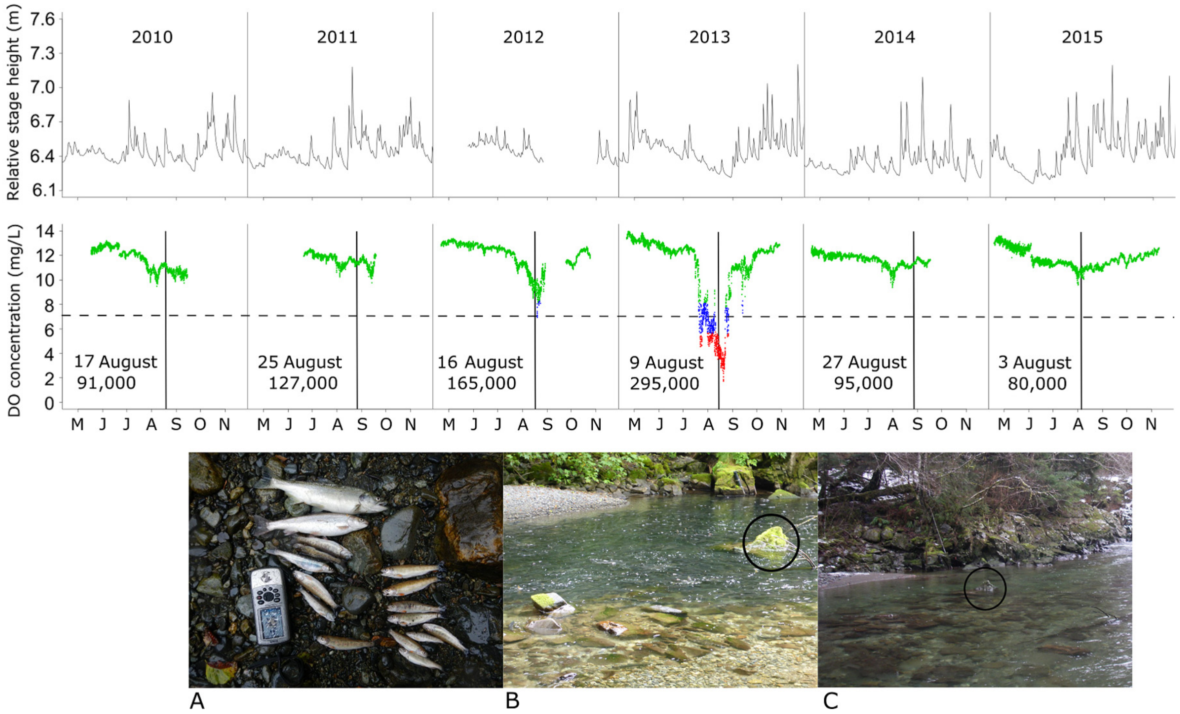

Fig. 2. Inter-annual patterns of Indian River dissolved oxygen (DO) concentration and saturation in comparison with relative river stage and salmon presence. In the lower panel, colored points represent DO saturation levels (green > 70%, blue 50–70%, and red < 50%). The horizontal dashed line represents a DO concentration of 7 mg/L, our threshold for defining hypoxic stream conditions for spawning Pacific salmon. Vertical lines represent the date of peak daily salmon counts collected via aerial survey. Peak counts are included below each peak count date. Photo (A) portrays juvenile cutthroat trout and Dolly Varden mortalities observed during an informal streamside survey conducted on 30 August 2013 (Photo courtesy of S. Gende/National Park Service), shortly after DO concentration at the Indian River study site reached a minimum of 1.7 mg/L at 16% saturation (average stage = 6.20 m). Open mouth and flared opercula in several individuals are typical signs of asphyxiation. Photo (B) was taken on 15 August 2013 and shows the high density of salmon present in the pool, where DO was measured for this study. For comparison, Photo (C) was taken on 19 November 2014 at the same location approximately three months after the peak spawning migration of pink salmon. The same rock is circled in photos (B) and (C) for spatial reference.

salmon (Davis 1975, Spence et al. 1996). Dissolved oxygen levels below 5 mg/L are likely to distress most freshwater species in cold-water systems (Davis 1975). Additionally, the Alaska Department of Environmental Conservation (ADEC) freshwater water quality regulations state that, “DO must be greater than 7 mg/L in waters used by anadromous or resident fish. In no case may DO be less than 5 mg/L. . .” (ADEC 2017).

Spawning salmon counts

In the Indian River, a relative index of spawning pink salmon abundance was reported each year of our study as a peak daily count derived from aerial surveys conducted by ADFG. Peak daily counts included the sum of pink salmon observed in the intertidal delta, river mouth, and main river channel. In Sawmill Creek, on-the-ground visual surveys conducted from the base of the waterfall downstream to the mean high tide line counted all visible chum salmon during periods when water clarity permitted. No spawning chum salmon were observed below mean high tide line. Due to their high density, pink salmon were counted along a 50-m index reach when water clarity and observer capacity allowed. The index reach was an active spawning area and provided surveyors with a

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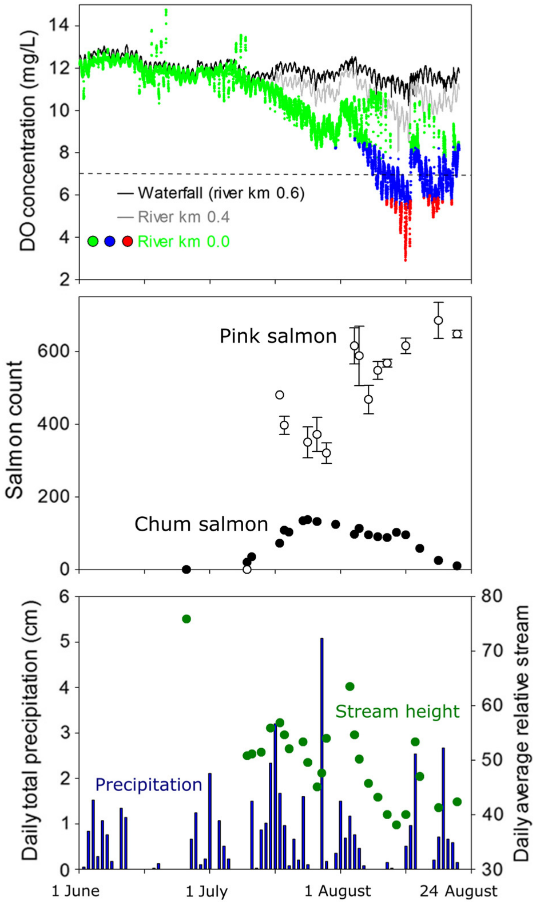

Fig. 3. Intra-annual patterns of Sawmill Creek dissolved oxygen (DO) concentration and saturation at three stream locations in comparison with stream height and salmon abundance. In the upper panel, colored points represent DO saturation levels at river km 0.0 (green > 70%, blue 50–70%, and red < 50%). Dissolved oxygen saturation levels at river km 0.4 (gray line) and river km 0.6 (black line) remained above 70% at all times during the study period. The horizontal dashed line represents a DO concentration of 7 mg/L, our threshold for defining hypoxic stream conditions for spawning Pacific salmon. In the middle panel, error bars represent ±1 SD (see *Methods* for differences in visual count methodology between species).

high bank and forested shoreline for optimum visibility. For pink salmon only, two surveyors counted spawners independently and averaged the two counts for the final index section abundance.

DO modeling

The effect of salmon on DO dynamics was simulated using a two-process model coupling atmospheric oxygen reaeration with salmon respiration of oxygen. The rate of change in DO as a function of both of these processes was given by:

$$\frac{d[\mathrm{O_2}]}{dt} = (k([\mathrm{O_{2sat}}] - [\mathrm{O_2}])) - R_{\mathrm{sal}}$$

where $[\mathrm{O_2}]$ is DO concentration (mg/L), $[\mathrm{O_{2sat}}]$ is the DO saturation concentration (DO concentration at atmospheric equilibrium), k is the rate of reaeration with the atmosphere (1/h), and R_{sal} is the instantaneous respiration rate of the salmon population (mg $\mathrm{O_2 \cdot L^{-1} \cdot h^{-1}}$). The concentration of DO at complete saturation varies with water temperature and was calculated with the equation in Benson and Krause (1980). The rate of oxygen reaeration with the atmosphere was calculated using the energy dissipation model (Owens et al. 1964):

$$k_{20^\circ\mathrm{C}} = \left[\frac{50.8 \times v^{0.67} \times d^{-0.85}}{d}\right]$$

where $k_{20^\circ\mathrm{C}}$ is the oxygen reaeration rate when water temperature is 20°C, v is water velocity (cm/s), and d is average water depth (cm). The reaeration rate at ambient water temperature (T) is calculated as follows (Elmore and West 1961):

$$k_{T^\circ\mathrm{C}} = k_{20^\circ\mathrm{C}} \times 1.024^{(T-20)}.$$

Salmon respiration was calculated using a bioenergetics model (Trudel et al. 2004, Holtgrieve and Schindler 2011) that relates oxygen consumption to individual salmon mass (W; g), swim speed (U; cm/s), and water temperature (T; °C) as:

$$R_{\mathrm{sal}} = N_{\mathrm{sal}}(\alpha W^{\beta} \times e^{\varphi T} \times e^{\nu U})$$

where R_{sal} is the amount of oxygen respired by spawning salmon (mg $\mathrm{O_2 \cdot L^{-1} \cdot h^{-1}}$); N_{sal} is the number of spawning salmon per liter of water (salmon/L = salmon/m^2 × 1/depth (m) × m^3/1000 L); α is the standard metabolic rate of 1 g fish at 0°C (0.060); and β, φ, and ν are coefficients describing the metabolic costs of mass, temperature, and swim speed, respectively (0.791, 0.086, and 0.0234; values that have been previously used for chum, pink, and sockeye salmon; Beauchamp et al. 1989, Trudel et al. 2004).

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All of the components that combine to generate overall ecosystem metabolism (gross primary production and all oxygen-consuming reactions in the ecosystem; Holtgrieve et al. 2010*a*) were not included in our model. Ecosystem metabolism can strongly influence DO dynamics in some rivers (Holtgrieve et al. 2010*a*), particularly diel dynamics; however, we hypothesized that a simpler model, one that only included atmospheric reaeration and salmon respiration, could reproduce observed seasonal patterns in DO in the oligotrophic rivers of southeastern Alaska (Kline et al. 1997, Sterling et al. 2000). In addition, because our goal was to understand the effect of live spawning salmon on DO dynamics, we did not include oxygen respiration associated with decaying salmon carcasses.

Model parameterization and simulation

We used the model to simulate hourly DO dynamics in the Indian River before, during, and after salmon spawning in years 2010–2015. We parameterized the model with hourly water temperature, discharge data, and salmon spawning counts. Discharge was calculated from relative river stage using a stage–discharge relationship established from 2014 wading discharge measurements (Sergeant and Schwarz 2017). The model converted discharge into its components of depth (d) and velocity (v) using the Manning equation (Gordon et al. 2004) parameterized with empirical channel morphology data collected in 2016 (bankfull width and depth, bank angle, channel gradient; C. Sergeant, *unpublished data*). While the stage–discharge relationship may have shifted as a result of high flow events modifying the channels in either study system, relative river stage remained an effective indicator of comparatively low vs. high discharge. To determine the sensitivity of modeled DO predictions to a shifting stage–discharge relationship for the Indian River, we altered discharge values ±20% and re-calculated modeled DO to examine model residuals between the primary and shifted stage–discharge relationships.

Spawning counts conducted by ADFG (see *Spawning salmon counts* sub-section above) were used to construct time series of salmon abundance within the spawning reach (Appendix S1). Estimates were converted to spawners/m^2 by dividing by the wetted area of the spawning reach (wetted length × average wetted width from Manning equation). Thus, spawning density can increase due to both salmon entering the spawning reach, as well as reductions in wetted area associated with lower discharges. In the respiration component of the model, we assumed an approximate individual pink salmon mass of 2 kg and a swim speed of 50 cm/s (approximately 1 body length/s). Once parameterized, model simulations were compared against empirical DO data for the Indian River.

