

LITERATURE SYNTHESIS ON ARTIFICIAL PROPAGATION ON CHINOOK

U.S. Fish & Wildlife Service

Review of the Effects of Artificial Salmon Propagation and Agency Perspective on Artificial Propagation of Yukon River Salmon



Female Chinook Salmon, Upper Chena River, Alaska, July 2015. Credit USFWS.

Fisheries and Aquatic Conservation and National Wildlife Refuge System – Alaska Region
October 2016



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Executive Summary

Due to over a decade of poor Chinook Salmon returns in the Yukon River basin, stakeholder interest in artificial propagation activities is increasing as a possible means to rebuild the stock complex to its historic levels, which would provide for more harvest opportunities. This document provides historical context on artificial propagation efforts in the Yukon River along with a review of the potential risks artificial propagation may have on wild stocks and their diversity. The Service uses best available science as a foundation to inform agency decisions and opinions. A review of the scientific literature has led the Service to conclude that at this time continuation of collaborative adaptive harvest management and habitat conservation for Yukon River Chinook Salmon are the preferred tools to rebuild the stock and ensure their sustainability. This position is consistent with the position of the Alaska Chapter of the American Fisheries Society (1993) and those described in the 1998 Yukon River Comprehensive Salmon Plan and Yukon River Salmon Agreement (2002) of the Pacific Salmon Treaty. If the current management approach for Yukon River Chinook Salmon appears to be unsuccessful and Yukon River Chinook Salmon populations experience further declines, a rigorous scientific investigation and planning process should be completed to avoid and minimize risks associated with artificial propagation to wild salmon populations, humans and the environment.

Introduction

Salmon are the lifeblood of much of the Alaska's economy, identity, and culture. Salmon contribute nearly \$5.1 billion annually to the national economy. Over 90% of surveyed Alaskan residents feel that wild salmon are linked to important Alaskan values (Salmon Project 2013). Fish make up over 50% of all the wild food harvest (by weight) of rural Alaskans. Salmon and whitefish species comprise the majority of that harvest annually, with Chinook Salmon (*Oncorhynchus tshawytscha*) one of the highest prized. The Service and other federal resource management agencies have been working with the state of Alaska and other partners since the early 1980s to maintain the natural diversity of these fish populations and the connectivity of quality fish habitat as mandated by the Alaska National Interests Lands Conservation Act of 1980 (ANILCA) and the Yukon River Salmon Agreement of 2002. Prior to and concurrent to these efforts, the Alaska Department of Fish and Game (ADF&G) and private non-profits have been conducting artificial propagation efforts of salmon as one way to rehabilitate some of the state's depleted and depressed wild salmon fisheries while minimizing risks on wild stocks (Naish et al. 2008; Heard 2012). Over the past 40 years, the majority of artificial propagation efforts have gone towards releasing Pink Salmon *O. gorbuscha*, Chum Salmon *O. keta*, and Sockeye Salmon *O. nerka* into rivers and lakes of Southeast and Southcentral Alaska (Stopha 2016). Chinook Salmon and Coho Salmon *O. kisutch* have also been artificially propagated, but to a lesser extent due to the space required to accommodate the species' extended rearing phase and the subsequent higher risk of disease and costs.

Despite these propagation examples, most of the salmon populations in Alaska are still comprised of solely wild fish because of the remoteness and largely still intact nature of the

state's salmon habitat, and successful adaptive fisheries management by state and federal managers. However, concern over the status of multiple stocks of Chinook Salmon throughout Alaska after a decade of poor or below average returns (Alaska Department of Fish and Game 2013; Schindler et al. 2013; U.S Fish and Wildlife Service 2016) has triggered increased interest in artificial propagation for Chinook Salmon, particularly in the Yukon River.

Yukon River Chinook Salmon Stock Restoration

The Yukon River Chinook Salmon stock complex has been depressed since the early 2000s resulting in a state designation as a Stock of Yield Concern and several failures to meet annual passage goals into Canada and tributary escapement goals (Lingnau and Bergstrom 2003; JTC 2016). Several plausible hypotheses to explain the declines of Chinook Salmon abundance were proposed in the Arctic Yukon Kuskokwim (AYK) Chinook Salmon Research Action Plan (Schindler et al. 2013). Hypotheses range from selective fishing practices altering demographic qualities of the population, natural environmental changes in freshwater habitats affecting survival, natural or human-caused ecological changes in marine habitats, changing growth patterns, bycatch in non-salmon marine fisheries, and pathogens such as *Ichthyophonus* affecting survival of returning adults. The range of possibilities encompassed by these hypotheses and others illustrate the uncertainty of the contributing factors to the decline and the complexity of the problem. Many scientists familiar with Yukon River fisheries believe there are likely multiple factors acting together causing the current Chinook Salmon declines.

Subsistence, recreational and commercial fisheries managers, and stakeholders have responded to the poor returns with harvest restrictions and closures (Estensen et al. 2015). Many people who fish along the Yukon River and its tributaries have accepted the recent fishing restrictions as a means to rebuilding the stocks and many are seeking alternative ways to fill their subsistence, cultural, recreational, and commercial needs. Alternatives considered have included directing harvest to other species, altering fishing gear types and periods, and artificial propagation of Chinook Salmon.

The Yukon River Salmon Agreement established the bilateral U.S. - Canada Yukon River Panel (Panel) and its Joint Technical Committee in 2002 (Yukon River Salmon Agreement of 2002). The Panel makes recommendations to managers in both countries, to ensure coordinated management of salmon originating from Canada. Canadian-origin Chinook Salmon stock restoration, through multiple means (including harvest management, artificial propagation, habitat restoration) is a current priority for the Panel as approximately 50% of all Chinook Salmon returning to the Yukon River spawn in Canadian waters (Wilcock 1984; Bromaghin and Bruden 1998; Lingnau 2000). To date, Service biologists serving on the Joint Technical Committee have advocated for adaptive, conservative harvest management and habitat restoration and protection as the preferred means of recovering Yukon River Chinook Salmon until limitations of productivity are better understood.

Eggs

- could not be done on a large enough scale to have an impact; difficulty of access to sites, difficulty in evaluation, & the need for specific groundwater conditions.

Fry

- difficulty transporting fry & collecting eggs
- can mark physically
- could compete for rearing habitat & food

SMOLTS

- most successful approach & most often used for Chinook
- much more expensive & greater need for infrastructure
- high transport costs/difficulty
- FWS - Alaska Region Artificial Propagation of Yukon River Salmon

Artificial propagation for stock restoration purposes has been occurring in the Yukon River basin to varying degrees since 1958. A hatchery at the Whitehorse Rapids Dam is currently releasing Chinook Salmon to the wild in the upper Canadian mainstem (Boyce 1997; JTC 2016). The facility began operations in 1985 as mitigation for the obstruction to migration imposed by the dam, which was completed in 1958 and equipped with a fish-ladder in 1959 (Gordon et al. 1960; Yukon Energy 2005). During its 31 years of operation, the hatchery has released an average of approximately 150,000 marked juvenile Chinook Salmon each year, mostly upstream of the dam and in Michie Creek (JTC 2016). To date, there have been no formal evaluations of hatchery production or possible impacts on wild stocks (de Graff 2015; JTC 2016). However, studies have shown that the juveniles produced in the hatchery are larger than wild conspecifics at release and migrate to sea earlier, i.e., age 0 versus age 1 (Healy 1991; Yukon Energy 2005; Murphy et al. 2009). Egg incubation facilities have also been used as a tool to restore stocks impacted by the dam in the upper Yukon River basin (Tanner 1997; JTC 2016). Formal monitoring programs designed to estimate production levels or impacts on wild stocks have not been implemented for any of these fry distribution sites.

Avg. 1.6% survival

The only artificial propagation of Chinook Salmon in the U.S. portion of the Yukon River drainage came from the Clear Fish Hatchery in the Nenana River drainage, a tributary of the Tanana River. The hatchery released Chinook Salmon juveniles into upwelling streams in the lower Nenana River between 1982 and 1987 (except 1983) (unpublished ADFG data). Broodstock were obtained from the Salcha River for three years of the program and from Clear Creek, an upwelling stream near the Clear Fish Hatchery, for the other two years. No production-monitoring program was designed to evaluate the success of the releases.

There are no current releases of artificially propagated salmon in the Alaska portion of the Yukon River. However, there has been increasing interest in stock restoration activities in the Yukon River basin due to record low returns. In 2010, ADF&G received an inquiry from the Alaska State Legislature regarding artificial salmon propagation opportunities within the Yukon River Basin. ADF&G provided a response with assessment and recommendations. Two years later, ADF&G assembled a group of agency scientists and representatives of the aquaculture industry to consider the use of artificial production to increase Chinook Salmon harvest opportunities in Alaska during periods of low production (Josephson et al. 2013). The group evaluated the use of artificial propagation programs (e.g., hatcheries, incubation facilities) and scientific investigations throughout the state with a section of the document and an appendix devoted specifically on the potential use of Yukon River hatchery-reared fish to improve the understanding of survival processes within freshwater and marine ecosystems. The group provided a comprehensive review on obtaining brood-stock, hatchery capacity, optimal release locations, and expected number of adult returns for a given number of juveniles released. However, their reports did not address the literature on the biological impacts of introducing artificially propagated fish to wild populations.

500,000 fingerlings released
no return info
hatchery reported ~ 200 ex yr 1985-89
 $\frac{1000}{20000} = 0.2\%$

Would need 3,000,000 fingerlings per yr, brood stock of 1,000 fish or 1,500,000 smolts

How many needed to make a noticeable difference in harvests w/out jeopardizing wild stocks?

Add 50,000 to run each year
50% typical harvest rate = 25,000^{extra for} harvest & 25,000 for escapement

- Entire SE AK return of hatchery kings is 90,000 - 170,000 over last 10 yrs
- Would need CAREFUL RELEASE SITES, while minimizing impact on wild stocks

In yrs of low abundance, may not be able to harvest all available hatchery fish while still achieving escapement goals. In years of high abundance, additional fish not necessary. May exceed

In addition, House Bill 220 was introduced to the Alaska State Legislature in January 2016 as a means to increase salmon returns statewide (<http://bit.ly/2dnW0FW>). The bill would allow the Commissioner of ADF&G to issue permits for applicants to collect, fertilize, and incubate eggs from fish captured in state waters and distribute the fertilized eggs or hatched fish into the same waterbody where they were originally collected or other waterbodies within the state. The House Special Committee on Fisheries discussed the bill on January 26, 2016 and accepted public testimony both in support and in opposition to the bill (<http://bit.ly/2dqb5tq>). Since that hearing no further legislative action has occurred.

Risks Associated with Artificial Propagation

The Service has been one of the pioneers of fish propagation and fish health since Congress established the National Fish Hatchery System (NFHS) in 1871. Since then, the NFHS has evolved to become a major network of hatcheries, laboratories, and research centers around the country that address a wide variety of species conservation needs. Artificially propagated fish are reared in an artificially enhanced environment to a juvenile stage and then released into the wild. Artificial propagation efforts such as hatcheries, incubation facilities, and egg boxes function to improve egg-to-juvenile survival (the most vulnerable life stage) by providing a stable, predator free environment. Egg-to-juvenile survival in the wild (i.e., fish that are offspring of parents that naturally spawned) can be as low as 10% due to environmental stochasticity and predation while eggs are in the gravel (Stopha 2016). Conversely, survival can reach 90% or higher in hatcheries.

While there are no federal fish hatcheries in Alaska, the Service and our partners have a long history with the propagation of salmonids in other North Pacific rim areas and in the North Atlantic. In the past 150 years, habitat alterations, hydroelectric development and consumptive fisheries have affected most of the salmon and Steelhead *O. mykiss* stocks in the Pacific Northwest and have resulted in lost fishing opportunities, altered ecosystem processes, and nine federally listed evolutionarily significant units of Chinook Salmon in the lower 48. In these areas, modern artificial propagation activities have been used to:

- restore depleted native fish stocks,
- restore declining populations of native fish and other aquatic species so as to prevent listing under the Endangered Species Act;
- provide for lost recreational fishing opportunities; and
- increase the number of fish available for harvest.

There are differing viewpoints of artificial propagation due to the potential benefits and risks to wild stocks and the people that depend on them (Waples 1999; Brannon et al. 2004). From one perspective, artificial propagation activities such as hatcheries are beneficial because they can help achieve some of the goals listed above and they create jobs. However, they are expensive to build and operate.

From the ecological perspective, artificial propagation activities often do not address the true cause of poor returns and can lead to further complications (e.g., competition for resources, increased mortality rates) with wild stocks as well as unknown long-term consequences (Waples 1999; Chilcote et al. 2010). Conserving the long-term sustainability of salmon through adaptive and strategic management of the wild stocks and their habitats can save significant economic resources and avoid potential adverse ecological consequences. Numerous interagency studies have evaluated the success of artificial propagation efforts and the effects on wild stocks of anadromous salmonids, primarily Chinook Salmon, Coho Salmon, and Steelhead. Literature reviews on the impacts of artificially propagated salmon on wild stocks in the Pacific Northwest (e.g., Naish et al. 2008; Kostow 2009; Araki and Schmid 2010) have recently led to major hatchery reform efforts to ensure that conservation goals and harvest were compatible (U.S. Fish and Wildlife Service 2013; Trushenske et al. 2015; HSRD 2014).

The following pages provide a synthesis of the literature from the Pacific Northwest and highlight the ecological consequences that could be experienced if artificial propagation of Chinook Salmon occurred in the U.S. portion of the Yukon River. Some of these effects may already be occurring due to releases of artificially raised juveniles within the Yukon Territory. While the following synthesis identifies risks, the Service recognizes that it is not easy to predict whether and to what degree the deleterious effects may occur in any given area and that the risks vary with the scale and type of the propagation efforts.

Artificial propagation through hatchery efforts entails releasing hatchery reared juveniles into streams that generally support wild stocks resulting in a number of ecological consequences. Hatchery fish eat a highly nutritious diet on a set schedule to improve growth and survival rates while in captivity. Therefore, these fish are larger than their wild conspecifics at time of release (Kostow 2004; Tatara and Berejikian 2012). The most immediate consequence is that juvenile wild fish are suddenly competing with large densities of larger hatchery fish for limited resources (e.g. food, refugia) in their freshwater rearing habitats, which limits growth potential and survival rates (Einam and Fleming 2001; Webber and Fausch 2005; Kostow 2009). Studies have documented that high densities of juvenile fish tend to attract predators that exploit wild and hatchery fish at elevated rates. Hatchery fish tend to experience greater mortality from predators than wild fish (Berejikian 1995; Collis et al. 2001; Ryan et al. 2003; Naisch et al. 2008). However, the mortality experienced by wild fish is still higher than normal due to the cumulative impacts derived from the increased densities (National Research Council 1996; Kostow 2009).