Sensitivity analysis

To evaluate conditions that may result in hypoxia, we conducted a global sensitivity analysis. We ran the model approximately 15,000 times with different values of salmon abundance, stream discharge, and water temperature to produce approximately 15,000 independent estimates of DO. The ranges of values used in this analysis were as follows: (1) salmon abundance, 0–100 spawners/m; (2) stream discharge, 0.01–20 m^3/s; and (3) water temperature, 0–20°C. These ranges fully incorporated the conditions observed in the Indian River, as well as conditions outside the observed range. These model runs were used to produce response surfaces that visually illustrate threshold values of temperature and discharge that may produce hypoxia at low (10 spawners/m), medium (40 spawners/m), and high (70 spawners/m) salmon densities. We report linear spawning densities (spawners/m), rather than areal densities (spawners/m^2), because linear densities are not influenced by discharge. Reductions in modeled discharge, however, concurrently influence modeled DO due to decreasing atmospheric reaeration rates as well as increasing areal estimates of salmon respiration (higher respiration per unit area).

RESULTS

Indian River

During the 2010–2015 ice-free seasons in the Indian River, DO regimes were highly variable but displayed periods of sharp decreases during July, August, and September when river stage was low and spawning pink salmon were present (Fig. 2). Across all measurements, hourly point measurements of DO concentration ranged from 1.7 to 14.0 mg/L and DO saturation ranged from 16% to 112% (Fig. 2). Hourly water temperature ranged from 2.2° to 12.6°C. Hypoxic conditions, which we defined as DO concentrations <7 mg/L and saturation <70% (Davis 1975), were observed over a five-day period in 2012 (28 August–1 September) and a 37-d period in 2013 (29 July–4 September). Brief periods (several hours to approximately one day) of DO conditions greater than our thresholds for hypoxia were included in these event summaries when they were bounded by periods of hypoxia. During the five-day 2012 event, DO levels were reduced below hypoxic thresholds for only 18% of hourly measurements. Dissolved oxygen concentrations ranged from 7.0 to 9.7 mg/L, DO saturations ranged from 60% to 84%, and the peak salmon density occurred approximately 12 d before hypoxia developed (16 August; Fig. 2). During the 37-d 2013 hypoxic period, DO levels were reduced below hypoxic thresholds for 91% of hourly measurements. Dissolved oxygen concentrations ranged from 1.7 to 10.1 mg/L, DO saturations ranged from 16% to 86%, and peak salmon density occurred in the middle of the event (9 August; Fig. 2).

Each year, peak daily salmon estimates in the Indian River occurred between 3 and 27 August and ranged from approximately 80,000 individuals in 2015 to 295,000 in 2013 (Fig. 2). Average August river stage from 2010 to 2015 ranged from 6.26 to 6.54 m with an August minimum single measurement of 6.19 m and maximum of 8.18 m. During the minimum DO measurement of 1.7 mg/L on 29 August 2013, river stage was 6.21 m (Fig. 2). A 15-min streamside survey conducted <24 h after the minimum DO measurement discovered juvenile cutthroat trout and Dolly Varden mortalities exhibiting signs of asphyxiation such as flared opercula (Fig. 2, Photo A; S. Gende, National Park Service, *unpublished data*). Concurrently, in the same stream reach, 88% of haphazardly surveyed body cavities of 100 dead female pink salmon had most of their ripe eggs intact, suggesting a large prespawn mortality event (S. Gende, National Park Service, *unpublished data*).

Sawmill Creek

From 1 June to 21 August 2015, DO loggers placed in three locations in Sawmill Creek revealed high longitudinal variability in DO regimes in relation to relative stream stage, seawater inundation due to tidal fluctuations, and spawning salmon (Fig. 3). Across all measurements, DO concentrations ranged from 2.9 to 14.8 mg/L and DO saturations ranged from 26% to 124% (Fig. 3). Water temperature ranged from 6.1° to 15.6°C. The two uppermost DO loggers did not record any hypoxic conditions during the study period, but DO trends progressively decreased moving downstream (Fig. 3). In the waterfall plunge pool at river km 0.6 and at river km 0.4, DO concentration ranged from 8.0 to 13.1 mg/L and DO saturation ranged from 70% to 103%. At river km 0.0 (mean high tide line), DO concentration ranged from 2.9 to 14.7 mg/L and DO saturation ranged from 25% to 124%. At this lowest DO logger, high tides occasionally inundated the site with seawater and created temporary DO spikes (Fig. 3).

Two hypoxic events occurred at river km 0.0. The first event occurred for approximately 1.5 h overnight on 25 and 26 July during a spike in pink salmon abundance, while the second event lasted for at least 22 d from 30 July to 21 August, when DO loggers were retrieved (Fig. 3). During the second event, DO concentration ranged from 2.9 to 11.3 mg/L, DO saturation ranged from 26% to 98%, and peak salmon density occurred in the middle of the event (17 August; Fig. 3). Brief periods of increased DO during this event corresponded with isolated precipitation and tidal seawater inundation (Fig. 3).

Peak daily salmon counts occurred on 20 July for chum salmon ($n = 137$) and 17 August for pink salmon ($n = 685$ for index reach; Fig. 3). During the monitoring period, relative river stage ranged from 38 to 76 cm. The minimum DO measurement of 2.9 mg/L was recorded on 9 August when river stage was between 38 and 40 cm (nearly the lowest observed) and temperature was 10.4°C (Fig. 3).

DO modeling

The magnitude and pattern of the oxygen reaeration–salmon respiration DO model generally matched field-observed DO trends, and the two time series were highly correlated across all study years (Spearman's rank correlation coefficient 0.73–0.97, all $P < 0.001$; Fig. 4; Appendix S2). Model residuals ranged from −2.11 to 5.87 mg/L and were largest during the peak spawning

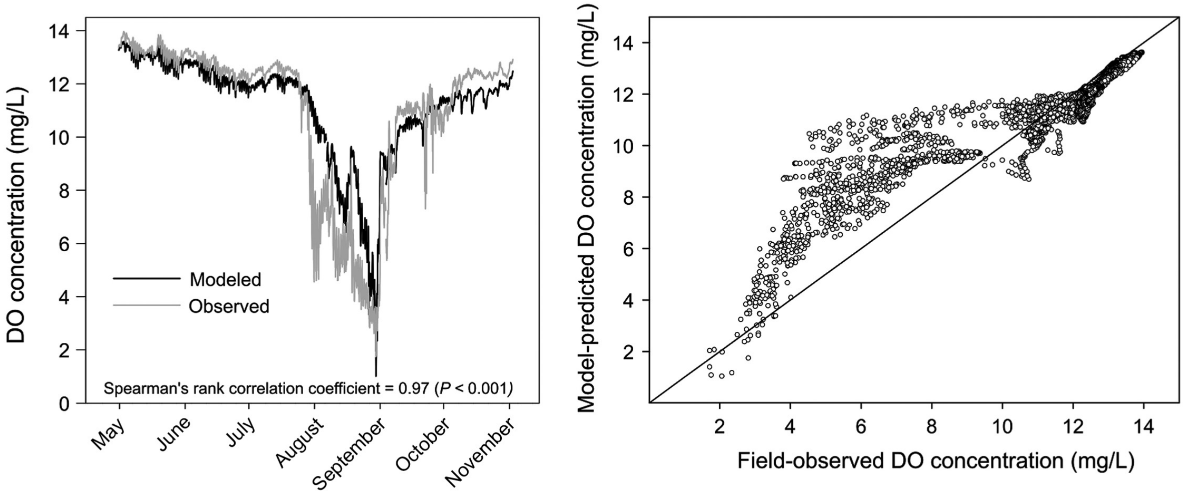

Fig. 4. Dissolved oxygen (DO) model vs. field DO measurements. Left panel compares modeled (black line) DO time series to field observations (gray line) during 2013. Right panel is a scatter plot of modeled vs. field DO measurements; black line represents 1:1 values.

months of August and September (Fig. 4; Appendix S2). The model tended to over-predict DO values from approximately 4 to 10 mg/L, which occurred during sharp transitions from high to low oxygen events. Model results most closely matched field-observed DO from 2–4 mg/L to 10–14 mg/L (Fig. 4; Appendix S2). In general, shifting discharge values by ±20% within the model had a minimal impact on predicted DO values. Across all modeled years except 2013, there was no notable difference in DO predictions across the range of tested discharge values, but some divergence was present in 2013 once DO levels dropped below 9.0 mg/L. During that year, residuals between modeled DO using the stage–discharge relationship and modeled DO using ±20% discharge ranged from −1.2 to 1.6 mg/L (Appendix S3).

Modeled sensitivity analyses revealed that the presence of spawning salmon, even in high densities, does not necessarily result in hypoxia or low DO (Fig. 5). When river discharge was relatively high, and/or water temperature low, salmon respiration did not appear to strongly influence on DO levels. Rather, hypoxia was only predicted when high salmon densities coincided with lower discharges and higher water temperatures. Specific combinations of discharge and temperature that induce hypoxia depend on the density of salmon in the stream. At low salmon densities for the Indian River (10 spawners/m), the thresholds of discharge (<0.01 m^3/s) and water temperature (>12°C) necessary to trigger hypoxia are limited and unlikely to occur (Fig. 5). A typical annual low discharge measurement in the Indian River ranges from 0.4 to 0.6 m^3/s (Neal et al. 2004, Sergeant and Schwarz 2017), and the maximum water temperature from the 2010 to 2016 monitoring seasons was 12.6°C. At medium salmon densities (40 spawners/m), salmon respiration was predicted to create hypoxia across a broader range of discharge (<0.2 m^3/s) and water temperature (>6°C; Fig. 5). At high salmon spawning densities (70 spawners/m), the range of discharge (<0.7 m^3/s) and water temperature (>6°C) that resulted in hypoxia were much greater (Fig. 5) and are well within the range of conditions that occur annually in the Indian River.

DISCUSSION

We provide compelling evidence that spawning salmon can create hypoxia, even in low-productivity streams with relatively cold thermal regimes. Our combination of field observations and modeling illustrates that low summertime river discharge is a precursor to salmon-induced hypoxia. In the rainfall- and snowmelt-dominated watersheds of southeastern Alaska,

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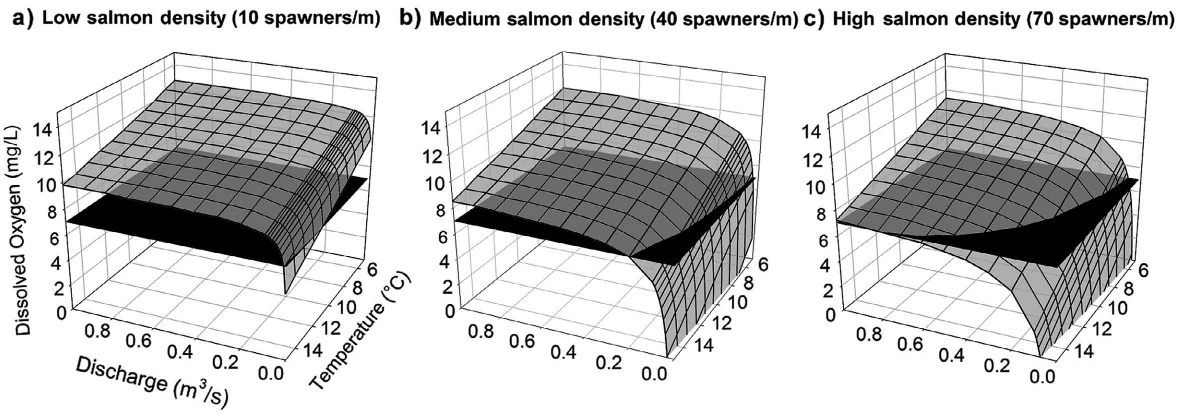
a) Low salmon density (10 spawners/m) b) Medium salmon density (40 spawners/m) c) High salmon density (70 spawners/m)

Fig. 5. Three-dimensional model representation of Indian River dissolved oxygen dynamics (mg/L) based on varying discharge (m^3/s) and water temperature (°C) across three pink salmon spawning densities (spawners/m). The flat black plane represents our defined hypoxic level of 7 mg/L.

we expect increases in the future frequency and magnitude of hypoxic events due to decreasing winter precipitation falling as snow, decreasing summer precipitation during warm PDO phases, and warming air temperatures (Neal et al. 2002, Shanley and Albert 2014, Shanley et al. 2015). Hypoxic events may also be intensified by human-mediated actions that further increase spawning densities such as straying hatchery salmon and water diversion. By combining high-frequency water quality monitoring data with a mechanistic model, accurate predictions of DO can be made using relatively simple datasets that include salmon counts and watershed habitat characteristics.

The results from our study systems illustrate that low discharge can be the primary physical driver of three phenomena that combine to deplete DO: (1) Reduced water turbulence decreases oxygen reaeration with the atmosphere, (2) reduced water volume for spawning salmon increases areal respiration rates, and (3) increased water temperature decreases DO saturation concentration and increases salmon respiration. Thus, similar numbers of spawning salmon may have very different effects on DO in different water years depending on flow and thermal regime variation.

Our model effectively predicted DO trends and magnitude in comparison with field measurements despite excluding primary production and overall ecosystem respiration (Fig. 4; Appendix S2). We hypothesize that under-predicted values in the spring resulted from excluding photosynthesis by primary producers, while over-predicted values in the fall may have been caused by excluding additional components of ecosystem respiration beyond live salmon respiration, particularly oxygen use by decomposing salmon carcasses. During periods of low discharge, the importance of decomposition increases as carcass retention is likely very high in slow-flowing habitat features such as deep pools. Although the model was coded specifically for the Indian River, its low gradient floodplain channel is typical of many pink and chum salmon streams in the NPCTR (Paustian 1992). Thus, we expect DO response surfaces (Fig. 5) to be broadly representative of the conditions that can produce hypoxia in small- to medium-sized watersheds with runoff dominated by rainfall and snowmelt. The mechanisms of hypoxia we describe were parallel to recent similar research conducted in a small southwestern Alaska stream (Tillotson and Quinn 2017). Our model may not perform as well in small- to medium-sized watersheds in the NPCTR with high percentages of wetland coverage (>30%) and more complicated groundwater dynamics or lake systems contributing significant flow to downstream channels (e.g., see Peterson Creek in Fellman et al. 2015).

In addition to the DO dynamics we describe here, past field observations of depleted DO conditions in southeastern Alaska streams were also caused by two additional mechanisms: (1) inundated intertidal stream channels becoming overcrowded with stranded salmon and hypoxic after tidal marine waters retreat and (2) elevated surface water temperatures originating from upper watershed lakes reducing oxygen solubility downstream (Murphy 1985). Lakes and dendritic intertidal channels were not present in either of our study systems. Our data from Sawmill Creek demonstrate that DO in tidally influenced channels with simple morphology can also be recharged during seawater inundation (Fig. 3). In similar systems, hypoxic events may result in intertidal spawners being the most successful spawning cohort during a given year. However, the success of fertilized eggs within the intertidal zone may be limited by high salinity (Bailey 1964).

Beyond natural drivers of DO depletion, human impacts such as hatchery straying and water diversion may increase the probability of hypoxia. Comprehensive data on salmon straying rates and mechanisms for straying behavior are sparse, but pink and chum salmon appear to have the highest propensity for straying among all Pacific salmon species (Quinn 2005). In Prince William Sound, Alaska, 77% of surveyed streams contained hatchery pink salmon from three or more hatcheries, and hatchery strays comprised 0–98% of pink salmon escapement within individual streams (Brenner et al. 2012). In the Indian River from 2013 to 2015, 0–62% of sampled pink salmon carcasses were hatchery strays (S. Gende, National Park Service, *unpublished data*). In Sawmill Creek during 2015, hatchery chum salmon strays comprised 51% of total number of spawning chum (C. McConnell, *unpublished data*), although they were a small percentage of total salmon escapement in comparison with wild pink salmon (Fig. 3). An earlier Sawmill Creek study conducted in 2009 and 2010 found that 78% and 44% of sampled chum salmon carcasses, respectively, were hatchery strays (Piston and Heinl 2012). Even though stray rates tend to decrease as the distance from hatchery release sites increases (Brenner et al. 2012, Piston and Heinl 2012), continuing hatchery production levels and widely distributed juvenile salmon release sites in southern Alaska will likely keep the potential for continued straying to many coastal river systems high (Stopha 2015). While hypoxia-induced mortality before successful spawning would potentially create a density-dependent decline in the productivity of wild salmon populations (Quinn et al. 2007, Tillotson and Quinn 2017), hatchery populations, which only require small numbers of spawners to maintain production goals, do not receive this population feedback and have the potential to continue supplying large numbers of strays to streams in years immediately following die-off events. Thus, resident fishes in streams that are repeatedly populated with high densities of straying salmon may experience long-term declines in productivity, but data are currently lacking to strongly support this possibility.

In some systems, water diversions may combine with hatchery strays to cumulatively deplete DO levels. The Sheldon Jackson Salmon Hatchery, which operates approximately 1 km from the mouth of the Indian River, diverts water from the Indian River to maintain operations. Data are limited, but from October 1998 to September 2000, daily diversion discharge ranged from 0.11 to 1.16 m^3/s, and during August 1999 and 2000, it ranged from 0.42 to 0.85 m^3/s (USGS gage 15087730, http://waterdata.usgs.gov/nwis). During August in years 2013–2016, the mean diversion rate was 0.25 m^3/s, while the maximum was 0.45 m^3/s (T. Schwarz, Alaska Department of Natural Resources, *personal communication* 10 November 2016). During these periods, an unknown amount of water was returned to the Indian River approximately 0.4 river km below our DO monitoring location. Our model demonstrates that during high salmon density periods (70 spawners/m), a discharge reduction from 0.6 to 0.3 m^3/s at 12°C can equate to a DO drop of 1.0 mg/L (Fig. 5), so it is likely that both strays from the hatchery and water diversion cumulatively contribute to seasonal DO depletion. Based on the evidence presented here, it appears that hypoxia in nearby streams could be an underappreciated risk stemming from hatchery operations.

Management applications

While the combinations of discharge, water temperature, and salmon density that trigger hypoxia will differ based on individual watershed variation in stream channel morphology and flow regime drivers, our model could easily be parameterized to specific streams to create real-time predictive models of DO trends based on current observed salmon density and short-term predictions of discharge. In watersheds impacted by flow diversion and hatchery stray salmon, local stakeholders could collaboratively examine the effect of future management actions on DO levels using an intuitive model visualization tool (we have developed an online example at https://goo.gl/WY3seH). For other watersheds with historical salmon density and habitat data, this model could also explore the past frequency of hypoxic events in comparison with future events and create watershed-scale predictions of hypoxia risk across the study region. Our general modeling approach could be built upon to be applicable in other systems, such as those with large-scale migrations of spawning suckers (Childress et al. 2014).

In addition to hatchery operations, mining and hydropower are two common land uses that also divert water. Many small-scale hydropower operations are planned for southeastern Alaska communities in response to rising costs of diesel power generation (Cherry et al. 2010, Ray 2011). Future and current hydropower projects should consider electrical generation methods that minimize flow diversion from spawning salmon reaches and mitigate for warm surface waters created by reservoirs (Olden and Naiman 2010). As these land uses progress in the NPCTR, careful consideration of best practices can assist in balancing community needs with the health of freshwater ecosystems.

These local drivers of hypoxia will likely combine with regional-climate trends to decrease discharge magnitude for some streams; thus, the prevalence of hypoxic events may increase in the future. Given this likelihood, it will be critical to understand how these events impact the future productivity of individual salmon populations. We are unaware of any studies evaluating the potential influence of hypoxia on the productivity of anadromous and resident stream fishes. A first step to achieving this goal is to assess trends across a greater number of streams and variety of watershed types to determine the extent to which hypoxia risk and impact are system dependent. Future modeling and mechanistic interpretation of DO trends within individual watersheds would benefit from more rigorous estimates of salmon density and collecting longitudinal DO time series across multiple years from above and below anadromous migration barriers. Understanding the level of threat to freshwater ecosystem integrity presented by hypoxia in the NPCTR and the appropriate management responses will involve continued commitments to long-term ecosystem monitoring, applied research, and cooperative adaptive management of aquatic resources among stakeholders.

In general, our data demonstrate the importance of collecting and maintaining long-term water quality data for rivers that go beyond water temperature and across varying gradients of human impact. These time series data, in combination with continued research on hatchery to wild salmon proportions on spawning grounds and rates of pre-spawn mortality (Quinn et al. 2007, Tillotson and Quinn 2017), will allow ecologists and managers to collaboratively develop and apply models that explore the potential for hypoxia-driven mortality to influence anadromous and resident stream fish population productivity. While preserving thermally suitable stream habitat for cold-water taxa facing climate change has become an important land management priority (e.g., see Isaak et al. 2016), managers should also consider that some protected watersheds may still be at risk of increasingly frequent hypoxia due to cumulative human impacts such as water diversion and artificially abundant salmon populations caused by hatchery straying.

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Hypoxia vulnerability in the salmon watersheds of Southeast Alaska

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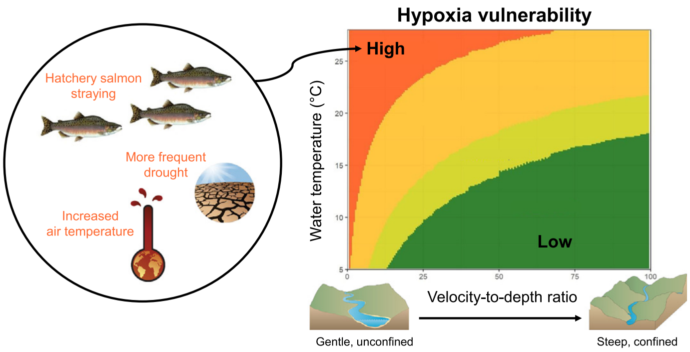
HIGHLIGHTS

- Freshwater hypoxia and implications for northern species remain poorly understood.
- Drought and artificially high fish densities can interact to cause hypoxia.
- Our hypoxia model combines channel hydraulics, water temperature, and fish density.
- Mapped spatial variability of watershed hypoxia vulnerability in 91,000 km^2 region
- Our repeatable methodology identifies watersheds at risk of hypoxia.

GRAPHICAL ABSTRACT



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ABSTRACT

The frequency of dissolved oxygen depletion events (hypoxia) in coastal aquatic ecosystems has risen dramatically since the late 20th century, yet the causes and consequences of hypoxia for some culturally and economically important species remain poorly understood. In rivers, oxygen depletion can be caused by high densities of spawning Pacific salmon (*Oncorhynchus* spp.) consuming oxygen faster than can be replaced by reaeration. This process may be exacerbated when salmon densities are artificially inflated, such as when hatchery-origin salmon stray into rivers instead of returning to hatcheries. In Southeast Alaska, hatchery salmon production has increased rapidly since the 1970s, with over 553 million chum salmon (*O. keta*) and 64 million pink salmon (*O. gorbuscha*) released in 2021 alone. Straying is pervasive in streams with outlets <25 km from nearshore marine hatchery release sites. Using a previously ground-truthed mechanistic model of dissolved oxygen dynamics, we examined how water temperature and low-flow channel hydraulics contribute to hypoxia vulnerability. We then applied the model to predict hypoxia vulnerability for watersheds within 25 km of hatchery salmon release points, where straying salmon spawner densities are expected to be higher and promote dissolved oxygen depletion. Our model predicted that low-gradient stream reaches, regardless of water temperature, are the most prone to hypoxia due to low reaeration rates. Our spatial analysis determined that nearly 17,000 km of anadromous-accessible stream reaches are vulnerable to high densities of hatchery-origin salmon based on 2021 release sites. To our knowledge, this study is the first to map the spatial variation of hypoxia vulnerability in anadromous watersheds, identify habitat conditions most likely to promote hypoxia, and provide a repeatable analytical approach to identify hypoxia-prone stream reaches that can be updated as empirical data sets improve.

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1. Introduction

In coastal aquatic ecosystems world-wide, the frequency of dissolved oxygen depletion events (also called, 'hypoxia') has increased dramatically since the late 20th century (Vaquer-Sunyer and Duarte, 2008). Hypoxia can result from causes such as drought (Magoulick and Kobza, 2003), decomposition of organic material (Dahm et al., 2015; Whitworth et al., 2012), high water temperature (Rabalais et al., 2010), or respiration by dense populations of organisms such as aquatic plants (Caraco and Cole, 2002) and Pacific salmon (*Oncorhynchus* spp., hereafter referred to as 'salmon'; Sergeant et al., 2017). As climate change and human competition for water increase the potential for drought and high water temperatures (Dudgeon et al., 2006), it is important to better understand the specific physical and biological conditions that expose groups of species to hypoxia. Bouts of hypoxia lasting hours to several days may lead to sublethal effects or large mortality events for aquatic organisms (La and Cooke, 2011). Therefore, improving our ability to predict hypoxia in various settings is important for conserving and managing the abundance and biodiversity of aquatic ecosystems. Here, we focus on culturally and economically important salmon populations in northern latitudes (Carothers et al., 2021; Johnson et al., 2019). Even though these fish remain generally abundant (Ruggerone et al., 2010), reports of hypoxia-related mortality from individual watersheds have become more frequent due to combinations of low streamflow, high water temperature, and dense spawning populations (Murphy, 1985; Sergeant et al., 2017; Tillotson and Quinn, 2017; von Biela et al., 2022).