Fish are subject to a variety of diseases which add to mortality rates. These include environmental and nutritional diseases, as well as infectious diseases caused by bacteria, viruses, or parasites. Under natural conditions, fish are exposed to diseases and sometimes get sick or die, generally keeping populations in balance with the diseases. Hatchery fish are exposed to the same diseases as fish in the wild but they may be more susceptible because the high densities or because environmental conditions in the hatchery may not be the same as in their natural

freshwater competition
high densities attract predators

environment. Diseases can become introduced into hatcheries then potentially introduced to wild populations through effluent discharge or transmission by hatchery fish (Mulcahy et al. 1983; Watanabe et al. 1988; Naish et al. 2008). Operational plans of most hatcheries minimize these risks; however disease outbreaks are not always detected and can result in significant ecological ramifications (Naish et al. 2008).

marine competition

Releases of artificially propagated juvenile Chinook Salmon also affect wild stocks in the marine environment through competition for prey sources. Studies have documented a negative relationship between the survival of wild juvenile Chinook Salmon and the number of hatchery fish released, with the negative effects amplifying in years with poor ocean conditions (Levin et al. 2001; Kostow 2009; Chilcote et al. 2011; HSRG 2014). Additionally, wild stocks can experience undesirable harvest levels in the marine and in-river fisheries due to the challenges associated in differentiating hatchery and wild stocks in these environments without fish in hand, thus leading to misinformed management actions (Lichatowich and McIntyre 1987; Flagg et al. 2004; Naish et al. 2008; Kostow 2009). Hatchery fish that do escape the fishery and successfully spawn produce young that compete for rearing space and food with their wild conspecifics which has long-term implications for genetic diversity.

genetics

Although hatchery fish are generally larger at age, they are less fit and suffer greater mortality at all life stages than wild fish (National Research Council 1996; Reisenbichler and Rubin 1999; Kostow 2009; Araki and Schmid 2010), even when broodstock was taken from the population where juveniles were subsequently released (Araki et al. 2008; Chilcote et al. 2011). Therefore, the wild fish should prevail due to natural selection. However, domestication of salmon, human selection of breeding pairs, and captive rearing often sidesteps natural and sexual selection experienced by wild fish that keeps them fit and resilient to changing conditions (Fleming and Gross 1994; National Research Council 1996; Ford 2002). These activities associated with artificial propagation allows survival through early life stages of large numbers of progeny that may be poorly adapted for life in natural environments (Einam and Fleming 2001; Kostow 2004; Christie et al. 2012a; Baskett and Waples 2013).

poorly adapted to changing conditions

Each year, a percentage of hatchery juveniles fail to migrate to sea, thus becoming freshwater residuals, further competing for resources with other wild juveniles and resident species (Kostow 2009; Tataara and Berejikian 2012). Of the hatchery reared juveniles that do go to sea, a percentage survive and return to natural spawning streams where they spawn with other returning hatchery fish and their wild conspecifics (Lichatowich and McIntyre 1987; Waples 1991; Kostow 2009; Christie et al. 2014). Hatchery reared males generally tend to early maturation rates due to the accelerated growth rates in hatcheries, thus causing skewed male to female ratios (Larsen et al. 2004). Once on the spawning grounds, hatchery fish are generally less successful at spawning compared to wild fish (Fleming and Petersson 2001; Araki et al. 2008; Araki and Schmid 2010; Christie et al. 2014). Those that are successful may spawn with wild fish, thus diluting heritable adaptations unique to the wild population (Fleming and Gross 1994; Ford 2002; Grant 2012; Christie et al. 2014). Over time, the effective number of spawners

skewed male:female
less fit to reproduce

(fish that actually produce young) may decline in populations with a history of artificial propagation and stocks may become dependent on expensive annual artificial supplementation (Ryman and Laikre 1991; Lichatowich et al. 1999; Reisenbichler and Rubin 1999; Kostow 2004; Myers et al. 2004; Araki et al. 2007; Christie et al. 2012b). For example, Williamson et al. (2010) documented that hatchery-origin Chinook Salmon spawning in the wild produced approximately half the juveniles per parent compared to a wild fish.

Genetic diversity in salmon populations is extensive and greatly influenced by gene flow and population size (Brannon et al. 2004; Templin et al. 2011). Releasing artificially propagated fish to streams with wild stocks can pose serious risks to a stock's genetic integrity, disease resistance, and overall fitness (Hemmingsen et al. 1986; Naish et al. 2008). Furthermore, the genetic consequences of artificial propagation often spread to other nearby populations through straying (Waples 1991; Brenner et al. 2012), the effects of which are compounded by the higher rates of straying by hatchery-origin fish compared to wild fish (Quinn 1993; Candy and Beacham 2000).

To maintain or restore a fishery it is necessary to manage for the abundance and the natural diversity of the stock complex. A stock complex with a high degree of biological diversity (i.e. comprised of many spawning groups or genetic groupings in one river basin) has a higher likelihood to be more temporally stable because of the complementary or independent dynamics of each group (Schindler et al. 2010). Schindler et al. (2010) refers to this variance damping effect as the portfolio effect, which is similar to having diverse financial assets. Even though hatchery supplementation may temporarily produce more anadromous salmonids to harvest, they jeopardize the sustainability and natural genetic diversity of the existing wild stocks; the effect of which may not be realized for a generation or two of Chinook Salmon. Maintaining as much genetic diversity as possible may become increasingly important as it provides a mechanism for wild stocks to be resilient to environmental changes.

Lessons Learned

Recent interagency hatchery reform efforts conducted by the Service and others acknowledge the potential consequences of hatchery fish interactions with wild populations, as discussed above (e.g., National Research Council 1996; Flagg et al. 2004; Mudrak and Carmichael 2005; USFWS 2013; Anderson et al. 2014; HSRD 2014; Trushenske et al. 2015). All provide similar procedural recommendations for those considering hatchery programs to increase the likelihood of achieving both hatchery and conservation goals. All advocate an initial public planning process that explicitly states the reason for considering a hatchery program (e.g., to supplement a faltering wild population, to mitigate anthropogenic impacts, to increase harvestable surplus) and a review of all wild populations with which the hatchery fish would interact.

The interagency hatchery reform teams provide a series of specific recommendations for hatchery operations to utilize to mitigate each of the various biological, behavioral, fishery,

diversity =
resilience

- 1) Realistic assessment of cost
- 2) probability of achieving goals (hatchery & conservation)
- 3) risks to wild population

U.S. FWS – Alaska Region
Artificial Propagation of Yukon River Salmon

genetics, and other consequences of hatchery and wild fish interactions. These hatchery reform efforts advocate realistic assessments of the cost of hatchery programs, the probability of achieving hatchery and conservation goals, and the risks to wild populations, all during the planning process. All suggest that if even if an anadromous salmonid population has declined to perilously low levels, or been extirpated, artificial propagation efforts for recovery are unlikely to succeed until the reasons for the decline have been identified and resolved.

These recent recommendations suggesting caution are consistent with the position taken by entities that have considered the prospect of propagation in the Yukon River. For example, the American Fisheries Society - Alaska Chapter (AFS; 1993) passed a resolution on the management of Yukon River salmon in response to requests for hatchery supplementation to support Yukon River fishery concerns in the 1980s (Appendix A). The resolution described the risks of introducing hatchery produced salmon and concluded that aquaculture techniques should be only used as a "last resort" if a "specific stock would become extinct without direct intervention." Instead, managers should look to rebuild depressed wild salmon stock "with proper management of the resources." (AFS 1993).

Additionally, ADF&G and the Yukon River Drainage Fishermen's Association led the development of the 1998 Yukon River Comprehensive Salmon Plan (Comprehensive Salmon Plan; ADF&G 1998). The mission of the original document was to "promote, using sound biological practices, activities which increase salmon production in a regional area for maximal social and economic benefits of the users consistent with the public interest." The document states the preferred avenue to increase salmon production in the Yukon River is through restored or expanded natural stock production rather than large-scale hatchery programs as used elsewhere in the state. Furthermore, the Comprehensive Salmon Plan identifies 12 guiding principles to achieve increased production levels, including: ensure the health and natural characteristics of the wild salmon stocks; preference for stock restoration (rebuild to historical abundance) over enhancement (production over natural levels); desired production levels; minimizing fish mortality during research; setting strict policies for genetics and disease management; and opposition to large-scale enhancement projects (hatcheries) that are designed to create new runs of fish (ADF&G 2001; Yukon River Salmon Agreement 2002).

Similarly, when the United States and Canada signed the Yukon River Salmon Agreement in 2002, the guiding principles for restoration, conservation, and enhancement programs specifically state "Artificial propagation shall not be used as a substitute for effective fishery regulation, stock and habitat management or protection."

U.S. Fish and Wildlife Position on Artificial Propagation in the Yukon River Basin

Whether to pursue artificial propagation for Chinook Salmon in the Yukon River has been raised in a couple different contexts recently. As mentioned above, the Yukon River Panel is evaluating artificial propagation and the State legislature introduced HB 220 to facilitate artificial

* Outcomes of mgmt & conservation efforts take time to be realized!

propagation throughout Alaska and Canada. Meanwhile, to further evaluate activities to increase Chinook Salmon production during periods of low returns, ADF&G has initiated the revision process of the 1998 Comprehensive Salmon Plan. A Yukon River Regional Planning Team (RPT) comprised of local stakeholders and ADF&G managers is reviewing the existing Comprehensive Salmon Plan and compiling information pertaining to Yukon River fisheries and habitat, and the statutes, regulations, and policies that will guide salmon fishery enhancement in Alaska. The Service is an ex-officio member of the RPT through the Service's role as the federal in-season fisheries manager in the Alaska portion of the Yukon River.

The social and economic pressures on the fisheries resources of the Yukon River and Alaska have changed since adoption or finalization of the AFS-Alaska Chapter resolution, the Yukon River Comprehensive Salmon Plan, and Yukon River Salmon Agreement. However, the science has only become more convincing that there are substantial long-term risks to wild salmon stocks from artificial propagation activities. While the mitigation hatchery at the Whitehorse Rapids Dam produces some returning fish, neither the production levels nor the impacts on wild fish have been fully evaluated and are therefore not understood. There is no indication at this time that any of the other artificial propagation projects within the Yukon River basin have been successful. Additionally, the Service recognizes there are significant information gaps regarding the cause of Chinook Salmon declines in the Yukon River and that the outcomes of management and conservation efforts take time to be realized. The Service suggests this warrants a precautionary approach when considering the long-term pros and cons of propagation.

The Service believes that the reasons for opposing artificial propagation of Chinook Salmon in the Yukon River as expressed in the AFS - Alaska Chapter resolution, the Yukon River Agreement, and the 1998 version of the Yukon River Comprehensive Salmon Plan are still valid. This position is based on a robust body of scientific research documenting risks posed by artificial propagation as well as recognition of critical knowledge gaps (e.g., understanding of genetic diversity, survival rates) associated with wild stocks in the Yukon River and the factors affecting productivity. It's also supported by recent successes with collaborative and adaptive Chinook Salmon harvest management strategies which has led to: 1) achievement of Canadian border passage goals (2014-2016); 2) satisfaction of tributary escapement goals; and 3) a moderate subsistence fishery in 2016 (Joint Technical Committee 2016).

Although the Service opposes artificial propagation in the Yukon River at this point, there are circumstances that would merit support including, but not limited to: 1) runs drop further despite harvest management practices; 2) productivity drivers in the system are well understood and are beyond human influence; and 3) risks to wild stocks from artificial propagation are well understood and deemed minimal.

The Service recognizes that all agencies and stakeholders have a role in recovering Yukon River Chinook Salmon. Effective management and conservation of these vital, yet vulnerable, resources demands strong collaboration between the Service, ADF&G, Alaskan tribes, DFO, 1st

Nations, and recreational and commercial fishermen throughout the Yukon River basin and beyond. To ensure that we are collectively prepared should the aforementioned situations arise, the Service proposes the appropriate course of action at this time is to:

- build on existing and potential partnerships to implement effective harvest management practices to increase Chinook Salmon population levels in the Yukon River basin;
- conduct further research to understand more about the drivers of productivity; and
- work with partners and stakeholders to undertake formal analyses to determine the critical threshold for Chinook Salmon that would warrant consideration of a well-thought out artificial propagation strategy.

If the proposed approach for Yukon River salmon appears to be unsuccessful and there is risk the stock complex or a component is at critically low spawning levels, a rigorous scientific investigation and planning process similar to the recent hatchery reform efforts (e.g., USFWS 2013; HSRD 2014; Trushenske et al. 2015) should be completed prior to any artificial propagation efforts.

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Appendix A: Resolution statement of the Alaska Chapter American Fisheries Society regarding artificial propagation of salmon in the Yukon River, 1998.

YUKON RIVER WILD STOCK MANAGEMENT ZONE

WHEREAS, the Yukon River is one of the largest producers of wild Chum Salmon and Chinook Salmon in North America; and

WHEREAS, supplemental hatchery production is being considered as a means to increase harvest levels of Yukon River salmon; and

WHEREAS, increased harvest levels have a potential to severely impact the many small wild stocks included in the mixed stock and mixed species fishery; and

WHEREAS, available scientific literature suggests that hatchery produced salmon can stray and interbreed with wild stocks altering the wild gene pool, reducing stock fitness, and threatening the survival of wild populations;

BE IT FURTHER RESOLVED, the American Fisheries Society, Alaska Chapter, urges the governments of Canada, United States, and Alaska to manage the Yukon River as a Wild Stock Management Zone and to implement the following resolutions:

1. Rebuilding of depressed wild salmon stocks should be accomplished with proper management of the resources and not accomplished through increased hatchery production;
2. In no instance should hatcheries be used as a means to increase harvest levels;
3. As a last resort, aquaculture techniques may be necessary if a specific stock would become extinct without direct intervention.

Create 10,000 extra kings in Andraafsky (need 600k fingerlings
which is ~5X Whitehouse)

150,000 + 10,000 moving through → 6% of kings available

Dip nets intercept 10,000 kings; ~~£~~

so 6% = 600 hatchery kings in District 1-2

9,400 remaining → would need to
be harvest @ EF Andy

CWT barely
caught @ Pilot,
so interception is low

Climate change, pink salmon, and the nexus between bottom-up and top-down forcing in the subarctic Pacific Ocean and Bering Sea

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Edited* by Robert T. Paine, University of Washington, Seattle, WA, and approved March 4, 2014 (received for review October 9, 2013)

Climate change in the last century was associated with spectacular growth of many wild Pacific salmon stocks in the North Pacific Ocean and Bering Sea, apparently through bottom-up forcing linking meteorology to ocean physics, water temperature, and plankton production. One species in particular, pink salmon, became so numerous by the 1990s that they began to dominate other species of salmon for prey resources and to exert top-down control in the open ocean ecosystem. Information from long-term monitoring of seabirds in the Aleutian Islands and Bering Sea reveals that the sphere of influence of pink salmon is much larger than previously known. Seabirds, pink salmon, other species of salmon, and by extension other higher-order predators, are tightly linked ecologically and must be included in international management and conservation policies for sustaining all species that compete for common, finite resource pools. These data further emphasize that the unique 2-y cycle in abundance of pink salmon drives interannual shifts between two alternate states of a complex marine ecosystem.

ocean ecology | exploitative competition | consumer front | interaction strength | carrying capacity

Predator control of community structure and ecosystem function became a tenet of intertidal and nearshore marine ecology following early studies of Paine and others (1–3), yet with few exceptions (4, 5), until more recent times the idea has been less well appreciated for open oceans. Growing attention now is being paid to the overexploitation of pelagic species, particularly those at higher trophic levels currently and in the past, and effects on ocean ecosystems of the loss, or development, of top-down forcing (6–12).