Salmon migrate from the ocean upstream to their natal rivers or lakes for spawning. These migrations may end abruptly at the intertidal mouth of small streams or range thousands of km into large watersheds (Quinn, 2018). At any point during these migrations, several known mechanisms lead to *premature mortality*, defined as the in-river death of adult salmon migrating upstream or holding on the spawning grounds before depositing their gametes (Bowerman et al., 2016). In many rivers, especially in the southern range of salmon, prolonged and elevated water temperatures >18 °C can increase the rate of premature mortality by delaying spawning migration, rapidly depleting energy reserves, increasing disease risk, and exceeding cardiovascular limits for delivering oxygen to body tissues at pace with increasing metabolic demand (Hinch and Martins, 2011; Strange, 2012; Bowerman et al., 2018). In the northern range of salmon (~>52°N), there is less historical evidence of in-river heat stress, but notable exceptions have recently been documented in the Yukon River basin (von Biela et al., 2020; Westley, 2020) and Bristol Bay watersheds (Quinn et al., 2007). Hypoxia is a related mechanism of premature mortality. Observations of hypoxia-related mortality dating back to at least the 1940s suggest that spawning salmon can respire oxygen faster than it can be replaced by the atmosphere when spawning densities are high and reaeration rates are low, even when water temperatures are relatively cool (<12 °C; Murphy, 1985; Sergeant et al., 2017).

Water temperature, streamflow, channel hydraulics, and spawning density are key predictors of summer and autumn dissolved oxygen dynamics (Fellman et al., 2018; Sergeant et al., 2017). The capacity for water to hold oxygen molecules decreases as water temperature increases (Benson and Krause, 1980). Thus, sufficient oxygen reaeration via gas exchange at the air-water boundary may not occur when periods of drought increase water temperature and reduce stream velocity and turbulence, especially in low-gradient stream reaches (Garvey et al., 2007; Hall and Ulseth, 2020). Broad-scale climate patterns also play an important role in dissolved oxygen dynamics. Future snowpack reductions will likely exacerbate the severity of drought by supplying less meltwaters to rain- and snow-fed watersheds in the summer. Even though mean annual precipitation is predicted to increase up to 18 % in Southeast Alaska by the 2080s, mean annual precipitation falling as snow may decrease as much as 58 % (Shanley et al., 2015). The combination of reduced snowpack and warmer summer air temperatures is expected to generally increase water temperatures during salmon spawning windows (Shaftel et al., 2020; Winfree et al., 2018) except in watersheds where substantial glacier coverage (>30 %) remains (Fellman et al., 2014). Based on this knowledge, we expect that hypoxic conditions harmful to salmon are most likely to occur in low-gradient streams with relatively warmer water (>~15 °C) that receive most of their flow from rain and are more prone to summer drought. In addition to these atmospheric and physical habitat controls, respiration by spawning salmon themselves can further reduce dissolved oxygen levels when stream reaeration rates are low. Oxygen consumption rates by individual salmon can range from 10s to 100s of mg O_2/kg/h depending on swimming speed and water temperature (Brett, 1972).

In southern coastal Alaska, where many salmon populations remain abundant, hypoxia-related mortalities can occur during periods of high wild-origin spawner abundance (Murphy, 1985; Tillotson and Quinn, 2017) or can be exacerbated by large numbers of hatchery-origin salmon that stray into natural spawning grounds instead of being harvested in fisheries or returning to hatcheries (Brenner et al., 2012; Josephson et al., 2021; Knudsen et al., 2021; Piston and Heinl, 2012; Sergeant et al., 2017). Hatchery salmon production in Southeast Alaska started during the 1970s, and total release numbers steadily increased leading up to the turn of the 21st century (Wilson, 2021). Since 2005, juvenile pink (*O. gorbuscha*) and chum (*O. keta*) salmon, which comprise most of Alaska's hatchery-raised salmon, have been released at 30 different nearshore marine sites across Southeast Alaska. Annual releases of juvenile chum salmon have ranged from approximately 0.2 to 87 million individuals per site, while juvenile pink salmon releases have ranged from approximately 0.1 to 97 million individuals per site (https://mtalab.adfg.alaska.gov/CWT/Reports/). In 2021 alone, over 553 million chum salmon were released from 21 sites across Southeast Alaska, while over 64 million pink salmon were released from three sites.

Hatchery-origin salmon mature in the ocean and migrate back toward their nearshore marine release sites. If not captured in a fishery, some individuals will enter rivers located near hatchery release sites and attempt to spawn naturally. Studies conducted in Southeast Alaska between 2008 and 2015 showed that the proportion of hatchery-origin conspecific spawners can be as high as 90 % in watersheds with coastal outlets <25 km from a release site, (Josephson et al., 2021; Piston and Heinl, 2012). From 2013 to 2015, 0.4–1.2 % of the total Southeast Alaska hatchery chum salmon returns were estimated to stray to 81 study streams (Josephson et al., 2021). Recent studies stress the potential effects of hatchery introgression on wild population fitness (reproductive success), but less attention is paid to the acute ecological impacts from hypoxia events, such as premature mortality of naturally spawning salmon and other resident stream fishes such as cutthroat trout (*O. clarkii*) and Dolly Varden (*Salvelinus malma*) (for example, as documented in Sergeant et al., 2017). These acute impacts may conflict with the Alaska salmon hatchery program's goal of protecting and maintaining the abundance of wild salmon stocks (Heard, 2012), but the empirical data necessary to quantify the ecological impacts and prevalence of hypoxia (e.g., stream density of hatchery- versus natural-origin spawners, continuous water temperature/streamflow/dissolved oxygen time series) are widely lacking. Considering these limitations, we present three related analyses that combine best available modeled and empirical datasets with a ground-truthed mechanistic model of dissolved oxygen dynamics to identify specific stream reaches and general habitat conditions where salmon-related hypoxia events are most probable:

(1) The first analysis calculates summertime hypoxia vulnerability across Southeast Alaska for 62 stream reaches with hourly water temperature data. These streams represent culturally important salmon populations and a range of watershed types across the region, although they are not statistically representative of the variability present in the region. The metric for hypoxia vulnerability was defined as the estimated density of spawning salmon necessary to create hypoxic conditions—defined here as a dissolved oxygen level of 7 mg/L or less, following Sergeant et al. (2017)—in each stream reach based on channel hydraulics, hourly water temperatures, and salmon bioenergetics.

(2) To explore a broader set of combinations of habitat characteristics than were present in the 62 monitored watersheds, we calculated and

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visualized hypoxia vulnerability over a range of low-water velocity, depth, and temperature conditions to illustrate the mechanistic interplay between these factors and hypoxia vulnerability. A realistic range of values for each characteristic was based on data from the 62 stream reaches.

(3) Lastly, for the tens of thousands of stream reaches in Southeast Alaska lacking water temperature data but at risk for high salmon spawning densities due to hatchery straying, we predicted and mapped hypoxia vulnerability for anadromous-accessible stream reaches in watersheds with outlets <25 km from 2021 hatchery release sites.

To our knowledge, this study is the first to map the spatial variation of hypoxia vulnerability in anadromous watersheds, identify habitat conditions most likely to promote hypoxia, and provide a repeatable analytical approach to identify hypoxia-prone stream reaches as empirical datasets improve.

2. Methods

2.1. Study area

The streams included in this study (Fig. 1) fall within Southeast Alaska, the southern boundary of which begins at the maritime zone known as Dixon Entrance (approximately 54.52°N, 131.65°W) and stretches northwesterly along the Alaska coastline to Icy Bay (approximately 59.96°N, 141.44°W). Based on climate normals calculated from 1991 to 2020 (https://www.ncei.noaa.gov/access/us-climate-normals/), average annual rainfall ranges from 64 cm in Skagway to 380 cm in Ketchikan. Much of this rainfall (63 %) occurs during salmon spawning and embryo incubation between September and February. Average annual air temperature across the region is approximately 6 °C, with an average June–August temperature of 13 °C (minimum and maximum average summer values range from approximately 9 °C to 18 °C). This region is part of the larger Northern Pacific Coastal Temperate Rainforest (O'Neel et al., 2015) and consists of four ecologically distinct regions: Alexander Archipelago, Boundary Ranges, Chugach-St. Elias Mountains, and Gulf of Alaska Coast (Nowacki et al., 2003). The extensive ice coverage, steep terrain, and abundant vegetation creates a diversity of watersheds exposed to climate patterns ranging from wet and mild maritime to drier and colder continental climates. Twelve distinct categories of streamflow patterns in approximately 2600 coastal watersheds ranging from 5 to 54,770 km^2 reflect different combinations of rain, snow, and glacier runoff (Curran and Biles, 2021; Sergeant et al., 2020).

2.2. Water temperature and channel hydraulics data

The hypoxia vulnerability calculation described in the next sub-section (Eq. (2)) requires inputs for water temperature and channel hydraulics that include width, depth, and velocity. We describe how we aggregated those inputs here. The 62 water temperature monitoring sites used in this analysis represented a wide range of watershed and stream channel characteristics across Southeast Alaska (Table 1). Water temperature data were aggregated by "site-summer," which we defined as a unique stream location having at least 90 % of hourly water temperature measurements during July 1–September 30 of a single year. This time frame overlaps with periods when spawning salmon densities, primarily pink and/or chum salmon, have the potential to be very high and contribute to hypoxic conditions via respiration. Individual stream locations across Southeast Alaska (n = 62) had from 1 to 12 site-summers available for analysis, totaling 275 site-summers of water temperature across the years 2008–2021 (Fig. 1).

Water temperature data were collected by many organizations across Southeast Alaska, including federal, state, Tribal, university, and non-profit groups. Most water temperature data were curated by the Southeast Alaska Freshwater Temperature Monitoring Network (https://www.alaskawatershedcoalition.org/southeast-alaska-stream-temperature-monitoring-network/). The network supplies data collectors with temperature loggers (Hobo TidbiT or Pro v2, Onset Computer Corporation, Bourne, Massachusetts), which have a precision of <0.2 °C and are validated against

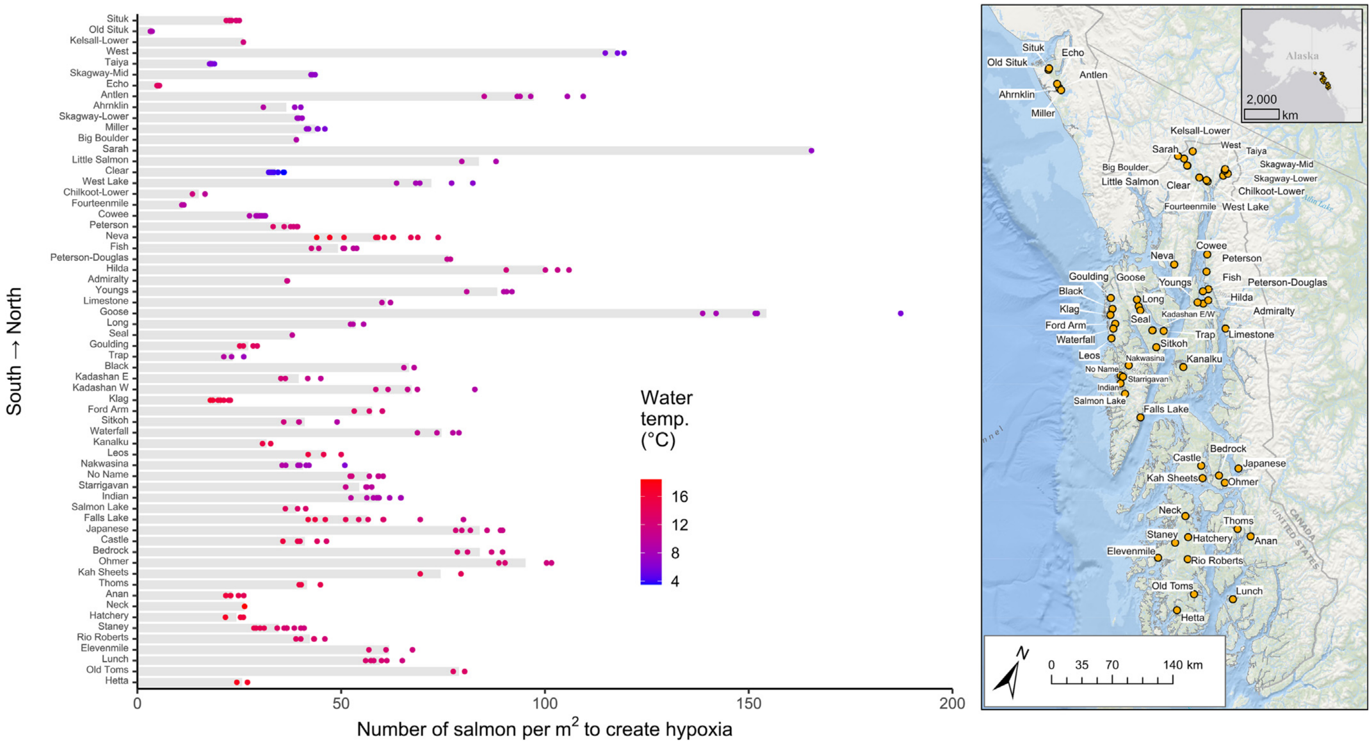

Fig. 1. Hypoxia vulnerability at each water temperature monitoring site in Southeast Alaska represented by the estimated number of pink salmon/m^2 to create hypoxia (7 mg/L). (A) Average hypoxia vulnerability across all monitored years for each site (gray bars). Sites are ordered from south to north. Individual points correspond to the average hypoxia vulnerability metric for a given site-summer and are color-coded by average summer water temperature. (B) Locations for all water temperature monitoring sites in Southeast Alaska (n = 62) used in this analysis. The map was created using the Ocean Basemap in ArcMap 10.8.2 (Esri, Redlands, California).