The prevailing view has long held that most biological change in ocean ecosystems, apart from human exploitation, is driven from the bottom up (13–16). One striking example that has been linked to bottom-up processes driven by climate change is the burgeoning abundance of wild Pacific salmon (*Oncorhynchus* spp.), and in particular pink salmon (*Oncorhynchus gorbuscha*), in the subarctic North Pacific Ocean and Bering Sea (SNPO/BS). Underpinning the notion initially were studies that found (i) strong coherence between decadal patterns in the Aleutian Low pressure system, which exerts a large influence over climate in the North Pacific Ocean, and patterns in salmon production across a broad region of the SNPO/BS (17, 18); (ii) decadal patterns in primary production that could be explained by the effect of the Aleutian Low pressure system on basin scale wind fields (19); and (iii) decadal patterns in zooplankton, squid, and pelagic fish production that also were correlated with meteorological forcing over the North Pacific Ocean and consistent with patterns in primary production (20). Thus, the general explanation for waxing and waning abundances of salmon over the record in the 20th century was that physical forcing by shifts in the strength and position of the Aleutian Low altered winds, ocean temperatures, and primary and secondary production to the benefit or detriment of salmon. A decadal scale oscillation in the Aleutian Low, now often referred to as the Pacific Decadal

Oscillation (PDO) (21), has been linked to numerous physical and biological variability in the SNPO/BS in addition to salmon abundance (21–23).

It was subsequently shown that salmon population responses and their relation to the PDO were out of phase between Alaska and the northwest coast of North America during much of the 20th century (24); that warm anomalies in coastal temperatures were associated with increased survival of salmon in Alaska; and that regional-scale variability in ocean temperature was a better predictor of salmon survival than large, basin-scale variability characterized by the PDO (25). A recent analysis from around the rim of the North Pacific Ocean found regional covariance in abundance of pink salmon, chum salmon (*Oncorhynchus keta*), and sockeye salmon (*Oncorhynchus nerka*) associated with the Aleutian Low, and with smaller scale spatially coherent, but regionally distinct, patterns in climate (26).

Water temperature can be important to the early growth and survival of pink salmon fry directly by its effect on physiology and indirectly by its effect on the timing and development of zooplankton prey stocks in nursery areas, which commonly is advanced and greater in warmer years than in cooler years. In cooler springs, fry grow more slowly and a greater number die both from lack of food and from an increased susceptibility to predators (27, 28). For example, a conceptual model for Prince William Sound, Alaska, holds that, in years of abundant spring zooplankton, fry grow faster and remain longer in the shelter of inshore nurseries where they are protected from walleye pollock (*Theragra chalcogramma*) and Pacific herring (*Clupea pallasii*), two chief predators that remain offshore feeding primarily on swarms of large calanoid copepods and other macrozooplankton.

Significance

Wild salmon in the North Pacific Ocean, particularly pink salmon, have grown greatly since the mid-1970s apparently due to bottom-up effects of climate change on ocean physics and production processes. Pink salmon spend less than 2 y at sea and most stocks alternate between high and low levels of abundance every other year. In years of high abundance, they now constitute a pelagic consumer front as they return to their spawning rivers, exert top-down control over the open ocean ecosystem by outcompeting other species for shared prey resources, and drive major ecological shifts between years of high and low abundance. Their effect on competing species must be considered in international conservation policies and when developing informed ecosystem-based management strategies.

Author contributions: A.M.S. and G.B.v.V. designed research, performed research, analyzed data, and wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1319089111/-DCSupplemental.

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Climate change, pink salmon, and the nexus between bottom-up and top-down forcing in the subarctic Pacific Ocean...

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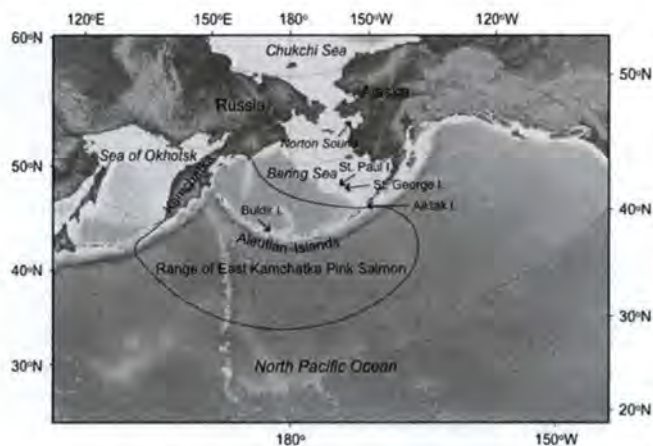


Fig. 1. The northern North Pacific Ocean and Bering Sea and locations of places discussed in the text. Salmon distribution is adapted from ref. 37.

In cooler years of lower zooplankton biomass inshore, fry grow more slowly, move offshore earlier, and suffer higher predation by pollock and herring due to spatial overlap, smaller size, and less alternative prey for those two predators (28).

Although the relationship between climate and pink salmon survival is likely complex, fluctuations in abundance appear to be modulated in large measure directly and indirectly by the thermal environment in which a stock lives. Such a fundamentally bottom-up explanation is bolstered by observations of high growth and survival rates of pink salmon during the period of warmer ocean temperatures and population increase (29, 30), and at this time provides a more parsimonious explanation for population dynamics than would explanations invoking strictly top-down control across such a broad region. Now, however, several lines of evidence indicate that pink salmon themselves are having a large top-down influence on other salmon species, other upper trophic level pelagic species, plankton standing stocks, and by inference, the functioning of the open-ocean ecosystem in the SNPO/BS.

Pink Salmon in an Ecosystem Context

Pink salmon are the most abundant of the wild Pacific salmon, representing about 70% of all returning fish each year across their range (31). They have several early life history characteristics that seem to explain their relatively great abundance, and a short 2-y life cycle from egg to spawning adult (30). Most stocks have interannually alternating weak and strong runs and strong runs can be in either even years or odd years: shifts between strong runs in odd years to strong runs in even years (and visa versa) have been documented in some stocks, even-year and odd-year brood lines are reproductively isolated, and the abundance of fish in strong runs is commonly far greater than in weak runs (32–36). The cause of this phenomenon is not known.

The majority of pink salmon in the northwestern and central SNPO/BS are of Asian origin, especially fish that spawn in rivers of the eastern Kamchatka Peninsula and western Bering Sea (Fig. 1) that are odd-year-dominant stocks (34). Although data are reported as “eastern Kamchatka,” more than 90% of those fish spawn in river tributaries of the western Bering Sea (38). The total run size (catch plus escapement) has been steady in even years for the past several decades, averaging about 17 ± 2 (SEM) $\times 10^6$ fish per y from 1972 through 2012, whereas runs in odd years rose from an average of about $47 \pm 6 \times 10^6$ fish per y in 1971–1987, to $83 \pm 7 \times 10^6$ fish per y in 1989–2007, and to 173×10^6 fish in 2009 and 225×10^6 fish in 2011 (34, 39) (Table S1). The increases were not augmented by hatchery releases (34). A

smaller stock of even-year-dominant pink salmon spawns in the eastern Bering Sea, primarily in Norton Sound, with run sizes there averaging 3.3×10^6 fish in even years and 0.56×10^6 fish in odd years between 1997 and 2012 (40).

Questions concerning the carrying capacity of the North Pacific Ocean in regard to salmon emerged in the early 1990s with increasing overall numbers of fish (41, 42). Differences in diets, growth, condition, distribution, and catch of three competing species—pink salmon, sockeye salmon, and chum salmon—in even years compared with odd years suggested that pink salmon were placing a disproportionately high demand on pelagic production (43–48). It was further suggested that biennial oscillations in standing stocks of phytoplankton and zooplankton in the central SNPO/BS, apparent by 1990 and out of phase with each other, represented a trophic cascade initiated in odd years by prey demand of pink salmon—during odd years, relaxed grazing pressure by depressed numbers of macrozooplankton, among the primary prey of pink salmon, led to an elevated standing stock of phytoplankton in summer (49, 50). This conclusion was reached after considering variability in physical indices and forcing factors, including the Northern Hemisphere Zonal Index, solar radiation flux, surface wind speed, sea surface temperature, salinity, density, and nutrient levels that were associated with interannual and decadal patterns in production at lower trophic levels, but not systematic biennial oscillations.

Such a relationship between zooplankton and phytoplankton abundance would explain a conspicuous biennial alternation in body size of *Neocalanus* copepods in the central North Pacific Ocean, during a study spanning the 1980s and 1990s, that generally was poorly correlated with climatological and environmental variables as well (integrated mean water column temperature from surface to 150 m, vertical stability index, North Pacific Index, and Southern Oscillation Index) (51). The authors found that individuals were larger in odd years, when competition for phytoplankton would have been less, than in even years when competition would have risen. The one significant correlation they did report was a positive one between body size of *Neocalanus cristatus* and chlorophyll *a* concentration, which would be expected in this scenario.

Seabirds in a Pink Salmon Context

Observations in the Bering Sea in odd years of lower body mass and liver mass of short-tailed shearwaters (*Puffinus tenuirostris*), a Southern Hemisphere seabird that spends the austral winter in the SNPO/BS and Chukchi Sea (52), and two to five times higher

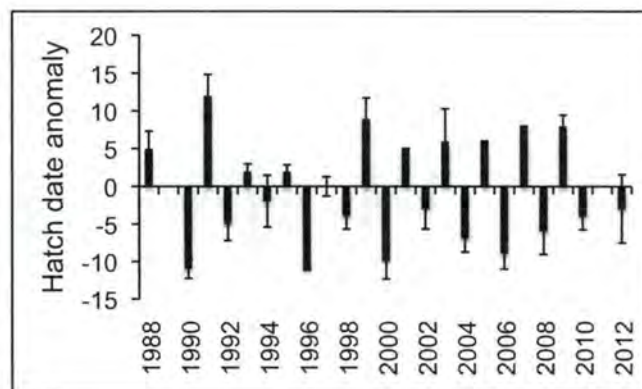


Fig. 2. Nesting phenology (mean hatch date anomaly, days) using the example of tufted puffins at Buldir Island. Positive values are late, and negative values are early; no data for 1989 or 2011. Error bars denote ± 1 SEM. Data are from ref. 67. See Tables S2 and S3 for phenology data for all species tested.

Table 1. Comparisons of seabird nesting parameters in even years versus odd years

Parameter	No. of tests	No. rejections (%)	No. expected
Clutch size	9	4 (44)	1
Hatch date	25	21 (84)	3
Laying success	8	6 (75)	1
Hatching success	27	9 (33)	3
Fledging success	21	6 (29)	2
Productivity	21	9 (43)	2
Overall	111	55 (50)	11

Number of tests of the null hypothesis of no difference between mean values of seabird nesting parameters in even years versus odd years, the number (percentage) of hypotheses that were rejected at $\alpha = 0.10$, and the number that would be expected to be rejected at $\alpha = 0.10$ due to chance alone.

strandings of shearwaters on the coast of eastern Kamchatka (53), provided the first evidence (to the authors' knowledge) of the influence of pink salmon over a competing species besides other salmon (and see ref. 54). Among the important prey of

pink salmon (29, 55, 56), copepods (*Neocalanus* spp.), euphausiids (*Thysanoessa* spp.), squids (Gonataidae), myctophids (Myctophidae), and Atka mackerel (*Pleurogrammus monopterygius*) are at times also important prey of shearwaters and of resident seabirds wintering in the subarctic North Pacific Ocean and nesting in the Aleutian Islands and Bering Sea (52, 57–66).

Systematic annual monitoring of nesting seabirds at four major colonies in the southern Bering Sea and Aleutian Islands (Fig. 1) began in 1984 at St. George Island and St. Paul Island (Pribilof Islands), 1988 at Buldir Island (western Aleutian Islands), and 1995 at Aikta Island (eastern Aleutians) (67–70). One of the most conspicuous patterns over the years, and the one that first alerted us to the possibility of a connection between the birds and pink salmon, is the alternating early (even year)–late (odd year) nesting phenology of tufted puffins (*Fratercula cirrhata*) at Buldir (Fig. 2). This led us to examine phenology and up to five additional elements of the breeding biology of tufted puffins and as many as 15 other seabird species of two feeding guilds—omnivores (12 species that consume a mixture of fishes, squids, zooplankton, and other invertebrates) and planktivores (4 species that consume primarily zooplankton)—at those islands for

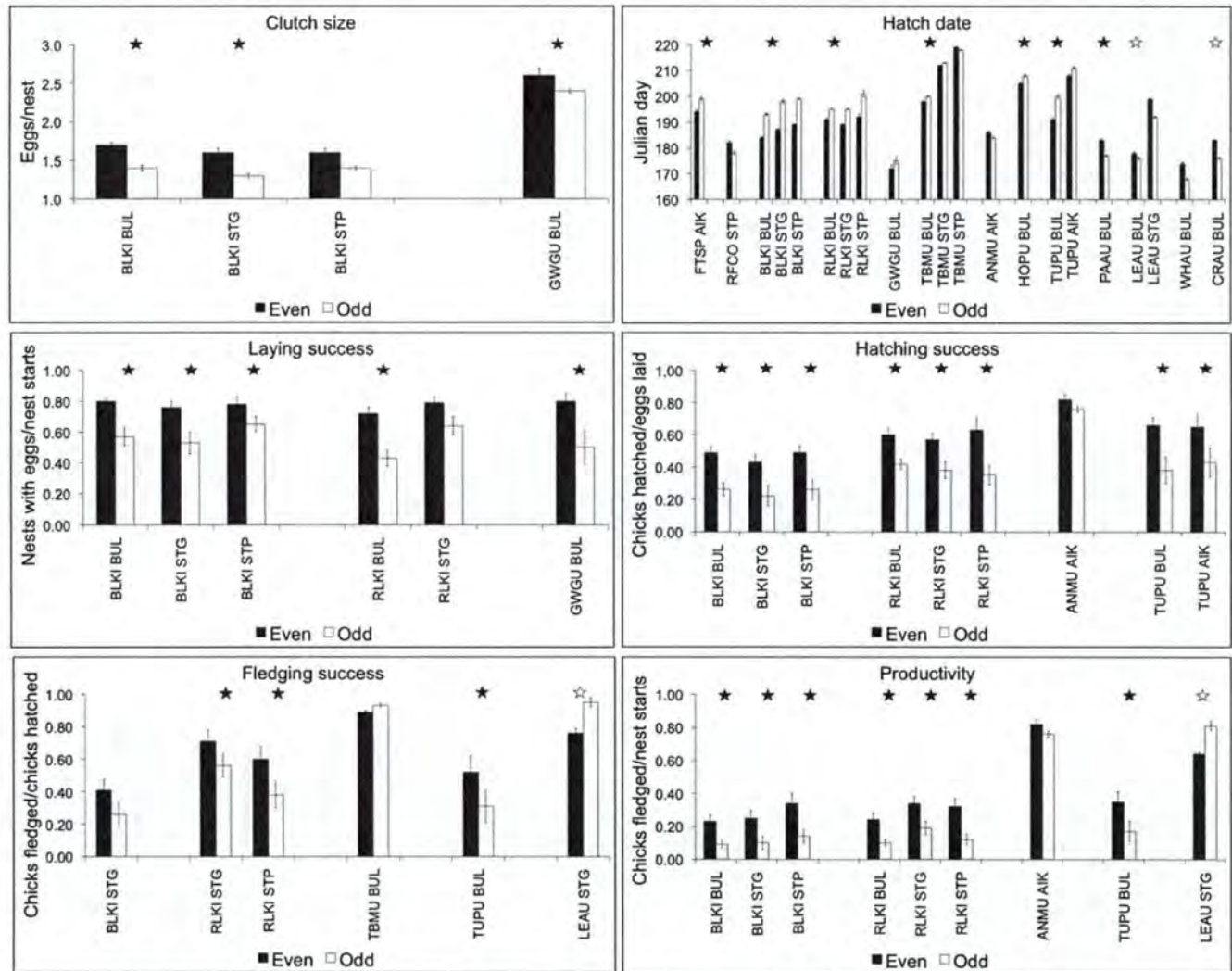


Fig. 3. Mean values of seabird breeding parameters that exhibited differences between even years and odd years at $\alpha = 0.10$. See Tables S2 and S3 for all parameter tests in all species and sample sizes. Error bars denote ± 1 SEM. Filled stars indicate relationships to eastern Kamchatka pink salmon abundance (linear regression, $\alpha = 0.10$); open stars indicate relationships to western Alaska pink salmon abundance at $\alpha = 0.10$ (Table S4). See Table S2 for species abbreviations. BUL, Buldir Island; STG, St. George Island; STP, St. Paul Island. Data are from refs. 67–70.

similar even-year–odd-year patterns. We further examined the possible connection between seabirds and salmon by comparing seabird nesting parameters to the annual run size of eastern Kamchatka pink salmon, and in particular cases to the annual run size of pink salmon in western Alaska. Using these approaches, we found compelling evidence that pink salmon have a major influence on diets, numbers, phenology, fecundity, and/or productivity of one or more species (in the order of 10^7 individuals) at one or more of these islands.

Results

We ran 111 tests of the null hypothesis that there was no difference in mean values of six nesting parameters of 16 species at four islands between even and odd years (Table 1 and Tables S2 and S3). Rejection of the null hypothesis for the individual parameters at $\alpha = 0.10$ ranged from 29% to 84% and was 50% overall. These rates exceeded in all cases the number that would be expected by chance alone and demonstrated strong directionality and the large magnitude of effect that we hypothesize pink salmon have on seabirds, and the ecosystem, of the SNPO/BS.

Omnivorous Seabirds. Phenology, as indexed by mean hatch date, was later (at $\alpha = 0.10$) in odd years than in even years for 13 of the 20 species/island samples and was seen on all islands: the difference was particularly pronounced in black-legged kittiwakes (*Rissa tridactyla*), which had mean hatch dates that were 9–12 d later in odd years (Fig. 3 and Tables S2 and S3). It was earlier by 4 d for red-faced cormorants (*Phalacrocorax urile*) at St. Paul, and earlier for ancient murrelets (*Synthliboramphus antiquus*) at Aiktak and for common murrelets (*Uria aalge*) and thick-billed murrelets (*Uria lomvia*) at St. Paul by 2, 4, and 1 d, respectively. Clutch size was smaller in odd years than in even years for black-legged kittiwakes at all three islands and for glaucous-winged gulls (*Larus glaucescens*) at Buldir. Laying success (number of nests with eggs per number of nest starts) was lower in odd years for black-legged kittiwakes at all three islands, for red-legged kittiwakes (*Rissa brevirostris*) at Buldir and St. George (and by 15% at St. Paul, although it missed the $\alpha = 0.10$ criterion), and for glaucous-winged gulls at Buldir. Hatching success (number of eggs hatching per number of eggs laid) was lower in odd years for both species of kittiwakes at all three islands, for tufted puffins at Buldir and Aiktak, and for ancient murrelets at Aiktak. Fledging

success (number of chicks fledged per number of eggs hatched) was lower in odd years for tufted puffins at Buldir, both species of kittiwakes at St. George, and red-legged kittiwakes at St. Paul (and black-legged kittiwakes by 12%, although it too missed the $\alpha = 0.10$ criterion), but was higher in odd years for thick-billed murrelets at Buldir. Productivity (number of chicks fledged per number of nest starts) was lower in odd years for both species of kittiwake at all three islands, for ancient murrelets at Aiktak, and for tufted puffins at Buldir.

Counts of nests of some species that build nests (not all species of seabirds do) at Buldir and the Pribilofs were made in sufficient numbers of even and odd years to compare differences, and in all cases more nests were built in even years than in odd years (Fig. 4). Although these are small sample sizes and not all differences had high significance levels (Table S5), they strongly support the other even-year–odd-year evidence of an effect of pink salmon on these birds. In addition, finally, black-legged kittiwakes at all three islands, red-legged kittiwakes at Buldir and St. Paul, and glaucous-winged gulls, horned puffins (*Fratercula corniculata*), and tufted puffins at Buldir laid conspicuously more eggs in even years than in odd years (Fig. 4).

Nesting parameters of several of the omnivores also exhibited negative correlations with the run size of eastern Kamchatka pink salmon (Fig. 3 and Table S4). Clutch size of black-legged kittiwakes at Buldir and St. George was well correlated with salmon abundance, and of glaucous-winged gulls at Buldir. The hatch date for five of six species at Buldir was highly correlated with salmon abundance, although not correlated at either of the Pribilof islands despite large differences in mean hatch dates between even and odd years. Laying success of black-legged kittiwakes at all three islands and of red-legged kittiwakes and glaucous-winged gulls at Buldir was correlated with salmon abundance. Hatching success of both species of kittiwakes at all three islands and of tufted puffins at Buldir and Aiktak was also correlated with salmon abundance. Fledging success was generally less well correlated with salmon abundance, reflecting the smaller, or lack of, differences between mean values in even and odd years, but still was correlated for black-legged kittiwakes at St. Paul, for red-legged kittiwakes at St. George and St. Paul, and for tufted puffins at Buldir. Productivity was strongly correlated with pink salmon abundance for both species of kittiwakes at all islands and for horned and tufted puffins at Buldir.

There were no consistent geographic patterns in the magnitude of differences between mean values of parameters in even and odd years for the three species that were sampled at Buldir, St. George, and St. Paul (Table 2), nor were there consistent geographic patterns in the strength of relationships of nesting parameters to eastern Kamchatka pink salmon run size (Table S4).

Planktivorous Seabirds. The limited data on breeding parameters of planktivores—four species at Buldir and one species at St. George—revealed either an opposite pattern to that of omnivores, or no pattern at all (Fig. 3 and Tables S2 and S3). Only the hatch date was very different between even years and odd years at Buldir, and in all cases it was earlier (by up to 7 d) in odd years. The hatch date for least auklets (*Aethia pusilla*) at St. George also was much earlier in odd years, and fledging success and productivity were higher. The hatch dates of least auklets and crested auklets (*Aethia cristatella*) at Buldir were well correlated with Norton Sound pink salmon abundance, as were fledging success and productivity of least auklets at St. George (Fig. 3 and Table S4).

Diets of least auklets at Buldir during the chick period (mid-June to mid-July) differed between even years and odd years (Fig. 5). In 1994–2009, the dominant prey of least auklets, the large calanoid copepod taxon *Neocalanus plumchus/flemingeri* (the two species are difficult to differentiate), had a mean frequency of occurrence of $97 \pm 2\%$ and there was no difference between

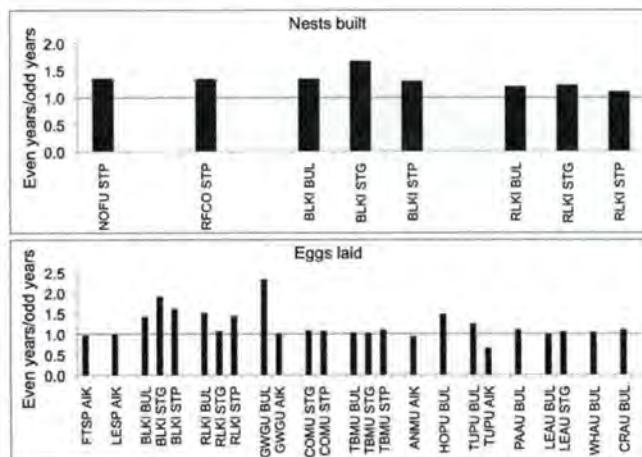


Fig. 4. Ratios of the numbers of nests built and eggs laid in even years compared with odd years across all years. See Table S2 for species abbreviations. AIK, Aiktak Island; BUL, Buldir Island; STG, St. George Island; STP, St. Paul Island. Data are from refs. 67–70.

Table 2. Values of nesting parameters in even years divided by values in odd years for omnivorous species that were each measured at Buldir (BUL), St. George (STG), and St. Paul (STP)

Species location	Clutch size	Hatch date	Laying success	Hatching success	Fledging success	Productivity
BLKI BUL	1.21	0.95	1.40	1.88	1.00	2.56
BLKI STG	1.23	0.94	1.43	1.95	1.58	2.50
BLKI STP	1.14	0.94	1.20	1.88	1.34	2.43
RLKI BUL	na	0.98	1.67	1.43	0.96	2.60
RLKI STG	na	0.97	1.23	1.50	1.28	1.74
RLKI STP	na	0.96	1.35	1.75	1.58	2.67
TBMU BUL	na	0.99	na	1.03	0.96	1.00
TBMU STG	na	1.00	na	0.98	1.00	1.00
TBMU STP	na	1.00	na	0.91	0.99	0.89

BLKI, black-legged kittiwake; RLKI, red-legged kittiwake; TBMU, thick-billed murre; na, not applicable. Data are from refs. 67, 69, and 70.

even and odd years. In 1994–2006, it made up an estimated $65 \pm 7\%$ of the biomass of prey brought to chicks; however, the proportion in even years (excepting 2000 when it was anomalously low at just 12%) was $77 \pm 6\%$, but $62 \pm 9\%$ in odd years ($P = 0.18$). Although the apparent difference did not have high statistical significance, it is consistent with even-year–odd-year differences found in the consumption of principal secondary prey—that is, with the exception of euphausiids, consumption of *N. cristatus*, decapods, hyperiids, and pteropods was generally

higher in odd years than in even years. The lower consumption of euphausiids in odd years may have been proportional to a lower abundance of euphausiids in odd years due to pink salmon predation.

Likewise, whiskered auklets (*Aethia pygmaea*) at Buldir (67) consumed more *Neocalanus cristatus*, their dominant prey, during the chick rearing period in even years than in odd years ($52 \pm 8\%$ versus $32 \pm 11\%$; $P = 0.18$). Although this difference also was not highly significant, it and the differences in least auklet diets

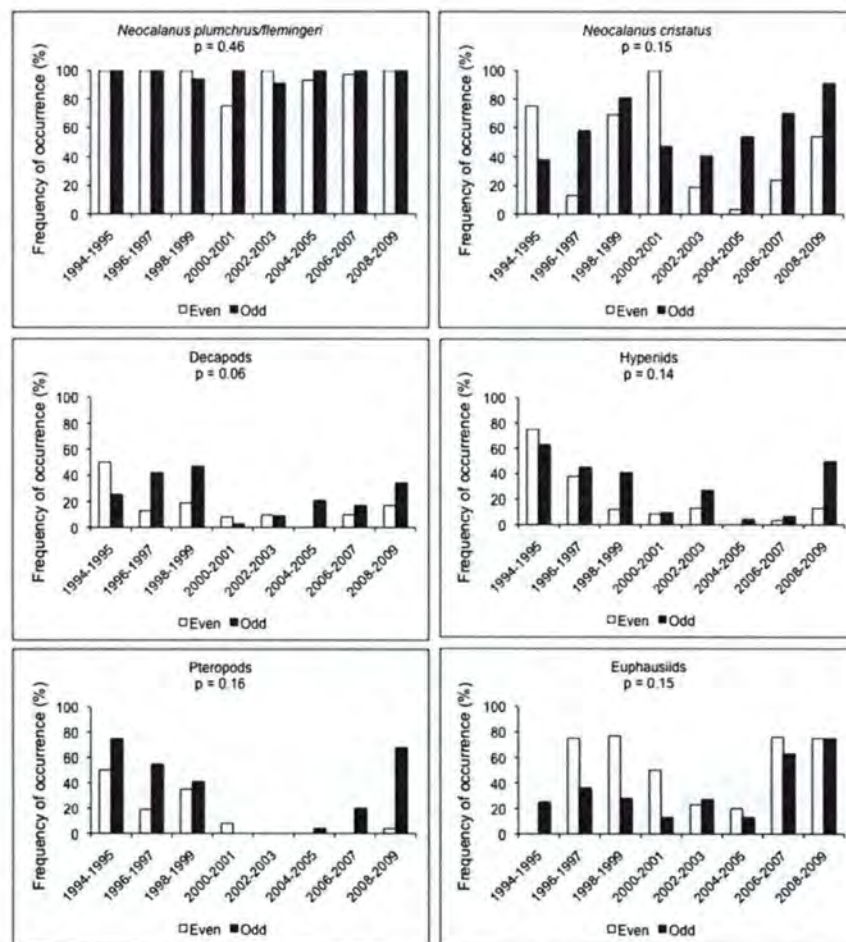


Fig. 5. Frequency of occurrence (percentage) of principal prey in diets of least auklets at Buldir Island. Significance levels (P , Student t test; $n = 16$ y) are for differences between mean values in even years and odd years across all years. Data are from ref. 67.

between even and odd years are likely biologically significant. Such a conclusion is supported by continuous plankton recorder data primarily from the southern Bering Sea (173 W \times 173 E, 52 N \times 54 N; appendix 5 in ref. 66) that show large differences in the abundance of *N. cristatus* and *N. plumchrus/flemingeri* across even and odd years— 4.8 ± 2.3 g versus 0.06 ± 0.01 g, $P = 0.14$; and 3.9 ± 0.6 g versus 0.6 ± 0.3 g, $P = 0.0071$, respectively (Fig. 6).

Discussion

The great interaction strength of pink salmon during years of high abundance apparently derives from voracious consumption to fuel exceptionally rapid growth in spring–summer of their second year—the mass of maturing fish increases by some 500%, from about 300 to 1,500 g, in just 4 mo between March and July when they spawn (29). Prominent among their prey are species important to the structure of the plankton community of the SNPO/BS and to other consumers, such as seabirds, both directly and indirectly as trophic links. Exploitative competition is common within many trophic levels in many ecosystems, but there are few cases where it has been identified or suspected among lower and higher trophic levels in the open ocean (e.g., refs. 71–74). Now we show evidence of strong exploitative competition by pink salmon visited upon pelagic species, besides other species of salmon, in the SNPO/BS: in years of high abundance pink salmon consume zooplankton and micronekton in sufficient amounts to compromise a variety of nesting parameters of resident seabirds, as well as the survival of migratory seabirds.

Most of the omnivorous seabirds considered here winter in the northern North Pacific Ocean and southern Bering Sea (59, 60, 75, 76). Thus, most species are exposed to competition with

pink salmon during much of the year, and competition would intensify rapidly in late spring and early summer when fish move back into the Bering Sea from the North Pacific Ocean. Any carryover effects of prebreeding food stress on nesting success (77) would exacerbate the effect of continuing competition through the early to mid stages of nesting.