a NIST-certified thermometer at 0 °C and room temperature (~20 °C), following standardized protocols for Alaska (Mauger et al., 2015). Loggers are shaded within a PVC housing with holes through which water may rapidly flow. Housings are either attached to a stable bank structure with steel cable or anchored to the streambed. Temperature data are not representative of surface water if a logger is exposed to air, frozen, or buried in sediment. To identify potential non-surface water temperatures, data were automatically flagged for large diurnal variability, rapid hourly temperature changes, and extreme low and high temperatures. All data were subsequently visualized, and suspect data were manually removed after reviewing automated flags, field notes, and comparing to air temperature data, when available. Values were averaged at a site when two loggers were deployed within 15 m of each other and not influenced by different water sources. Other water temperature data were downloaded from publicly available sources following published monitoring protocols and quality control procedures such as the U.S. Geological Survey (https://waterdata.usgs.gov/nwis) and the U.S. National Park Service (Goodwin et al., 2021).

For each water temperature monitoring location and anadromous stream reaches without water temperature data, we used the NetMap synthetic stream network (Benda et al., 2016, 2007) for the Tongass National Forest (derived from a 20-m or finer resolution digital elevation model) to extract watershed attributes of interest (Clarke et al., 2008), including channel gradient (m/m), bankfull width/depth (m), bankfull velocity (m/s), bankfull discharge (m^3/s), roughness (unitless Manning's n), upstream basin area (km^2), mean basin elevation (m), and mean annual precipitation (m). For each water temperature monitoring site, attributes were averaged across all reaches surrounding the logger location from the first upstream tributary junction to the first downstream tributary junction. At two low-gradient sites (Taiya River and Clear Creek) NetMap reported channel gradients of 0 m/m, which we adjusted to 0.001 m/m to ensure the hydraulic simulations described provided a non-zero value for the low flow calculation. The 98-percent duration flow is defined as the level of discharge that is equaled or exceeded 98 % of the time over a given water year. We estimated 98-percent duration flow for the July–September time frame ($J-S98$) using a regionally calibrated regression (Wiley and Curran, 2003):

$$J - S98 = 2.532 \times 10^{-9} A^{1.142} P^{1.521} E^{1.674} \quad (1)$$

where $J-S98$ is discharge (ft^3/s), A is upstream drainage area (mi^2), P is mean annual precipitation (in), and E is upstream mean basin elevation (ft). Discharge was converted to m^3/s for subsequent calculations.

We computed the wetted channel depth (d) and velocity (V) associated with low flow conditions (98-percent duration flow) for each reach based on the estimated bankfull width, bankfull depth, bank angles (assumed 45°), channel gradient, and roughness (Manning's n) for a given site, using the Manning equation (Gordon et al., 2004). The final combination of reach-specific water temperature and low-flow channel velocity and depth were used to calculate hypoxia vulnerability.

Table 1
Minimum (Min), maximum (Max), and mean of watershed and stream channel characteristics across all water temperature monitoring sites (n = 62) in Southeast Alaska. Upstream basin area and mean basin elevation are calculated for the watershed upstream of the monitoring site.

	Min	Max	Mean
Upstream basin area (km^2)	0.2	751	70
Mean basin elevation (m)	26	1124	435
Mean annual precipitation (m)	1.0	5.6	2.7
Mean summer water temperature (°C)	3.5	18.4	10.9
Gradient (m/m)	0.001	0.111	0.032
Bankfull width (m)	4.4	43.3	18.7
Bankfull depth (m)	0.4	0.8	0.6
Bankfull velocity (m/s)	1.3	5.0	3.6

2.3. Calculating hypoxia vulnerability at water temperature monitoring sites

We defined the metric for hypoxia vulnerability as the density of pink salmon necessary to reduce dissolved oxygen in a given stream reach at ambient water temperature from full saturation (which ranges from 14.6 mg/L at 0 °C to 7.8 mg/L at 28 °C) to 7 mg/L, which is the threshold at which biologists have observed decreased swimming performance and delayed upstream migration of spawning salmon (Davis, 1975; Spence et al., 1996). State of Alaska freshwater water quality regulations also state that, "DO [dissolved oxygen] must be greater than 7 mg/L in waters used by anadromous or resident fish. In no case may DO be less than 5 mg/L…" (Alaska Department of Environmental Conservation, 2020). Even at water temperatures as high as 28 °C, fully saturated dissolved oxygen levels are approximately 7.8 mg/L (Benson and Krause, 1980); therefore, until water temperatures in Southeast Alaska begin exceeding 28 °C, 7 mg/L always represents a reduction from full saturation due to biochemical oxygen demand. We chose pink salmon for this calculation because they tend to be the most numerically dominant natural spawners (Ruggerone et al., 2010) and are the most commonly documented species in mass mortality events (Murphy, 1985; Sergeant et al., 2017). There is evidence that pink salmon may have the highest respiration rates among Pacific salmon species, but comparative studies of metabolism across species and body sizes are limited (Abe et al., 2019). Our calculations could be modified to accommodate other salmon species, but this would not change the relative differences in hypoxia risk due to physical habitat characteristics across sites.

For each stream site, the number of pink salmon necessary to incite hypoxic conditions was calculated using water temperature, discharge, physical habitat characteristics, and pink salmon bioenergetics. The final metric equation was derived from a previously used model that successfully estimated dissolved oxygen in a snow-fed watershed based on atmospheric oxygen reaeration and salmon respiration (Sergeant et al., 2017; full derivation in Appendix A):

$$\frac{salmon}{L} = \frac{\frac{\left(50.8 \times V^{0.67} \times d^{-0.85}\right)}{d} \times 1.024^{(T-20)} \times \left([O_{2sat}] - 7\frac{mg}{L}\right)}{78.957 \times e^{0.086T}} \quad (2)$$

where $salmon$ is the number of pink salmon (individual mass = 2000 g), V is water velocity (cm/s), d is average water depth (cm), T is water temperature (°C), and $[O_{2sat}]$ is the dissolved oxygen concentration at atmospheric equilibrium (mg/L). In the Indian River in Sitka, Alaska, USA—where this model was originally implemented—the correlation between observed and modeled dissolved oxygen concentrations ranged from 0.73 to 0.97 across 6 years of water quality monitoring, which included a hypoxic event (Spearman's rank correlation coefficient, all $P < 0.001$; Sergeant et al., 2017).

To create a fish density with units that are more intuitive to visualize in a stream channel, we converted $\frac{salmon}{L}$ to the final response variable, $\frac{salmon}{m^2}$, using:

$$\frac{salmon}{m^2} = \frac{salmon}{L} \times d \times \frac{1000\ L}{m^3} \quad (3)$$

In Eq. (3), d is expressed in m instead of cm (as in Eq. (2)).

The hypoxia vulnerability metric was reported as the density of pink salmon (number of salmon/m^2) needed to create hypoxic conditions ($\leq$7 mg/L) averaged across all hourly water temperature measurements for a given site-summer. Therefore, *lower* values of the metric represent *higher* vulnerability to hypoxia. Hypoxia vulnerability metric values were compared against the average summer water temperatures and velocity-to-depth ratios for each site at the 98-percent duration flow for July–September, which encompasses the primary spawning timeframe in these systems. Velocity-to-depth ratios provide an indication of the general reaeration potential for a given stream reach. High values imply more turbulence and a higher potential for gas exchange at the air-water boundary.

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High velocity-to-depth ratios generally represent a steeper stream channel within a confined floodplain, while low velocity-to-depth ratios represent lower gradient stream channels with unconfined, broader floodplains (Montgomery, 1999). Quantile regressions describing relationships between hypoxia vulnerability, velocity-to-depth ratio, and water temperature were conducted in R statistical software version 3.6.2 (R Core Team, 2019) using the "quantreg" package (Koenker, 2020).

2.4. Calculating hypoxia vulnerability for combinations of velocity, depth, and water temperature

The water temperature monitoring sites provided a range of potential velocity, depth, and water temperature values that represent relevant habitat conditions for spawning salmon across the study region. We used these ranges to calculate how the hypoxia vulnerability metric (Eq. (2)) varies across all realistic combinations of channel hydraulics and water temperature. For the analysis, we considered all combinations of low-flow velocity from 1 to 100 cm/s, low-flow depth from 1 to 25 cm, and water temperature from 5 to 28 °C.

2.5. Calculating hypoxia vulnerability in stream reaches near hatchery release sites

After overlaying coastal watershed polygons in the NetMap synthetic stream network (Benda et al., 2016, 2007) with 2021 hatchery chum and pink salmon release points (n = 21; https://mtalab.adfg.alaska.gov/CWT/Reports/), we used the Euclidean Distance tool in ArcMap 10.8.2 (Esri, Redlands, California) to identify all watersheds with coastal outlets <25-km over-water distance from release sites. Within those watersheds, we conservatively assumed that all reaches with downstream channel gradients <10 % were accessible to salmon (Pitman et al., 2021). Since this portion of our analysis moved beyond just the field-monitored sites, water temperature data were not available for these reaches. To solve for the hypoxia vulnerability metric in Eq. (2), we set $T = 10^{\circ}\mathrm{C}$ and calculated V and d for low-water conditions using the same Manning equation approach described for the 62 sites where water temperature was monitored (see Section *2.2 Water temperature and channel hydraulics data*). Since the relationship between water temperature and dissolved oxygen saturation concentration is nearly linear (Benson and Krause, 1980), the calculated hypoxia vulnerability metrics for all reaches will have the same relative differences using any realistic water temperature. This created a relative metric of hypoxia vulnerability within each ~100-m stream reach delineated by NetMap. To visualize hypoxia vulnerability at the watershed-scale, we color-coded watershed polygons by discrete ranges of the mean number of pink salmon/m^2 necessary to create hypoxic conditions across all reaches. This metric calculation isolates the importance of physical habitat factors in hypoxia risk and does not consider the potential for some streams to be more vulnerable to warm water temperatures. For data interpretation, it is also important to note that in this steep coastal region, some watershed polygons do not always represent one coastal stream outlet but rather multiple coastal stream outlets from small catchments where drainage areas are often <5 km^2.

3. Results

3.1. Hypoxia vulnerability at water temperature monitoring sites

Across all site-summers (n = 275), hourly water temperatures from July through September ranged from 1.9 °C to 26.2 °C. The mean site-summer water temperature across all hourly measurements at individual sites (n = 62) ranged from 3.5 °C to 18.4 °C (site-level SD ranged from 0.2 °C to 3.9 °C with CV from 5 % to 26 %). Water temperatures tended to be cooler at northern sites where a larger number of watersheds with relatively higher mean elevation and greater extent of glacier coverage provided a greater volume of cooling meltwaters (Fig. 1). Mean site-summer water temperature across the 31 northernmost-sites was 9.5 °C (SD = 1.3 °C), while the mean for the 31 southernmost-sites was 12.2 °C (SD = 1.7 °C). Velocity-to-depth ratios at 98-percent duration flows across individual sites ranged from 0.2 to 49.1 (mean = 19.7). The estimated number of pink salmon/m^2 to create hypoxia (i.e., the hypoxia vulnerability metric) increased with higher velocity-to-depth ratios and resulted in a wedge-shaped scatter due to the influence of water temperature (Fig. 2). The hypoxia vulnerability metric ranged from 3.2 to 187.3 salmon/m^2 across all site-summers (Figs. 1 and 2). While higher velocity-to-depth ratios generally represented decreased vulnerability to hypoxia at an individual stream site, increasing mean summer water temperature for a given ratio increased hypoxia vulnerability (i.e., lowered the value of the metric). For example, at Staney Creek, which had a velocity-to-depth ratio of 17.1, the hypoxia vulnerability metric was 41 salmon/m^2 at a mean summer water temperature of 11.6 °C but 29 salmon/m^2 at 14.5 °C (Figs. 1 and 2). Across all site-summers, incidents of hypoxia vulnerability metrics above the 90th percentile range (quantile regression; $P = 0.0003$; Fig. 2) (i.e., low vulnerability) had a mean site-summer water temperature of 6.4 °C (SD = 1.7), while incidents of hypoxia metrics below the 10th percentile ($P = 0.0002$; Fig. 2) (i.e., high vulnerability) had a mean site-summer water temperature of 14.2 °C (SD = 3.4). These 90th and 10th percentile thresholds represented mean summer water temperatures where hypoxia vulnerability was especially low or high regardless of channel hydraulics.

3.2. Hypoxia vulnerability for combinations of velocity, depth, and water temperature

Modeling hypoxia vulnerability based on realistic combinations of low-flow velocity, depth, and water temperature provided insights into the non-linear, dynamic relationship among habitat conditions that create the greatest hypoxia vulnerability (Fig. 3). For example, across the lowest values of reaeration potential (represented by velocity-to-depth ratios ranging from approximately 0–10), conditions creating hypoxia at spawning densities of 0–10 salmon/m^2 become rapidly more limited in a non-linear fashion until water temperatures become >20 °C. In general, sites with high velocity-to-depth ratios appear unlikely to become hypoxic unless temperatures are high (Fig. 3). At very low stream velocities (1 cm/s), hypoxia vulnerability is high across all realistic water temperature and depth values due to a lack of reaeration. Whereas, at higher velocities (50–75 cm/s), hypoxia vulnerability becomes high primarily when water temperatures increase to >15 °C (Fig. 3).

3.3. Hypoxia vulnerability in stream reaches near hatchery release sites

We identified 157 watersheds with coastal outlets <25 km from 2021 hatchery release sites. This numerically represents 6 % of the approximately 2600 coastal watersheds >5 km^2 in Southeast Alaska (Sergeant et al., 2020) and encompasses 16,806 ~ 100-m reaches accessible to spawning anadromous salmon (Fig. 4). Velocity-to-depth ratios across all reaches ranged from 0.01 to 89.6 (mean = 11.3). This represents a broader diversity of channel hydraulics than the 62 water temperature monitoring sites described above (maximum ratio = 49.1).

Hypoxia vulnerability varied widely across watersheds and individual stream reaches. The mean hypoxia vulnerability metric ranged from 3.1 to 98.4 salmon/m^2 (mean = 40.5) across individual watersheds, while individual reaches ranged from 0.5 to 187.1 salmon/m^2 (mean = 37.4). Across all reaches, 16 % had values of the hypoxia vulnerability metric from 0.5 to 10 salmon/m^2, 46 % from 10 to 40 salmon/m^2, 24 % 40 to 70 salmon/m^2, and 13 % >70 salmon/m^2 (Fig. 5).

While Fig. 4 illustrates hypoxia vulnerability averaged across stream reaches at the watershed-scale, it does not convey the variability present at the stream reach-scale within watersheds, or the extent of anadromous stream reaches that contributed to the averages. A more detailed examination of the watersheds adjacent to the Gunnuck Creek (near Kake, Alaska) and Southeast Cove hatchery chum salmon release sites provides some insights into the types of stream reaches that influence the wide range of average hypoxia vulnerability metrics across watersheds in this area (Fig. 6).

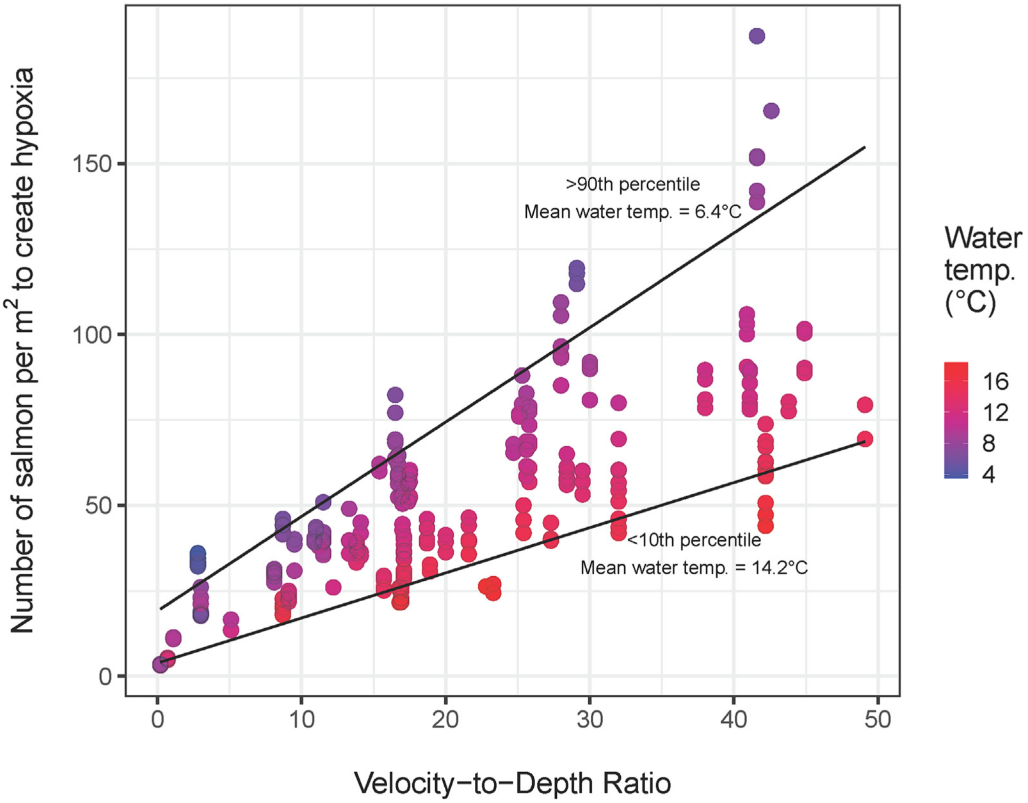

Fig. 2. Velocity-to-depth ratio vs. estimated number of pink salmon/m^2 to create hypoxia in Southeast Alaska streams. Points represent average hypoxia vulnerability across all hourly measurements for an individual site-summer and are color-coded by average summer water temperature. Black lines represent quantile regressions of sites in the 10th (high hypoxia vulnerability) and 90th percentile (low hypoxia vulnerability) of the number of pink salmon/m^2 to create hypoxia.

Hypoxia vulnerability tended to follow spatial patterns within each stream network: small tributaries and reaches near the coastal watershed outlets (where channel gradients are often low) tended to have the highest vulnerability to hypoxia while vulnerability in larger mainstem reaches with higher velocity-to-depth ratios was comparatively low (Fig. 6). In some cases, the presence of potential anadromous barriers lower in a watershed's stream network led to average watershed-scale hypoxia vulnerability metrics based on a relatively small numbers of reaches. For example, the

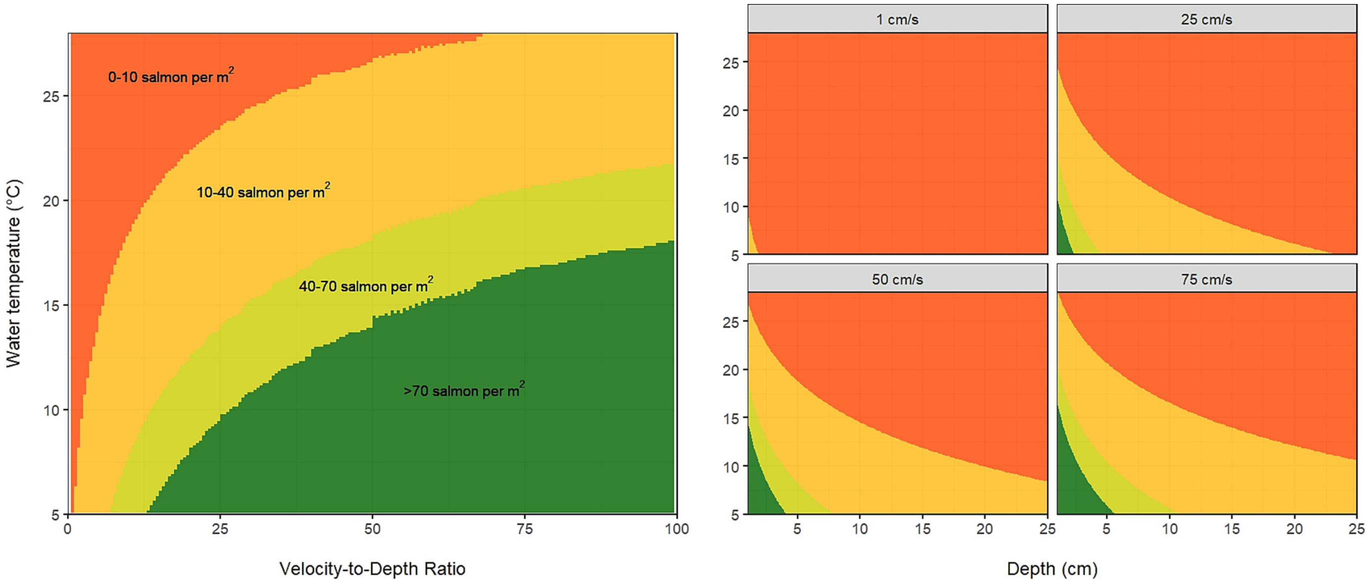

Fig. 3. Modeled contours of the estimated number of pink salmon/m^2 to create hypoxia in Southeast Alaska streams across all potential combinations of velocity, depth, and water temperature. (Left) estimated number of pink salmon/m^2 to create hypoxia based on velocity-to-depth ratio and water temperature. Cells with multiple values of the hypoxia vulnerability metric for each discrete value of velocity-to-depth ratio (e.g., $V = 5$ cm/s, $d = 1$ cm and $V = 50$ cm/s, $d = 10$ cm both have ratios $= 5$) were averaged. (Right) To avoid averaging within individual cells, the estimated number of pink salmon/m^2 to create hypoxia can also be modeled across the full range of depths and water temperatures but using discrete velocities (1, 25, 50, and 75 cm/s). Colors in both panels represent the same range of pink salmon/m^2 to create hypoxia.