This comportment reasonably well with the timing of the migration of eastern Kamchatka pink salmon (78). Most fish are in the northern North Pacific Ocean through May (coincident with prelaying), which would explain the strong relationships of phenology and laying success with salmon abundance. The fish begin moving back into the Bering Sea through the Aleutian Islands and Bering Sea basin in June (coincident with laying and incubation), and by July (coincident with peak hatch) they are moving into the central and western Bering Sea. Thus, by the chick period (July–August) the bulk of the fish are in or approaching their spawning rivers and their influence is apparently diminished. Their distribution and the timing of migration vary between years depending on oceanographic conditions, particularly temperature (79), which would be expected to lead to interannual variability in the strengths of relationships with various elements of seabird breeding biology.

There is the question of why planktivorous seabirds exhibit the opposite pattern in phenology—that it is advanced in odd years and delayed in even years and why least auklets on St. George have higher fledging success and productivity in odd years. However, the consistent differences between mean values in even years and odd years also suggest a connection to pink salmon. One possibility is that the differences are due not to effects of eastern Kamchatka pink salmon, but to effects of pink salmon from western Alaska that spawn in rivers emptying into the eastern Bering Sea and that have strong runs in even years (34). These fish appear to move out of the Bering Sea and into the northeastern North Pacific in winter, and maturing fish return in spring through the central and eastern Aleutian Islands and southeastern Bering Sea (78, 79). Although the western Alaska stock is smaller than the eastern Kamchatka stock, as they return in spring and early summer their numbers are concentrated in a comparatively smaller geographic region, which would concentrate possible effects on resource pools shared with auklets and other species. Thus, least auklets on St. George would compete with them from prelaying through much of the breeding season, which would explain the correlations between their breeding parameters and western Alaska pink salmon abundance. Auklets from elsewhere that winter in the eastern Aleutian Islands, for example, whiskered auklets (80, 81), would be exposed to competition with western Alaska pink salmon in winter–spring, but likely not in summer, which would explain why only phenology differs between even and odd years and why it is delayed in even years. Alternatively, auklets from the western Aleutian Islands, if they winter in the western North Pacific Ocean off Japan and the Kurile Islands (82), might be exposed to competition with Sea of Okhotsk pink salmon, which also are dominant in even years and highly abundant (34).

Neocalanus plumchrus/flemingeri and *N. cristatus* commonly dominate the biomass of zooplankton in the SNPO/BS and are major conduits of energy between phytoplankton and higher trophic levels, in large measure because they accumulate a high lipid content in summer in preparation for overwinter diapause (83). They are thus high-quality prey for planktivores including least auklets, whiskered auklets, pink salmon, and others. Although some of the secondary prey of least auklets and whiskered auklets also have comparatively high lipid concentrations, e.g., euphausiids, many are of much lower energy density (84). The rise in occurrence of secondary prey in auklet diets in odd years is presumably related to the same phenomenon in chum salmon in the SNPO/BS—in even years chum salmon diets include high lipid copepods, euphausiids, and other crustaceans,

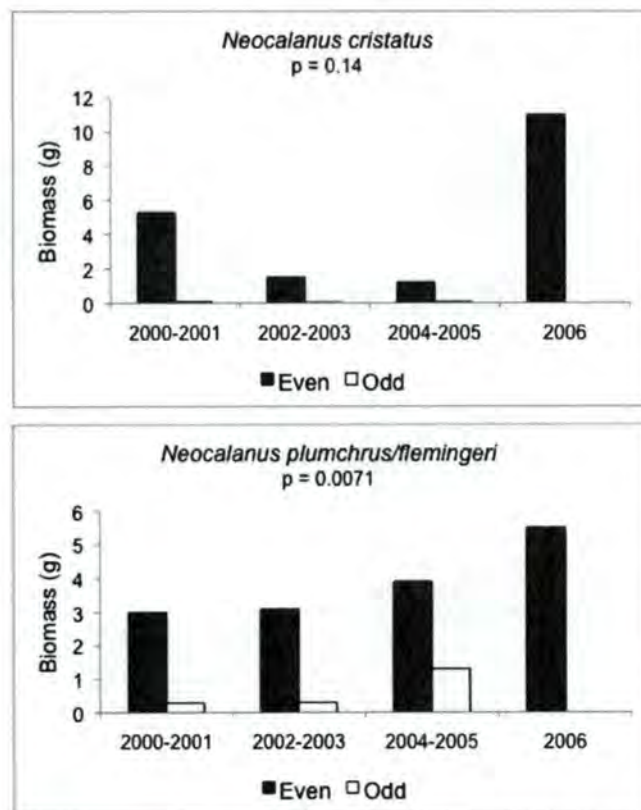


Fig. 6. Biomass of *Neocalanus* copepods in continuous plankton recorder standardized tows in the southern Bering Sea. Significance levels (P , Student t test; $n = 7$ y) are for differences between mean values in even years and odd years across all years. Data are from ref. 66.

but in odd years their diets are dominated by lower lipid prey, primarily gelatinous taxa such as pteropods, appendicularia, and coelenterates, due apparently to the depressing effect on crustacean biomass of pink salmon predation (43). Similarly, diets of pink, chum, and sockeye salmon in the northeastern North Pacific Ocean and Bering Sea contain different levels of important prey in even and odd years (46, 56).

Depression of seabird productivity cannot be tied to long-term trends in the abundance of any of the species, trends that vary among species and islands (67–70, 85). However, the combination of fewer birds attempting to nest in odd years; fewer eggs being laid, and later, by those that do attempt to nest; and poorer reproductive success by some species raises questions for the future. Seabirds are long-lived, K-selected animals, a strategy that dampens effects of interannual variability in productivity on abundance, but increases the sensitivity of populations to adult mortality. However, over the long term they do depend on reproduction, and the combination of depressed productivity every other year, by as much as 62% for both species of kittiwake, coupled with possible deleterious effects of physiological stress on developing chicks and reproductive life spans of adults experiencing biennial physiological stress (86) could lead to declines in the abundance of the more sensitive species if pink salmon numbers remain at high levels and seabird mortality begins to outpace recruitment. That not all seabird species were affected equally likely reflects differing degrees of ecological separation from pink salmon, which could include the extent of dietary overlap and spatial and temporal physical overlap, and the behavioral ability of some (e.g., murre in particular) to buffer effects of variability in prey quantity and quality on breeding success (87).

Ocean temperature has steadily risen in the western Bering Sea since the middle of the last century, with a pronounced increase in the 2000s that corresponded to the most recent increase in pink salmon abundance (39). One would expect that there is an optimum thermal window above and below which salmon populations cease to prosper (88–91), although the unusually large aerobic scope and cardiorespiratory capacity of pink salmon significantly broadens their range of thermal tolerance (92). However, even if pink salmon abundance experienced no further growth, important questions remain concerning their impact on ecosystem function in the SNPO/BS and the capacity of ocean production processes to support the current biomass of many higher trophic level species including salmon, other fishes, seabirds, and recovering populations of great whales. The potential problem may grow over the course of this century if habitat shrinks due to projected ocean warming and competitive dominance of pink salmon increases if they and other species become more tightly crowded (91).

The resource vacuum and altered community composition left behind as pink salmon migrate back through the SNPO/BS in spring–summer are functionally equivalent to effects of consumer fronts described in a variety of terrestrial and marine ecosystems (93). Although consumer (fish) density would not be as high per square meter as in other ecosystem types, at the geographic scale over which the process occurs (about 1.3×10^6 km² in the Bering Sea basin alone) it bears a resemblance, particularly if pink salmon tend to coalesce as their migration progresses. In this case, the movement of the consumers is not necessarily driven by serial depletion of resources at the “front,” but by the biological imperative to return to their natal streams to reproduce. Consumer fronts in open ocean ecosystems previously have not been described (93), and the indication that the return migration of eastern Kamchatka pink salmon now effectively constitutes one in odd years apparently derives from the role that climate change has played in the growth in their abundance. In aggregate, the direct, indirect, and cascading effects of pink salmon suggest that they have a destabilizing effect on the ecosystem of the SNPO/BS.

Additional pressure in the North Pacific comes from the growing number of hatchery produced pink and chum salmon—

e.g., some 3×10^9 chum smolts are released each year in Japan and the annual run size has been in the order of $50\text{--}80 \times 10^6$ fish since the 1980s, plus there are many more in the ocean given their multiyear life history strategy, and most of them spend the summer–fall feeding period in the Bering Sea (31, 37, 45). A recommendation has been made to increase Russian hatchery production of chum salmon (94), which currently is negligible. In the northeastern North Pacific, hatchery production of pink salmon in Prince William Sound began in the mid-1970s and has grown to annual runs as high as nearly 70×10^6 fish (34). Record-breaking runs of wild pink salmon in summer 2013 from Washington State to the Gulf of Alaska (95–97) highlight the continuing trend.

Interannual switching between alternate ecosystem states of the SNPO/BS driven by pink salmon must be accounted for when attempting to explain patterns of change in populations of species at lower and higher trophic levels and when building ocean ecosystem models. Key forcing from the salmon is additive to, perhaps dominant to in some cases, whatever other drivers are important in the environment. The abundance of pink salmon, owing to their life history strategy, is an uncommon case of too many fish in the sea, and the ecosystem-scale effect they have needs to become part of international resource common-pool policy discussions that include seabirds, and by extension additional competing species (98). The response of wild salmon, and other commercially targeted fishes, to climate change has important management implications (98–102) and conservation implications as revealed by this study. The large and growing number of hatchery-reared salmon raises additional concern about the carrying capacity of the SNPO/BS, although such concern is not universally embraced (103).

Pacific salmon has considerable societal importance, as the commercial fishery is a multibillion dollar industry employing tens of thousands of people (104) and feeding millions of people. There is an obvious strategy in using the oceans as unattended feedlots, but we know that the feed troughs will not be perpetually full, and despite the nutritious protein and fatty acids of free-range salmon, it is time to consider additional issues as well. The need to sustainably accommodate not only salmon but other denizens of the sea could potentially turn salmon fishery management in certain cases from the now common practice of imposing catch limits and raising hatchery production to enhance stocks, to relaxing catch limits and encouraging larger harvests and smaller hatchery releases to help maintain equity among all of the trophically linked consumers—in other words, to devise a broad-scale ecosystem-based management strategy.

Materials and Methods

Values of seabird breeding parameters at the four monitoring colonies are reported annually by the US Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge (67–70). Unless otherwise noted, all seabird data were from these sources—additional data were available in ref. 66 as cited. We used the data as reported for all parameters except number of eggs laid, which we calculated by adjusting the reported number of chicks hatched annually on phenology monitoring plots by the average hatching success of eggs in even and odd years. We compared mean values of nesting parameters in even years to those in odd years using Student *t* test.

Annual run sizes (catch plus escapement, millions of fish) of wild eastern Kamchatka pink salmon were reported for 1952–2005 in ref. 34, and catch only (tonnes) for 1971–2009 in ref. 39 and 2010–2012 (as shown in Table S1). We estimated the run size in 2006–2012 using the relationship between run size and catch in 1971–2005 ($r^2 = 0.90$, $P < 0.0001$). We used the annual run size of wild pink salmon in Norton Sound from 1997 to 2012 (40) as an index of run size in western Alaska. There are no hatchery programs in eastern Kamchatka or western Alaska. Run sizes were log normal transformed to compute values of linear regressions against nesting parameters.

We used $\alpha = 0.10$ to parse the full dataset for discussion and clarity in presentation in figures—it does not imply a firm judgment about the statistical or biological significance of differences between mean values in even and odd years or the slopes of regressions of nesting parameter values against salmon abundance. Significance levels of all tests of null hypotheses are reported in Tables S2–S5.

ACKNOWLEDGMENTS. We thank J. Estes, K. Myers, B. Agler, S. Iverson, and one anonymous reviewer for constructive comments that improved this manuscript, and G. Khen for providing eastern Kamchatka pink salmon harvest data. We are indebted to V. Byrd for establishing the long-term seabird monitoring program

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RESEARCH ARTICLE

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

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Abstract

The *Exxon Valdez* oil spill occurred in March 1989 in Prince William Sound, Alaska, and was one of the worst environmental disasters on record in the United States. Despite long-term data collection over the nearly three decades since the spill, tremendous uncertainty remains as to how significantly the spill affected fishery resources. Pacific herring (*Clupea pallasii*) and some wild Pacific salmon populations (*Oncorhynchus spp.*) in Prince William Sound declined in the early 1990s, and have not returned to the population sizes observed in the 1980s. Discerning if, or how much of, this decline resulted from the oil spill has been difficult because a number of other physical and ecological drivers are confounded temporally with the spill; some of these drivers include environmental variability or changing climate regimes, increased production of hatchery salmon in the region, and increases in populations of potential predators. Using data pre- and post-spill, we applied time-series methods to evaluate support for whether and how herring and salmon productivity has been affected by each of five drivers: (1) density dependence, (2) the EVOS event, (3) changing environmental conditions, (4) interspecific competition on juvenile fish, and (5) predation and competition from adult fish or, in the case of herring, humpback whales. Our results showed support for intraspecific density-dependent effects in herring, sockeye, and Chinook salmon, with little overall support for an oil spill effect. Of the salmon species, the largest driver was the negative impact of adult pink salmon returns on sockeye salmon productivity. Herring productivity was most strongly affected by changing environmental conditions; specifically, freshwater discharge into the Gulf of Alaska was linked to a series of recruitment



OPEN ACCESS

Citation: Ward EJ, Adkison M, Couture J, Dressel SC, Litzow MA, Moffitt S, et al. (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 12(3): e0172898. doi:10.1371/journal.pone.0172898

Editor: João Miguel Dias, Universidade de Aveiro, PORTUGAL

Received: November 4, 2016

Accepted: February 10, 2017

Published: March 15, 2017

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Data Availability Statement: All data and code to replicate the analysis and figure is on a public github site, <https://github.com/NCEAS/pfx-covariation-pws>.

Funding: This project was funded as an NCEAS working group (National Center for Ecological Analysis and Synthesis, <https://www.nceas.ucsb.edu/>) by Kristin Marshall, "Applying portfolio effects to the Gulf of Alaska ecosystem". Funding for the

working group was provided by the Exxon Valdez Oil Spill Trustee Council (EVOSTC).

Competing interests: The authors have declared that no competing interests exist.

failures—before, during, and after EVOS. These results highlight the need to better understand long terms impacts of pink salmon on food webs, as well as the interactions between nearshore species and freshwater inputs, particularly as they relate to climate change and increasing water temperatures.

Introduction

Impacts of human-caused environmental disasters—such as oil spills or nuclear accidents—are often realized immediately, but may also result in lasting change over decades or longer [1,2]. Detecting impacts of these disasters relies on dedicated funding and long-term monitoring; however, attributing change to these singular catastrophic events may be difficult when environmental and ecological variables measured in long-term monitoring efforts are simultaneously affected by other external pressures (e.g., climate variability, removals from fishing). Inference about impacts may be further complicated by how species are prioritized for monitoring, and how the allocation of monitoring effort is distributed in space and time [3].

One of the most well-known and documented environmental catastrophe with available long-term monitoring studies is the *Exxon Valdez* oil spill (EVOS). On March 23, 1989, the oil tanker *Exxon Valdez* ran aground in Prince William Sound (PWS), in southcentral Alaska (Fig 1). This region represents an ecosystem where multiple complex interactions between environmental conditions and terrestrial, nearshore, and pelagic components drive high rates of productivity [4,5]. The tanker spilled an estimated 42 million liters of crude oil into the area, contaminating marine waters for more than 800 km to the southwest [6–8,8–10]. Nearly 40 percent of the oil landed on beaches within PWS, affecting over 780 km of shoreline [11]. In the more than 25 years since the EVOS disaster, resource managers and researchers from federal, state, university, and non-profit organizations have collected a vast amount of information to quantify the effects of the spill and evaluate recovery of injured resources. Despite these monitoring efforts, the direct and indirect environmental impacts attributable to EVOS are still hotly debated by the scientific community [12,13].

The most scrutinized effects of EVOS have been related to direct exposure effects of oil, affecting species or populations closely associated in space and time with the obvious presence of oil. Clean-up efforts, combined with the dynamic marine tidal and weather patterns, were expected to remove or displace much of the spilled oil from the environment in several years [14]. Studies conducted a decade after EVOS estimated the remaining oil to be < 1% of that originally estimated, but lingering toxicity effects were still considered to be a concern [15]. More recent work has provided a mechanism by which this residual oil can have chronic effects on species that depend upon nearshore rearing and spawning areas. In particular, species such as Pacific herring (*Clupea pallasii*) and pink salmon (*Oncorhynchus gorbuscha*) that use nearshore habitats may be affected by crude oil through physiological defects that lead to reduced growth rates and higher larval and juvenile mortality [16]. While experimental studies have found support for toxic effects of oil on individuals, a larger challenge is identifying persistent effects at the population level, where duration and magnitude of oil exposure is unknown.

Herring and multiple species of salmon have been the focus of a large number of research studies in PWS, both because of their value to commercial fisheries and because of population-level changes observed in PWS during or after the EVOS disaster. For example, the PWS population of herring suffered a well-documented collapse in 1993, resulting in a closure of the

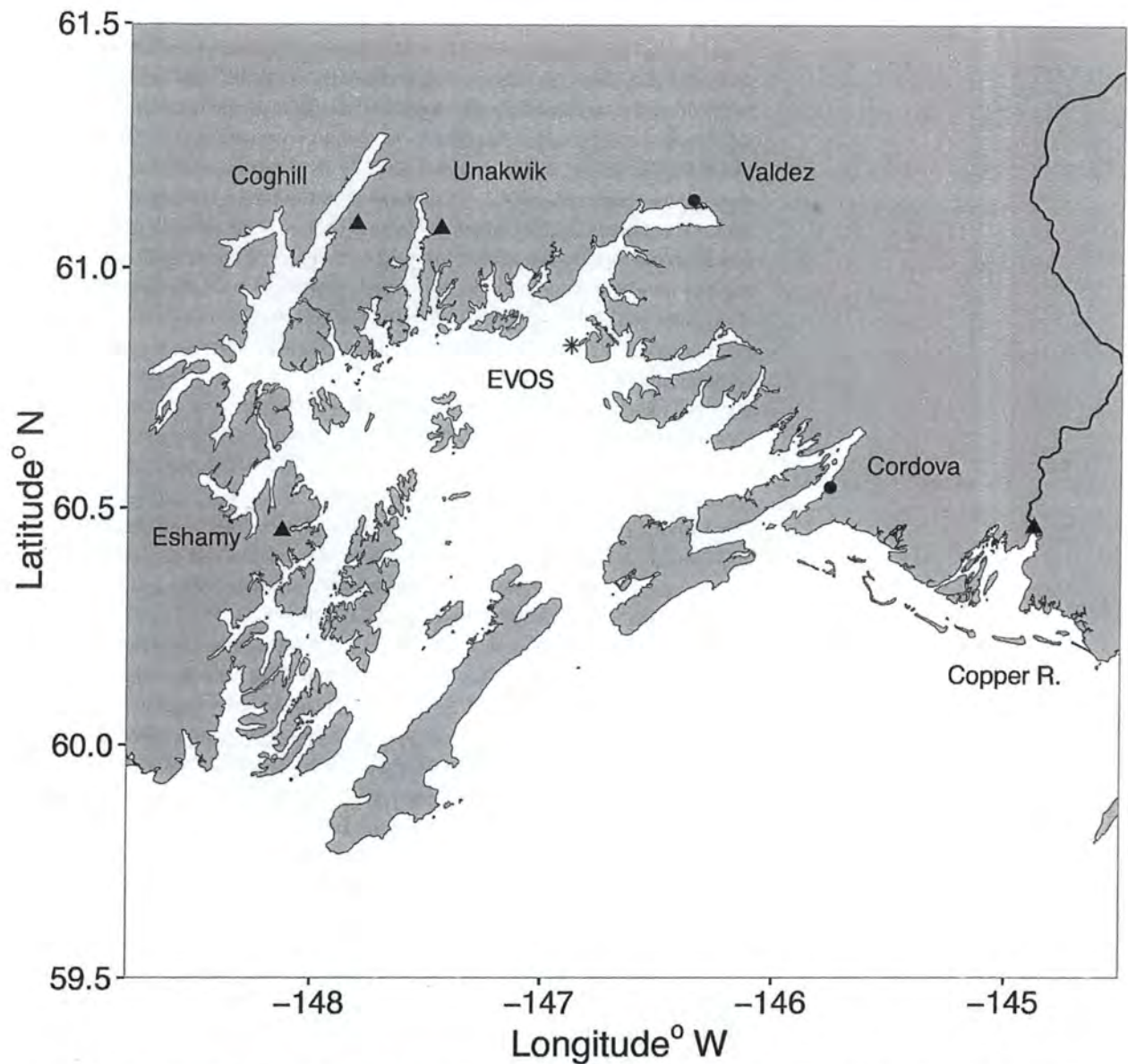


Fig 1. Map of Prince William Sound, and the adjacent Copper River Alaska. Triangles indicate the location of wild salmon stocks included in our analyses, circles show towns, and the asterisk shows where the *Exxon Valdez* ran aground in 1989.

doi:10.1371/journal.pone.0172898.g001

commercial fishery, and to date, the population has not recovered [17,18]. Similarly, low returns of pink salmon to PWS also occurred in 1992 and 1993, [19,20], and Willette et al. [21] proposed that Coghill Lake sockeye had been impacted by EVOS as juveniles in the nearshore environment. While the majority of studies investigating EVOS impacts have not found strong effects [12,22], a number of confounding hypotheses have been proposed for explaining observed changes in fish population dynamics; these include disease, variation in the ocean environment, changes in spawning habitat, changes in interactions between species, intraspecific density dependence, and increases in predation from higher trophic level species, such as marine birds and mammals [12,13,23].

Alternative hypotheses for herring and salmon declines

Over the last four decades, the PWS region has experienced a number of changes or regime shifts that may have also affected the productivity of species such as herring and salmon. In 1976–77 the coastal North Pacific experienced a dramatic increase in temperature that coincided with the large-scale realignment of marine communities [24,25]. Like the rest of the North Pacific Ocean, water temperatures have also been gradually increasing, resulting in anomalously high values [26,27]. Of particular interest to this study was the climate regime shift that occurred in 1989, which led to an ecosystem state thought to be less productive [28], thereby confounding assessments of the direct impact of the oil spill. Periods of warm and cool regimes in ocean temperature have also been correlated with changes in freshwater input, wind patterns, and water column stability that lead to shifts in marine productivity [29–32]. Over the past 40 years, the northern Gulf of Alaska has undergone a general warming and freshening in the upper 100 m of the water column; with an increase in salinity in depths between 100–200 m. This suggests that vertical stratification in the upper water column in the Gulf of Alaska has increased substantially [33]. In coincidence with the changes in the physical environment, higher water temperatures impact metabolism and consequently growth, energy demands, and ultimately, behavior and survival of larval and juvenile fishes [31,34]. Thus, these environmental changes in bottom-up forcing resulting from changes in temperature and productivity add to the variability in survival of both adult and juvenile herring and salmon.

In response to poor runs of wild salmon during the late 1960s and early 1970s, state and non-profit hatcheries began releasing salmon into areas of PWS in 1976 [35,36], with possible consequences to wild salmon and herring. A substantial increase in hatchery pink salmon production occurred during the late 1980s, just prior to the spill; thus representing another potential confounding effect (S1 Fig). Ecological impacts of this change have been speculated to impact both wild salmon and forage fish that compete for similar prey resources or serve as prey to adult returning fish [22,34,37,38]. Studies from other regions in the Northeast Pacific have demonstrated evidence for dietary overlap between pink salmon and herring [39] and pink salmon in particular are known to consume a diversity of prey items in the marine environment, from zooplankton to herring and other fish [40,41], and compete with salmon species including chum (*O. keta*), Chinook (*O. tshawytscha*) and sockeye salmon (*O. nerka*) [42].

In addition to the possibility of increased competition or predation from hatchery released salmon, the population dynamics of herring and salmon in PWS may also have been affected by other predators. Potential predators include populations of humpback whales (*Megaptera novaeangliae*) or piscivorous marine birds [23,43,44]. Effects of these predators on herring and salmon may be direct, or indirect through apparent competition. Combined with climate drivers, recoveries of these predators throughout the Northeast Pacific Ocean have the ability to alter the ecosystem state relative to the 1980s (e.g. alternating from a period of high productivity and low predation to low productivity and high predation).

Linking covariates to herring and salmon productivity

Previous studies on herring and salmon juvenile mortality in PWS have focused on finding effects within a narrow geographic or temporal window [45–47] less on impacts at the population or stock level. Additionally, previous testing and review of hypotheses on the collapse and recovery failure of PWS herring primarily focus on adult survival [3,22,48]. Because of relatively high uncertainty concerning what factors are primarily responsible for variation in herring and salmon recruitment, we adopted a statistical approach to evaluate multiple hypotheses about lasting effects of EVOS, and long term productivity change in PWS and the adjacent Copper River. The purpose of our analysis is to synthesize and review the working

hypotheses about changes in productivity, and to use time series methods to evaluate the data support for each, 25 years after the oil spill. These hypotheses include: (1) effects of intraspecific density dependence, or increasing per capita population growth rate at decreasing population density (2) immediate and/or prolonged impacts of the EVOS event, (3) impacts of changing environmental conditions, (4) effects of interspecific competition on juvenile fish, and (5) effects of competition and predation from adult fish or, in the case of herring, humpback whales.

Methods

Data

We examined the evidence of drivers affecting recruitment in Pacific herring and three species of salmon within the Prince William Sound management area: Chinook salmon, pink salmon, and sockeye salmon (Fig 2). Specifically, we examined the amount of recruitment divided by the total reproductive component of the population, measured as spawning biomass for herring or as the number of spawning adults for salmon (Fig 3); this ratio of recruits to the spawning population is referred to as productivity. We conducted the analysis for each species separately, using the longest time series possible that also allowed similar drivers to be compared. For Pacific herring, we analyzed recruits per spawning stock biomass (R/SSB) from PWS as the response, where recruits (defined as the number of mature and immature age-3 fish) and SSB are estimated from the Alaska Department of Fish and Game (ADF&G) age structured stock assessment model (ADF&G, pers. comm., <https://github.com/NCEAS/pfx-covariation-pws>) for brood years 1981–2011. For each of three salmon species, we calculated the total adult returns, summed across all ages of return, which were the offspring of spawning adults in a particular year (i.e., total brood year returns per spawner). For Chinook salmon, we used wild spawning escapements and wild brood year returns from the Copper River for brood years 1981–2005. For wild pink salmon, we used estimates of total run size and escapement in PWS. Due to the harvest of migrating fish, productivity of PWS pink salmon can only be calculated for the entire area and not for individual stocks or districts. Finally, for wild sockeye salmon, we examined spawner and recruitment data from three populations (Coghill Lake and Eshamy Lake in PWS and the adjacent Copper River), both separately and combined. These salmon stocks were included based on the availability of data on recruitment and age structure and because they transit PWS—or have the possibility to transit PWS—as juveniles and/or as returning adults. Data from ADF&G and others suggest that adult and juvenile salmon from throughout PWS use the southwestern passages of PWS as a primary migratory corridor [49–51], which were heavily oiled during EVOS [6,7]. The adjacent Copper River was not directly oiled during EVOS; however, we included Copper River stocks in our analyses because of the potential for juvenile salmon from the Copper River to be pushed into PWS by the Alaska Coastal Current [52] and into oiled areas by the cyclonic current within PWS [53]. It is not known if adult salmon returning to the Copper River transit through PWS. Limited data are also included for other populations in the region (PWS wild chum salmon, Unakwik district sockeye salmon, S4 and S5 Figs, <https://github.com/NCEAS/pfx-covariation-pws>) but missing age and escapement data prevents estimation of recruitment. All salmon data are provided in ADF&G reports [54,55].

For each of the five hypothesized mechanisms included in our analyses, we were interested in quantifying the data support for each hypothesis and species. The five hypotheses are explained in detail as follows:

Hypothesis 1: Patterns in productivity are driven by density dependence. To evaluate the hypothesis about intraspecific density dependence, we fit null models with constant

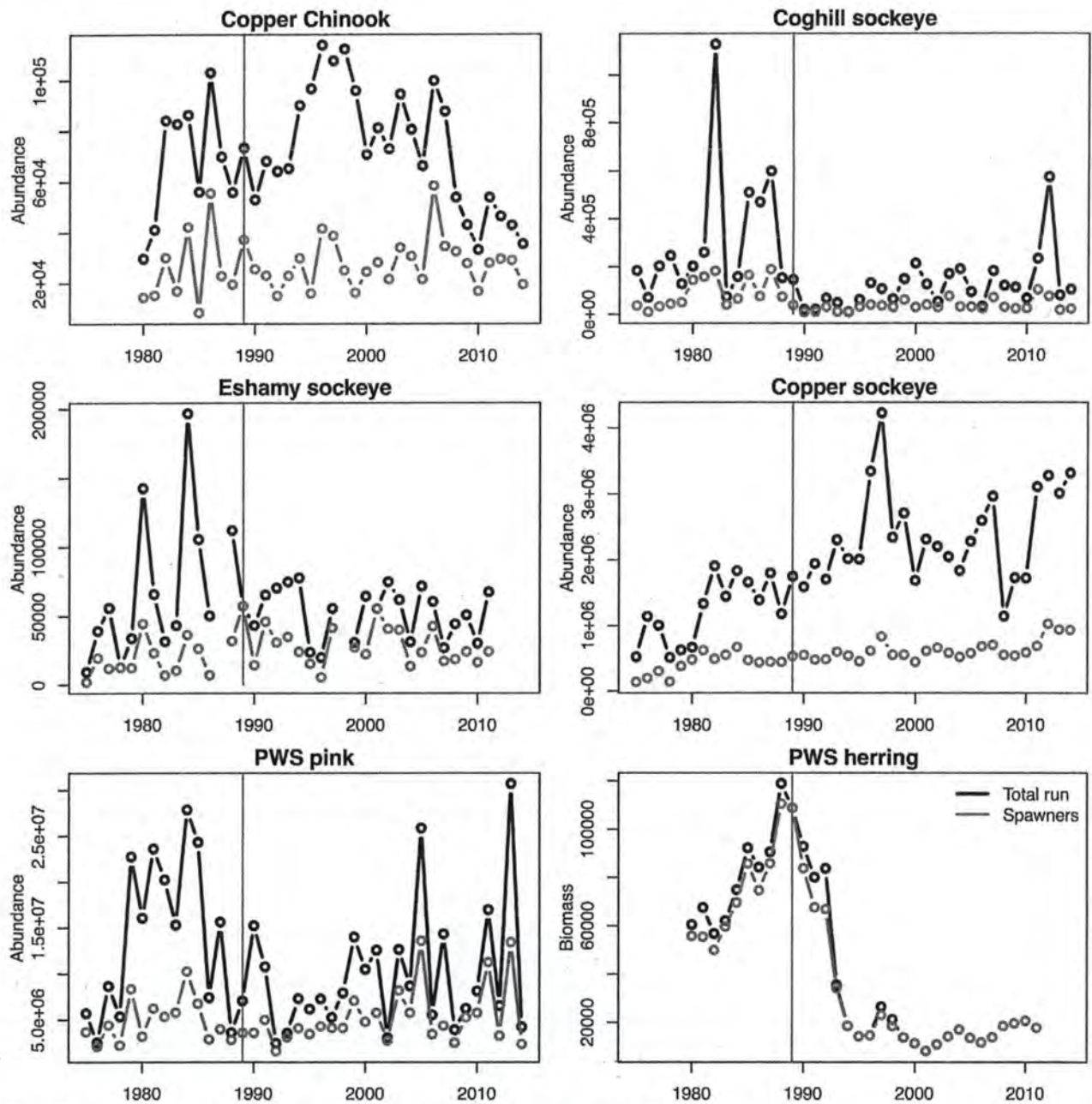


Fig 2. Time series of total run and escapement (or spawning biomass, herring). Total population size and escapement (salmon, in numbers of fish) or total population biomass and spawning stock biomass (spawning herring, in metric tons) for the six populations and four species in our analysis. Harvest for each population can be interpreted as the difference between total (black) and spawning (grey) lines. Red vertical lines are used to indicate 1989 (corresponding to the year of the EVOS event).

doi:10.1371/journal.pone.0172898.g002

productivity to time series for each species, and compared results to those of models that included spawners (or for herring, spawning biomass) in a Ricker stock-recruit relationship (Figs 2–4).