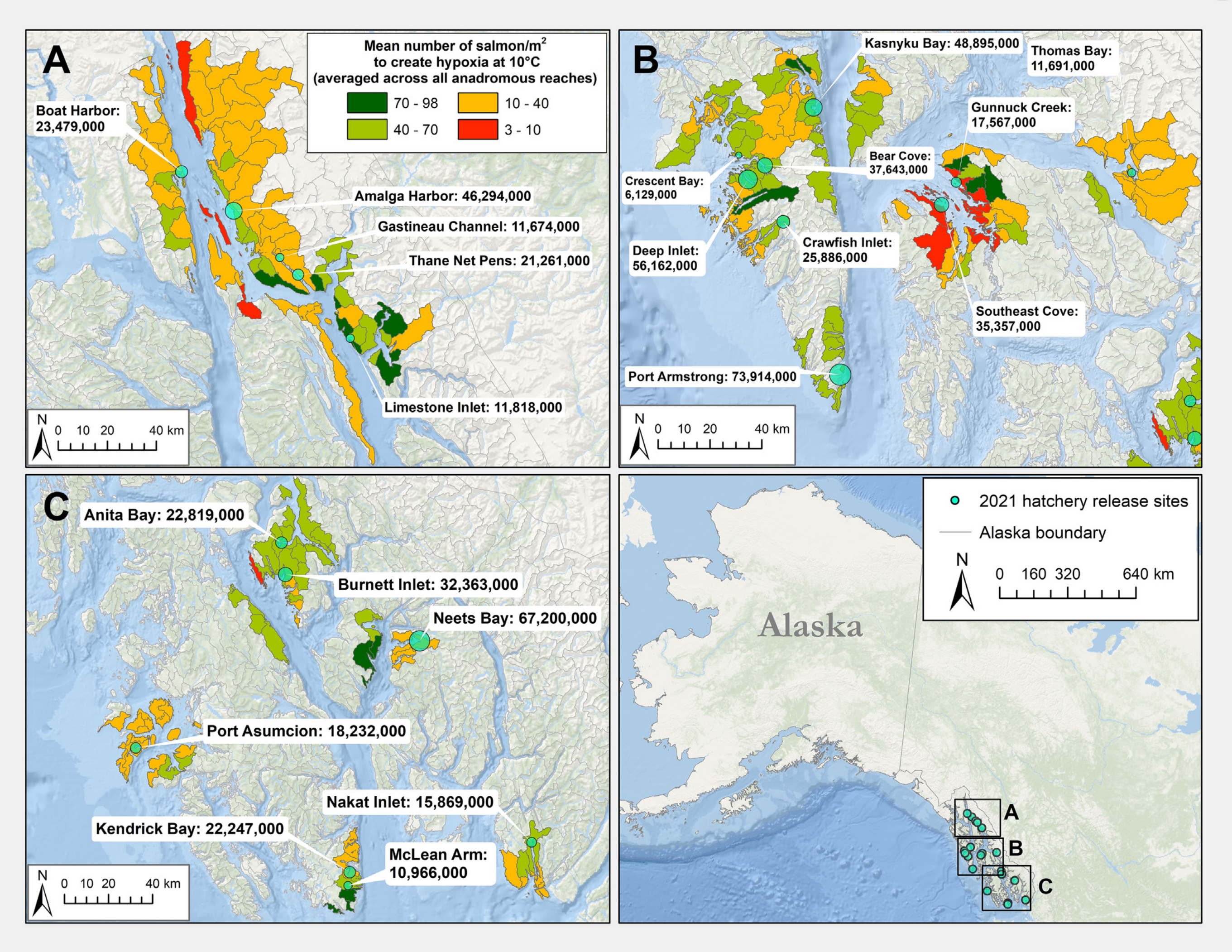

Fig. 4. Watersheds in the northern (A), central (B), and southern (C) portions of Southeast Alaska with coastal outlets <25 km from 2021 salmon hatchery release sites. Watersheds are color-coded by the hypoxia vulnerability metric calculated at 10 °C and averaged across all anadromous reaches within the watershed; see legend in (A). The labeled teal points represent 2021 hatchery release sites and are sized proportionally according to the total number of pink and chum salmon released (rounded to the nearest thousands). The map was created using the NetMap synthetic stream network and Ocean Basemap in ArcMap 10.8.2 (Esri, Redlands, California).

large watershed south of the Southeast Cove hatchery release site includes Kadake Creek (labeled in Fig. 6) and several smaller drainages that were not individually delineated by NetMap. In this example, <1600 m of anadromous reaches were used in the average hypoxia risk calculation for the entire watershed (Fig. 6). Although Kadake Creek has documented anadromous reaches above the sections included in this analysis (Harding and Coyle, 2011), most of these were excluded from this analysis because the downstream-most reach in the watershed had a channel gradient >12 % (this analytical artifact is discussed further in Section 4.4 *Study limitations*).

4. Discussion

Premature mortality in salmon populations due to hypoxia is a natural phenomenon, yet determining its mechanisms and the extent to which human activities increase vulnerability to mortality remains an active field of study with implications for salmon hatchery management and water diversion activities. We used a previously ground-truthed model based on first-principles calculations to describe dissolved oxygen dynamics and estimate hypoxia vulnerability for streams across Southeast Alaska using a repeatable analytical framework that simultaneously considers low-flow channel hydraulics, water temperature, and spawning salmon bioenergetics. Using the framework in concert with contemporary hatchery salmon release sites, we demonstrated that thousands of stream km in the study region adjacent to release sites may be exposed to greater numbers of stray spawning salmon, which have the potential to reduce dissolved oxygen in watersheds. More broadly, our framework could be adapted in other regions where high fish densities combined with low reaeration precipitate hypoxia.

4.1. Channel hydraulics

Channel hydraulics play a critical role in the dissolved oxygen estimates produced by our model (Eq. (2)) by controlling reaeration rate. Similar to empirical studies, our estimates suggest that hypoxia can occur even when water temperatures are relatively cool (<15 °C) in locations with low velocity-to-depth ratios. For example, the Indian River, which is on the outer coast of central Southeast Alaska, had a maximum summer water temperature of 12.6 °C, a mean across all hourly summer measurements of 8.7 °C, and relatively moderate hypoxia vulnerability across nine site-summers (mean = 59.4 salmon/m^2 to create hypoxia). Yet, severe hypoxia events (as low as 1.7 mg/L and 16 % saturation) have been measured in the Indian River due to low reaeration rates during low water and unnaturally high fish densities caused by hatchery-origin pink salmon returning

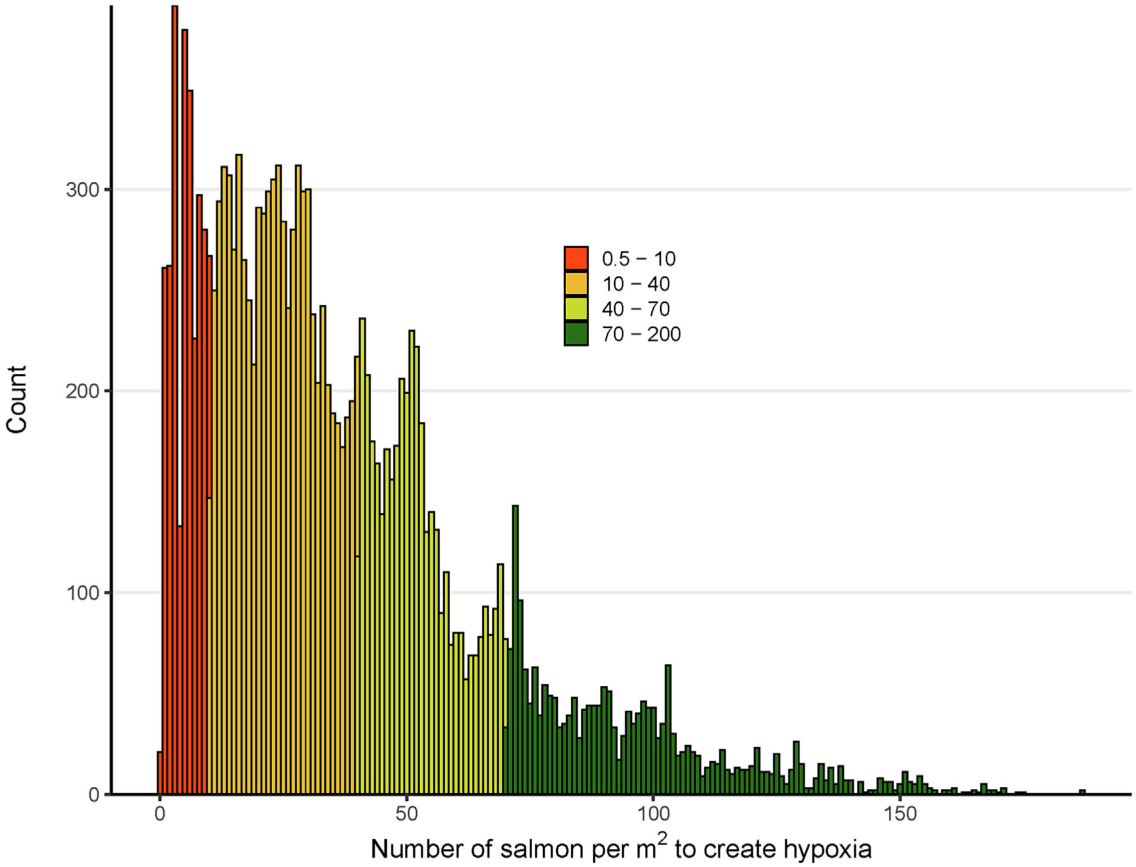

Fig. 5. Histogram of the hypoxia vulnerability metric for all anadromous-accessible stream reaches (n = 16,806) in Southeast Alaska watersheds with coastal outlets <25 km from 2021 pink and chum salmon hatchery release sites. Color scales for the metric match those in Figs. 3, 4, and 6.

to spawn in the river instead of the hatchery, which is located only 1 km from the river mouth (Sergeant et al., 2017).

Low-gradient reaches such as the estuarine and floodplain channels common to the outlets of small watersheds (<40 km^2) in southern coastal Alaska (Paustian, 2010) are often locations where mass mortality events are documented. Such events may occur due to different combinations of low-water migration blockage, warm water, or low dissolved oxygen (Murphy, 1985; Sergeant et al., 2017; von Biela et al., 2022). In these coastal habitats, velocity-to-depth ratios—and therefore, reaeration rates—tend to be low, while water temperature may vary widely depending on the influence of intertidal marine waters. Our study suggests that these lower watershed reaches are among the most hypoxia-prone due to their channel hydraulics, and under the right conditions may represent seasonal migratory barriers that prevent or reduce access to spawning habitat in the upper reaches of watersheds.

4.2. Salmon-spawner densities estimated by the hypoxia vulnerability metric

Modeled spawner densities predicted to result in hypoxia varied widely across stream reaches. These estimates should be interpreted as the relative risk of hypoxia. In other words, a stream reach with a metric value of 5 fish/m^2 is much more vulnerable to hypoxia than a reach with a metric value of 70 fish/m^2, regardless of whether the potential spawning density at a specific site is realistic. Additionally, the salmon-spawner densities represented by the hypoxia vulnerability metric are most relevant at smaller spatial scales (one to several 100-m stream reaches) where individuals in the reach experience similar fish densities. For example, spawners clustered in a pool experience the spawner density in that pool. The lead author (CJS) has visually estimated that dense pink salmon spawning aggregations in the Indian River can reach 10–30 fish/m^2 in depths of 0.5–1 m. These densities contrast with studies that report salmon-spawner densities averaged over the entire length of a surveyed stream channel, which is often several km in length. When averaged over a larger spatial scale, “high” salmon-spawner densities measured in previous studies of small Alaska streams are typically <3 fish/m^2 (e.g., Gende et al., 2001; Tillotson and Quinn, 2017; McConnell et al., 2018), which is lower than most of the range of our hypoxia vulnerability metric values.

4.3. Hatchery supplementation and other human influences

Human activities have the potential to exacerbate hypoxia risk, especially for streams with outlets located <25 km from hatchery release sites. Depending on the spatial arrangement of hatchery release sites and number of fish released at each site for a given year, the number of watersheds and stream reaches vulnerable to artificially increased spawning salmon density can be geographically extensive. Using the 2021 hatchery release sites, nearly 17,000 km of anadromous-accessible stream reaches met our distance criterion for increased straying potential, and this is likely a conservative estimate (see the Section 4.4 *Study limitations* section below). Any water diversion for human-use in these stream reaches—including hatcheries, mining operations, drinking water, or hydropower—would further increase hypoxia vulnerability by reducing stream discharge and increasing spawner density (e.g., Sergeant et al., 2017). In addition, while the effects of logging on streamflow patterns are complex and context-dependent, it is generally believed that extensive forest harvest within a catchment leads to reduced summertime baseflow (Gronsdahl et al., 2019). The potential severity of these human uses may be further compounded by climate change impacts in watersheds affected by reduced ice or snow runoff and increasing drought frequency (Cherry et al., 2017; Schoen et al., 2017; Vynne et al., 2021).