Hypothesis 2: Population productivity was negatively impacted by the oil spill. To model the potential negative impact of the EVOS event on productivity, we constructed three

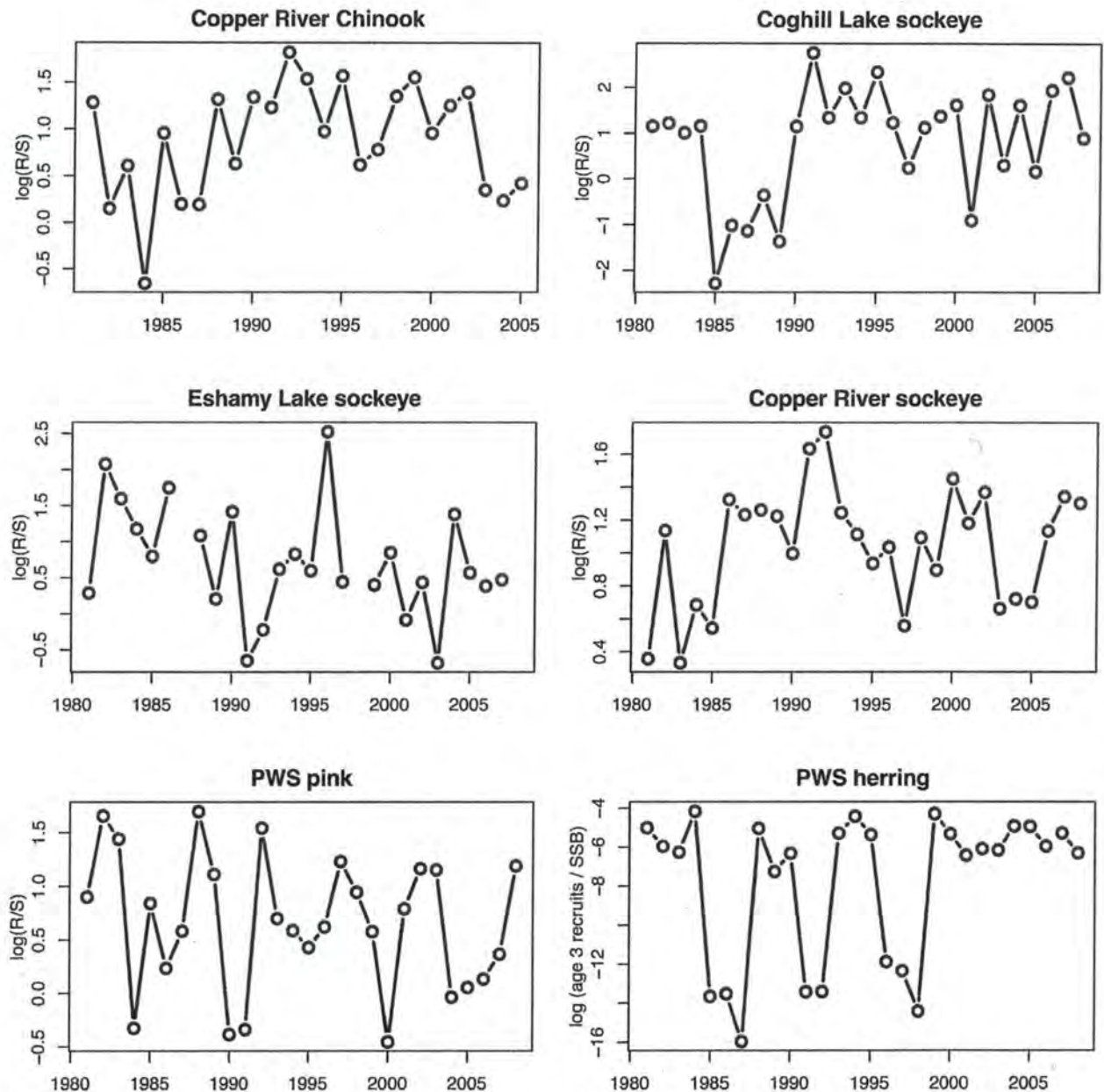


Fig 3. Time series of recruits-per-spawner relationship for data included in our analysis. Raw data are shown for the years included in our analysis. R = recruits, S = spawners, SSB = spawning stock biomass, age-3 recruits = millions of mature and immature age-3 herring, and PWS = Prince William Sound.

doi:10.1371/journal.pone.0172898.g003

alternate forms of the impact: a pulse perturbation (the impact of the event lasted one year), a press perturbation (EVOS decreased the long-term mean productivity), and a pulse perturbation followed by a gradual 20-year recovery (length chosen to correspond to a lengthy recovery but fit within the ~25 years of available data, Fig 5). For the herring and salmon species in our analysis, we also included the impacts of the EVOS event with a lag of 0, 1, and 2. All three lags were examined for herring, as spawners, eggs, and larvae may have been immediately impacted in 1989 and juveniles residing in nearshore areas from age 0 to 2 [56] may have been exposed

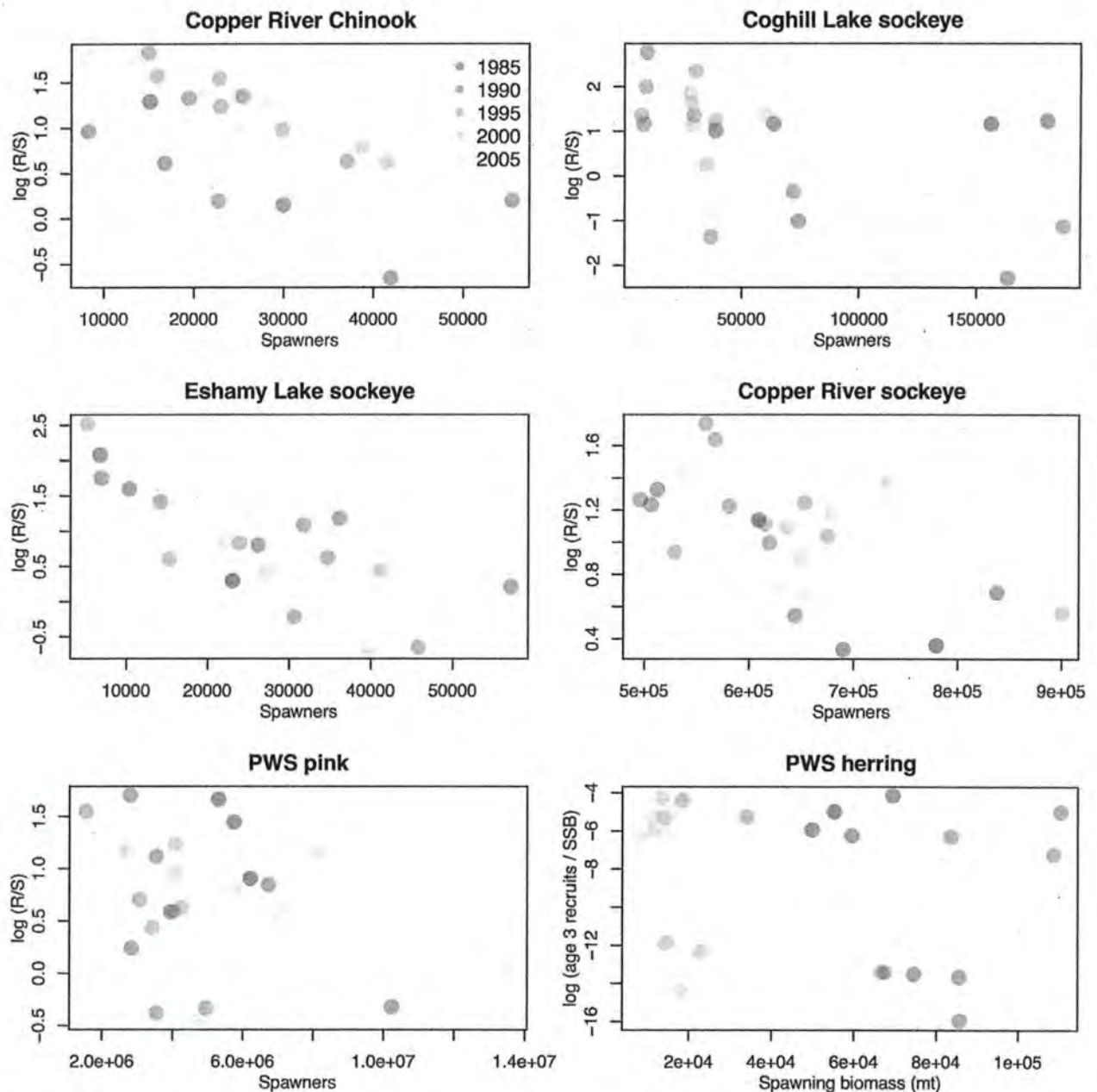


Fig 4. Relationships between spawners (salmon) or spawning stock biomass (herring, in metric tons) and recruits-per-spawner. Raw data are shown for the years included in our analysis, with each year assigned a unique color. R = recruits, S = spawners, SSB = spawning stock biomass, age-3 recruits = millions of mature and immature age-3 herring, and PWS.

doi:10.1371/journal.pone.0172898.g004

to oil. To model the potential effect of EVOS on salmon species spawning in 1989, we did not lag the indicator covariates. To account for species that may have been exposed to the spill as juveniles, we also considered versions of the EVOS impacts lagged by 1–2 years. For example, species that migrate to the ocean a year after spawning (pink and chum salmon) would have been exposed as 1-year olds, so we allowed the EVOS perturbation to affect the productivity of fish spawning in 1988. Similarly, for species that generally migrate to the ocean as 2-year olds

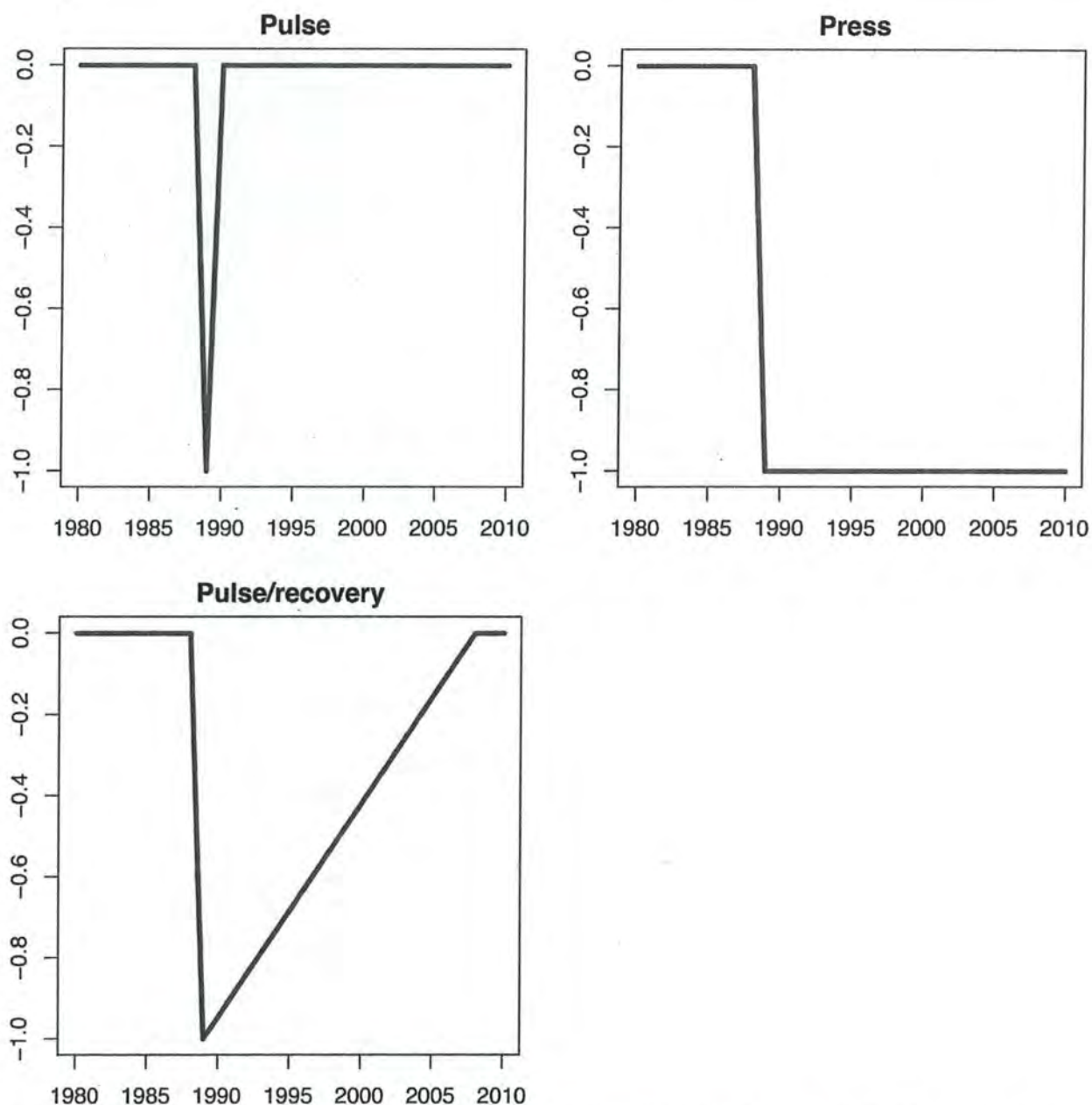


Fig 5. Models of potential impacts (pulse, press, and pulse/recovery) associated with the Exxon Valdez oil spill. Impacts here are shown for a time lag of 0, however lag-1 and lag-2 equivalents were also considered as predictors in our models.

doi:10.1371/journal.pone.0172898.g005

(Chinook, sockeye salmon), we allowed the EVOS perturbation to affect the productivity of fish spawning in 1987.