A clear question that arises from this study is whether hatchery-driven hypoxia events in streams like the Indian River are rare or common. In

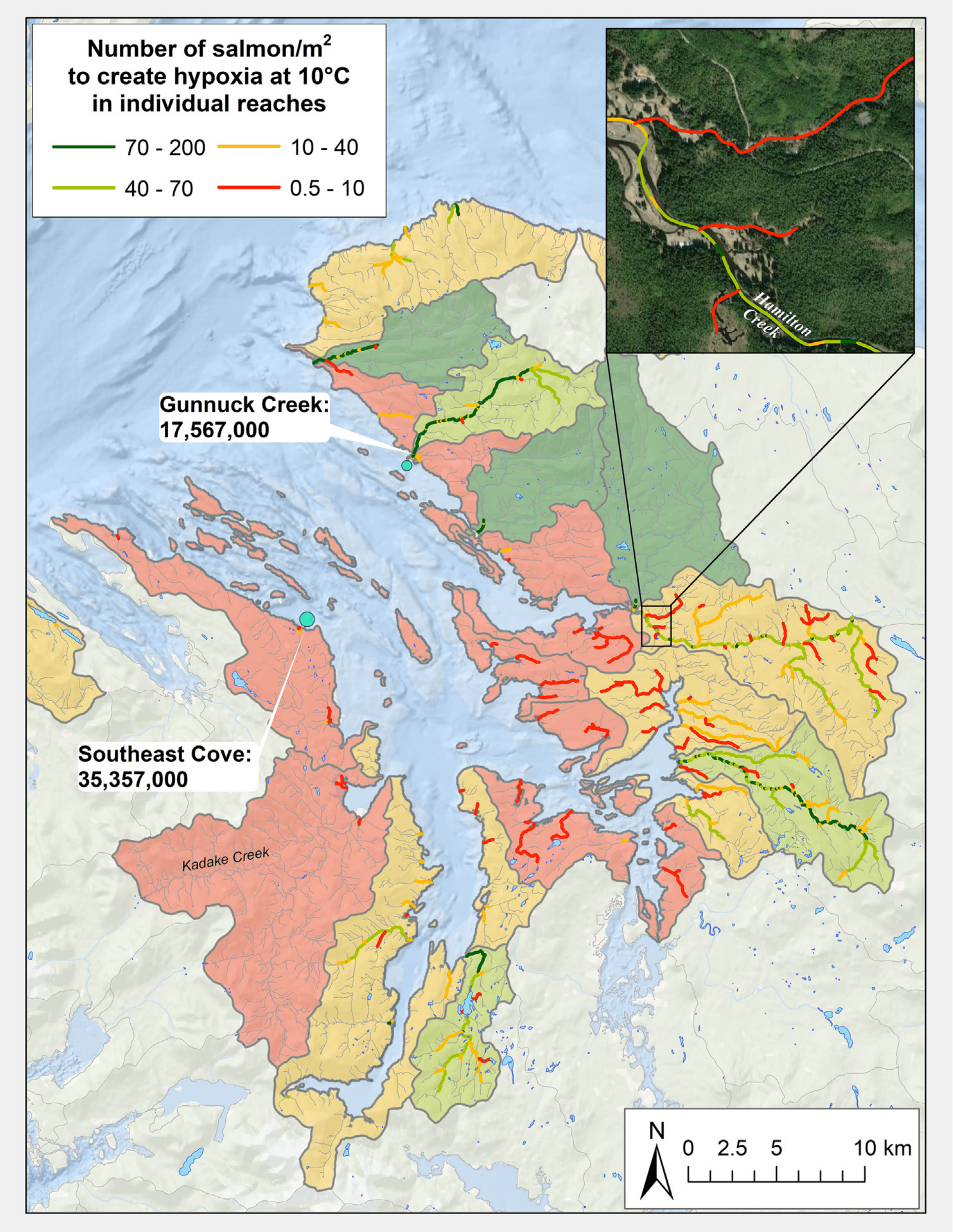

Fig. 6. Detailed view of a central Southeast Alaska area adjacent to Gunnuck Creek (near Kake, Alaska) and Southeast Cove hatchery release sites (teal points; labels represent 2021 total number of hatchery-released chum salmon rounded to the nearest thousands). See Fig. 4B for geographic location in Southeast Alaska. In this example, stream reaches are color-coded by the number of salmon/m^2 to create hypoxia. Watershed polygons from Fig. 4 follow the same color coding but are muted to better highlight stream reach-scale variability in the hypoxia vulnerability metric. The inset combines reach-scale hypoxia vulnerability in Hamilton Creek with satellite imagery to illustrate habitat variability within the watershed. Light gray stream lines within colored watersheds represent reaches upstream of reaches with >10 % channel gradient and therefore not considered anadromous reaches in this analysis. The map was created using the Ocean Basemap and default satellite imagery (18 April 2020) in ArcMap 10.8.2 (Esri, Redlands, California).

other words, how frequently do stray hatchery salmon crowd streams at sufficient densities to incite hypoxia that otherwise would not occur if only natural spawners were present? For a given stream and year, answering this question using our dissolved oxygen model would require a time series of areal spawner density for all species separated into hatchery- and natural-origin individuals, channel dimensions, discharge, and water temperature. We are not aware of any studies that provide these data. Instead, we briefly review previous research to support the notion that pink and chum salmon stray rates for individual streams can be very high across years and geographically wide-ranging.

A study from Prince William Sound using data collected from 1997 through 2010 demonstrated that hatchery-origin pink salmon can comprise up to 98 % of spawners and hatchery-origin chum salmon up to 63 % of total spawner abundance in a single stream; in the same study, hatchery-origin chum salmon at two weirs comprised 93–100 % of sampled fish (Brenner et al., 2012). A follow-on study conducted from 2013 to 2015 in Prince William Sound estimated that annual proportions of hatchery-origin pink salmon in single streams were as high as 90 % and chum salmon as high as 97 % (Knudsen et al., 2021). In two Southeast Alaska studies conducted from 2008 to 2010 and 2013 to 2015, the maximum proportion of hatchery-origin chum salmon in a single stream were 88 % and 85 %, respectively (Josephson et al., 2021; Piston and Heinl, 2012). In 2018 and 2019, unexpectedly large chum salmon returns to a new hatchery release site in Southeast Alaska (Crawfish Inlet on the west coast of Baranof Island) led to concerns that the marine fishery could not keep pace with harvesting the majority of the estimated 3.5 million and 2.1 million returning fish,

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respectively (Piston and Heinl, 2020). Many of these hatchery-origin fish were observed straying to the adjacent West Crawfish Inlet where their run timing overlapped with wild fish. In September of 2018 and 2019, sampling demonstrated that the main spawning stream in West Crawfish Inlet had 99 % and 94 % hatchery-origin spawners, respectively. In 2019, biologists conservatively estimated that over 10,000 chum salmon attempted to spawn in this stream (Piston and Heinl, 2020). In 2008 and 2009, before any nearby hatchery releases occurred, peak spawner count estimates in this same stream were only 4300 and 3500, respectively, with accompanying hatchery-origin proportions of 4 % and 0 % (Piston and Heinl, 2012).

4.4. Study limitations

While the dissolved oxygen model used here relies on established functional relationships and has been validated within the study region using empirical data (Sergeant et al., 2017), the accuracy of hypoxia vulnerability metrics may be limited in some reaches by the digital elevation models used to estimate habitat conditions and the lack of consideration for other components of ecosystem respiration that create or use oxygen. Some Southeast Alaska stream channel characteristics in NetMap are based on 2-m digital elevation models that use light detection and ranging (LiDAR) techniques, but most habitat data used here are based on a 20-m digital elevation model. Coarse elevation models may, for example, lead to incorrect estimates of gradient by averaging over sharp breaks in channel slopes (knickpoints) that could underestimate reaeration estimates. However, digital elevation models for Alaska are improving (https://elevation.alaska.gov/) and will be less likely to limit future studies. Bank angles and migration blockage thresholds are additional components of the analysis that remain widely unmeasured and uncertain in our study region.

In order to estimate low flow channel velocity and depth, all bank angles were assumed to be 45°. Increasing bank angle from 45° to 90° while maintaining the original bankfull width decreases velocity, while decreasing bank angle to <45° increases depth and velocity. In most instances, decreasing bank angles would result in a higher salmon density and increase hypoxia risk. For the analysis of stream reaches near hatchery release sites, we chose 10 % gradient as a conservative barrier threshold for migration that is similar to previous studies in the region (Romey, 2018; Pitman et al., 2021). There is no widely used channel gradient threshold at which upstream migration by anadromous salmon is blocked. In some places, this choice may exclude known anadromous waters from analysis. For example, Kadake Creek near Kake, Alaska (Fig. 6), is a known anadromous stream, but because the lowest stream reach channel gradient was estimated at >12 %, the upstream network was excluded from analysis. In future analyses, measurements of characteristics such as channel gradient barriers to migration and bank angles using field measurements or finer-scale digital elevation models would improve estimates and mapping of hypoxia vulnerability.

Since a goal of our study was to explore the role of spawning salmon respiration in dissolved oxygen dynamics, we did not consider other components of ecosystem respiration that create or remove oxygen such as photosynthesis, salmon carcass decomposition, or respiration by other aquatic organisms (Gende et al., 2002; Holtgrieve and Schindler, 2011). Additionally, we did not consider groundwater inputs that may either supply low dissolved oxygen water or provide micro-refugia during summer by providing cooler temperatures (Power et al., 1999). Groundwater and stream channel habitat complexity are known to play important roles in the thermal regimes of salmon watersheds, but data describing groundwater sources and thermal micro-refugia are often lacking (Mauger et al., 2017; Torgersen et al., 1999). Nevertheless, our relatively simple model analysis highlights opportunities for more nuanced modeling and empirical measurements that account for other factors that contribute to dissolved oxygen dynamics.

5. Conclusions: looking ahead to monitoring and managing dissolved oxygen in streams

While current concerns around the impacts of hatchery-origin salmon spawning with natural-origin salmon have focused primarily on genetic consequences (Christie et al., 2014; Josephson et al., 2021; Shedd et al., 2022), our analysis supports the additional concern that hypoxic stream conditions brought about by artificially high spawner densities have the potential to create a suite of acute ecological impacts across a broad geography, including premature mortality of spawning salmon and other resident fishes (Murphy, 1985; Tillotson and Quinn, 2017; von Biela et al., 2022), mortality or reduced diversity of benthic macroinvertebrate communities (Davis, 1975), inhibited salmon embryo growth (Shumway et al., 1964), and sublethal physiological stress of numerous aquatic organisms (Davis, 1975). In wild salmon populations with no hatchery straying influence, hypoxia-induced mass mortality events during periods of high abundance may only temporarily decrease population productivity due to a density-dependent decrease in successful spawning. In contrast, hatchery salmon populations lack this density-dependent feedback on the spawning grounds and have much higher egg-to-smolt survival rates than natural populations (Bradford, 1995; MacKinlay et al., 2004). Where straying salmon continue to return to streams near hatchery release points in high abundance year-after-year, the acute ecological impacts to that stream ecosystem and productivity of wild salmon may occur with greater frequency and become more chronic than streams with only naturally spawning populations.

Small rain- and snow-fed watersheds, where meltwaters from snow and ice are limited or non-existent during the summer, are likely the most important places to conduct hypoxia monitoring (Bellmore et al., 2023; Sergeant, 2022). These watersheds will be most prone to drought during salmon spawning periods, which can inhibit upstream migration, create warmer waters that hold less oxygen, and promote higher fish densities (Sergeant et al., 2020; von Biela et al., 2020).

Looking ahead, this research calls attention to three key questions that can guide future ecological monitoring programs: 1) Where and in how many places do straying salmon increase the frequency and intensity of hypoxia events? 2) Do hypoxia events result in observable ecosystem responses such as decreased natural spawning productivity or decreased diversity of aquatic macroinvertebrates? 3) Are climate change and associated extreme events creating physical habitat and flow conditions that decrease the ability of streams to reaerate efficiently? Our repeatable analytical framework for identifying hypoxia vulnerability can be used to address these questions and refined with empirical habitat and salmon density data at the reach and watershed scales. We see an opportunity to integrate research on these emerging ecological questions with existing long-term monitoring programs in regions like Southeast Alaska, where the focus to-date is mainly on juvenile and adult salmon enumeration. Government agencies such as the Alaska Department of Fish and Game and National Oceanic and Atmospheric Administration have research infrastructure in place throughout Southeast Alaska that could be leveraged to support monitoring programs geared toward the key ecological questions posed above. Future monitoring programs could be designed to assess the prevalence and ecological impacts of hypoxia events intensified by high rates of salmon straying. In streams where hatchery-induced hypoxia vulnerability is high, fisheries managers can take actions such as constructing in-stream weirs to control the number of hatchery fish straying into the stream. Macaulay Hatchery in Juneau, Alaska currently operates two weirs to limit straying (https://www.adfg.alaska.gov/index.cfm?adfg=fishingHatcheriesPlanning.annual). Pressures on the salmon watersheds of southern coastal Alaska brought about by climate change and hatchery supplementation increase the urgency to determine the ecological impacts of freshwater hypoxia. Our research strives to illuminate the degree to which hatchery strays may induce hypoxia-related mortality and create conflict with salmon hatcheries' goal of protecting and maintaining the abundance of wild salmon stocks.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.165247.

CRediT authorship contribution statement

Christopher J. Sergeant: Conceptualization, Methodology, Formal analysis, Writing – original draft, Visualization. **J. Ryan Bellmore:**

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Conceptualization, Methodology, Formal analysis, Writing – original draft. **Rebecca A. Bellmore:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – review & editing. **Jeffrey A. Falke:** Conceptualization, Methodology, Formal analysis, Project administration, Writing – review & editing. **Franz J. Mueter:** Formal analysis, Writing – review & editing. **Peter A.H. Westley:** Writing – review & editing.

Data availability

The following data will be available as a single .zip file stored on ScienceBase at LINK: 1) Hourly hypoxia vulnerability calculations at water temperature monitoring sites; 2) Hourly hypoxia vulnerability calculations near hatchery release sites; 3) Habitat characteristics at water temperature monitoring sites; 4) R code for reproducing the hypoxia conditions analysis in Fig. 3.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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