Hypothesis 3: Productivity has been affected by environmental variability. Our third hypothesis involved evaluating data support for effects of changing environmental conditions on herring and salmon productivity. Climate shifts have been suggested as drivers for both salmon and forage fish such as herring [25,57].

For all species, we considered Royer's annual index of freshwater discharge near Seward [58], because freshwater input has been identified as a potential bottom-up forcing mechanism determining the timing and abundance of zooplankton blooms [59]. For salmon, we constructed species-specific indices of sea surface temperature (SST) and upwelling, depending on life history information and previous work [29,60,61]. For sockeye, we included Jan–Apr SST with a 2-year lag, and the average upwelling from both the winter before and after outmigration (winter defined as Oct–Mar). For pink salmon, there is more uncertainty about whether climate has stronger influences on adult or juveniles, so we included average SST both in the year and season of spawning and the first year in the ocean, as well as upwelling indices in winter (Oct–Mar) and spring (Mar–May) [60]. Because of similar uncertainty with respect to Chinook salmon, we included SST in both the first and second years of ocean life and upwelling indices in both winter and summer (May–Sept) in the first and second years in the ocean. For herring, we considered winter SST (Nov–Mar) immediately before and 1 year prior to spawning, and summer upwelling (May–Sept) 1 and 2 years before spawning [62].

Hypothesis 4: Productivity has been shaped by intra- and interspecific interactions among juvenile fish. One of the ecological drivers that may explain trends in herring and salmon productivity (Figs 3 and 4) may be intra- or inter-specific competition as juveniles. Recent trends in hatchery releases in PWS have been dominated by chum and pink salmon (S1 Fig). Research in other regions has suggested that pink salmon may have a competitive advantage over other species, negatively impacting other species' growth and survival [63–65]. Similarly, interspecific effects of pink salmon on juvenile herring have been hypothesized in PWS [22].

We examined evidence of relationships between productivity and juvenile interactions for herring and the five PWS salmon stocks in our analysis by including time series of hatchery releases of dominant species (pink and chum salmon). For instance, with herring as a response, one hypothesis might be that hatchery pink or chum salmon compete with juvenile herring (age 1). Given the available data, we used hatchery releases in year t as a predictor of productivity in year $t-1$ (e.g. hatchery salmon from brood year 1980 would be 1 in 1981 and compete with herring in that year).

Hypothesis 5: Predation and adult competition (intra- and inter-specific) has impacted productivity. As our fifth hypothesis, we evaluated support for predation and competition by adults on juveniles of the same or different species and support for predation on herring by humpback whales. For example, predation and competition from returning adult salmon may directly affect juvenile herring and salmon and their prey [38,41]. As a proxy for adult predation on/competition with juveniles, we used estimates of total returning salmon abundance as covariates in our model [54,55]. We further stratified returning pink and chum salmon into wild and hatchery components to evaluate whether either component, or the combined run size, appeared to impact outmigrating juvenile salmon through predation or competition. Examples of these effects included using adult salmon (pink, chum, coho *O. kisutch*) returning in year t as a predictor of the brood year production from year $t-1$ in the herring models (e.g. herring produced by spawners in 1980 would have been age 1 in 1981, and subject to predation and competition from returning adult salmon that year). For herring, we also included PWS humpback whale abundance [43] as an additional covariate, as they have increased in number since 1970 and may be responsible for additional mortality in other regions [66].

Statistical analysis

For models of fish recruitment, we assumed that the herring and salmon stock-recruit relationship followed a Ricker model [67]. This model has been widely used in fisheries, because it

allows a flexible parameterization but can also be linearized [68]. This stock-recruit model can be written as $\log(R/S)_t = a + bS_t + cX_t + v_t$, where a represents maximum per capita (abundance or biomass) productivity or growth rate of the population, b is the negative effect of density dependence, X_t are optional time-varying covariates (e.g. SST, upwelling), c represents coefficients linking those covariates to productivity, and v_t represents residual error, assumed to be $v_t \sim \text{Normal}(0, \sigma)$. Additional models, including dynamic linear models, were also explored. Parameter estimation and model selection was conducted in a maximum likelihood framework, using the MARSS package in R [69,70]. To evaluate the data support for various hypotheses described above, we used the small sample version of Akaike's Information Criterion (AICc) [22,71]. Code and data to replicate these calculations, as well as the model selection described above, and additional detail is provided: <https://github.com/NCEAS/pfx-covariation-pws>.

Results

We found variable support for intraspecific density dependence (Hypothesis 1) in herring and salmon populations in PWS. Herring, Chinook and sockeye (Eshamy Lake and Copper River populations) exhibited strong evidence of increasing productivity at lower densities (Table 1, S1 Table), and pink salmon showed little support for the density dependent model, suggesting that variation may be better explained by other covariates (or that pink salmon escapements have been below thresholds needed to induce density dependence). For the sockeye populations in our analysis, the best model allowed the strength of density dependence to vary by population, (Figs 2–4, S1 Table).

We found little support for any negative impact of the EVOS (Hypothesis 2) on long term productivity in these populations (Table 1, S2 Table). Chinook salmon supported the inclusion of the EVOS covariate in explaining variation in productivity relative to the models that only included density dependence (Table 1), but the estimated impact of EVOS was slightly positive and opposite of what we might expect from other studies [16]. Coefficients for these impacts and all hypotheses are included online, <https://github.com/NCEAS/pfx-covariation-pws>.

The strongest relationship between the environmental covariates (Hypothesis 3) we examined and productivity was the estimated effect of freshwater discharge on herring (Table 1, S3 Table; Fig 6). The estimated productivity was lower than average in years of high discharge. Discharge into the Gulf of Alaska was episodic both before and after the EVOS event, and periods of high discharge generally coincided with three multi-year herring productivity failures (Fig 6; 1985–1987, 1991–1992, and 1996–1998). Our results showed less evidence for environmental drivers of salmon productivity; although, summer and winter upwelling were identified as predictors of Chinook and sockeye salmon productivity, respectively (Table 1, S3 Table). In both cases, however, models with environmental covariates performed worse when compared to all hypotheses (Table 1).

In evaluating hypotheses about effects of juvenile-juvenile competition (Hypothesis 4), we found little support for linking hatchery or wild pink or chum salmon to declining productivity of examined species (S4 Table). Including hatchery releases slightly worsened the fit of our model of wild pink salmon productivity, but was within 1 log likelihood of the best model (constant productivity). The effect of hatchery pink salmon releases was estimated to be slightly positive on juvenile Chinook salmon. Statistically, the inclusion of this predictor was an improvement over the null model for Chinook salmon (S4 Table); however, there was no support in including it in the model that also included the EVOS pulse/recovery impact.

We found a negative relationship between adult hatchery pink salmon returns on sockeye salmon productivity, supporting the predation and adult competition hypothesis

Table 1. Table of delta-AIC values used for model selection (S1–S5 Tables include raw values).

Model	Pink	Chinook	Sockeye	Herring
Null (productivity constant)	0	20.707	25.896	24.715
1 Ricker 'b' estimated	0.113	10.689	21.405	6.439
Ricker 'b' varies by population			10.581	
EVOS				
EVOS pulse (lag 0)	2.858	13.644	11.087	7.638
EVOS press (lag 0)	1.624	1.817	12.817	9.296
EVOS pulse/recovery (lag 0)	1.205	0	13.179	9.095
EVOS pulse (lag 1)	0.98			7.481
EVOS press (lag 1)	3.052			8.516
EVOS pulse/recovery (lag 1)	2.867			7.946
EVOS pulse (lag 2)	2.9	10.877	12.395	7.72
EVOS press (lag 2)	2.793	7.926	13.28	6.071
EVOS pulse/recovery (lag 2)	2.546	7.732	13.217	5.327
Environmental				
SST (lag 0)	2.826	12.235		2.915
SST (lag 1)	0.423	13.91		8.684
SST (lag 2)			12.875	
Upwelling winter (lag 1)	3.104	11.469	13.018	
Upwelling winter (lag 2)	3.085	13.425	13.202	
Upwelling spring (lag 1)	3.088			
Upwelling spring (lag 2)	2.664			
Upwelling summer (lag 1)		8.887		7.32
Upwelling summer (lag 2)		13.315		9.195
Freshwater discharge (lag 0)	2.346	13.327	12.582	0
Freshwater discharge (lag 1)	2.459	12.405	13.435	9.448
Juvenile competition				
Hatchery pink releases	0.304	8.311	13.14	7.965
Hatchery chum releases	2.764	11.195	13.039	9.243
Competition and predation				
Wild chum	3.071	12.778	12.518	8.54
Wild pink	2.975	9.867	11.872	6.099
Hatchery chum	3.095	6.464	12.93	5.352
Hatchery pink	1.488	12.391	0	9.093
Total pink run	2.106	13.84	3.5	8.105
Humpback whales				7.851

Models with the most support are indicated with a zero; all models within one log-likelihood unit highlighted in bold.

doi:10.1371/journal.pone.0172898.t001

(Hypothesis 5) (Table 1, Fig 7, S5 Table, and S3 Fig); however, this effect was not found for herring, Chinook, or wild pink salmon. The lag-2 model of hatchery returns was most supported, suggesting that adult hatchery pink salmon returning in year *Y* had a negative effect on the sockeye recruitment of brood year *Y*-2 (the 2 year lag a result of sockeye rearing in freshwater for 2 years before emigrating to the ocean). To understand the magnitude of these estimated hatchery pink salmon effects, we used the mean number of pink hatchery returns over the time series ($2.5e+07$) and mean log-productivity across the 3 sockeye populations in our analysis (0.87) to calculate the effect size of a 10% increase in pink salmon

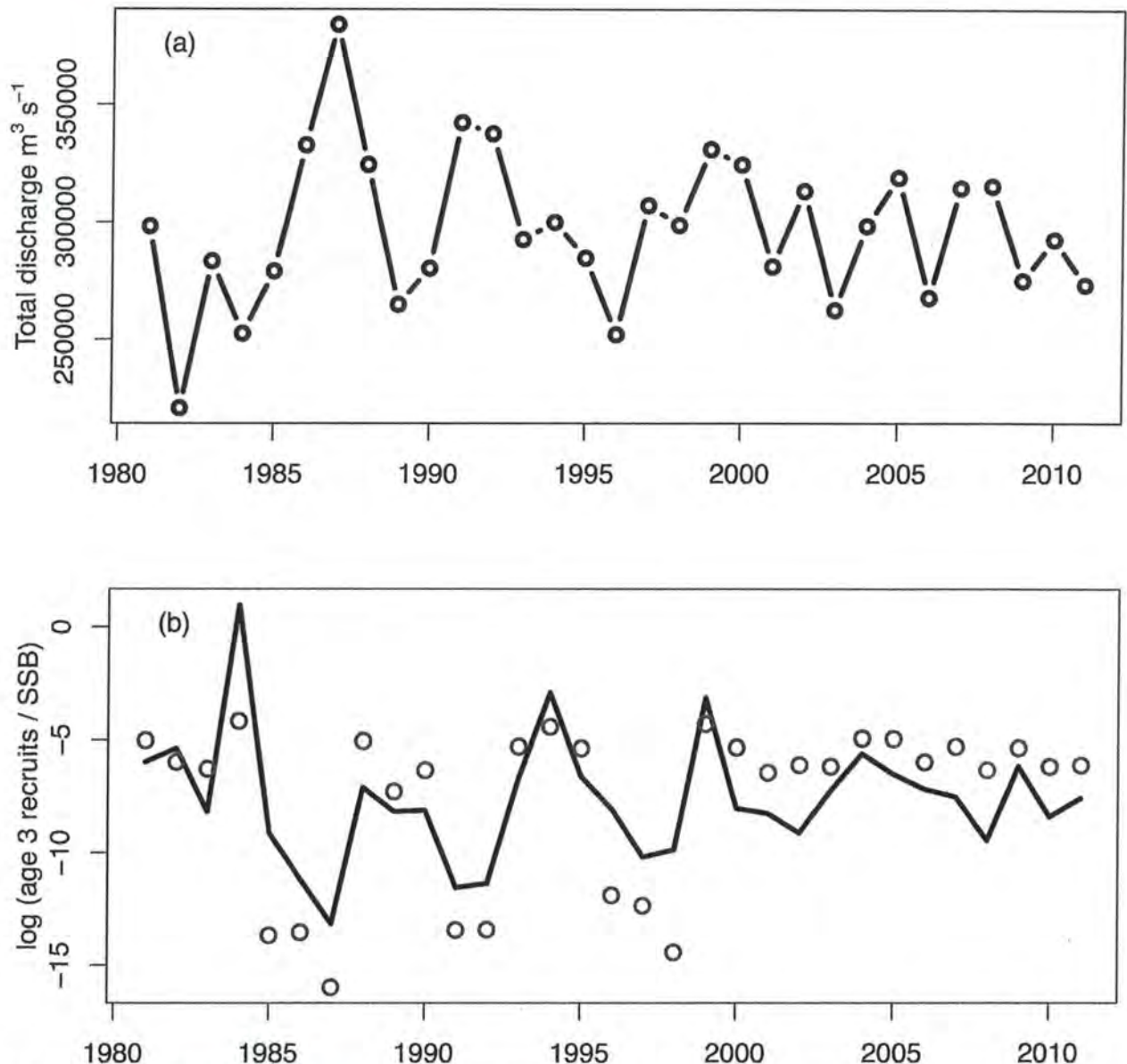


Fig 6. Gulf of Alaska freshwater discharge (Royer 1982, IMS 2016) as a driver of Pacific herring productivity. Shown are (a) the total freshwater discharge ($\text{m}^3 \text{s}^{-1}$) and (b) log of observed age-3 recruits per spawning biomass (mt)— $\log(\text{recruits}/\text{SSB})$ —in grey circles, and the model predicted $\log(\text{recruits}/\text{SSB})$ using freshwater discharge as a covariate ($R^2 = 0.55$). High discharge events correspond to reduced productivity (fewer recruits to the population as three year olds). For historical reference, the discharge time series starting in 1931 is shown in S2 Fig. R = millions of mature and immature age-3 herring, SSB = spawning stock biomass in metric tons.

doi:10.1371/journal.pone.0172898.g006

returns; this translates to $\log(R/S)$ declining to 0.938 of the status quo. For wild pink salmon productivity, including predation and competition from hatchery pink salmon worsened the fit of the models slightly (S5 Table). We found a slight improvement in models of herring productivity when interactions with adult wild pink salmon or hatchery chum salmon were included, although these effects were contrasting, with a negative effect of chum and a positive effect of wild pink salmon.

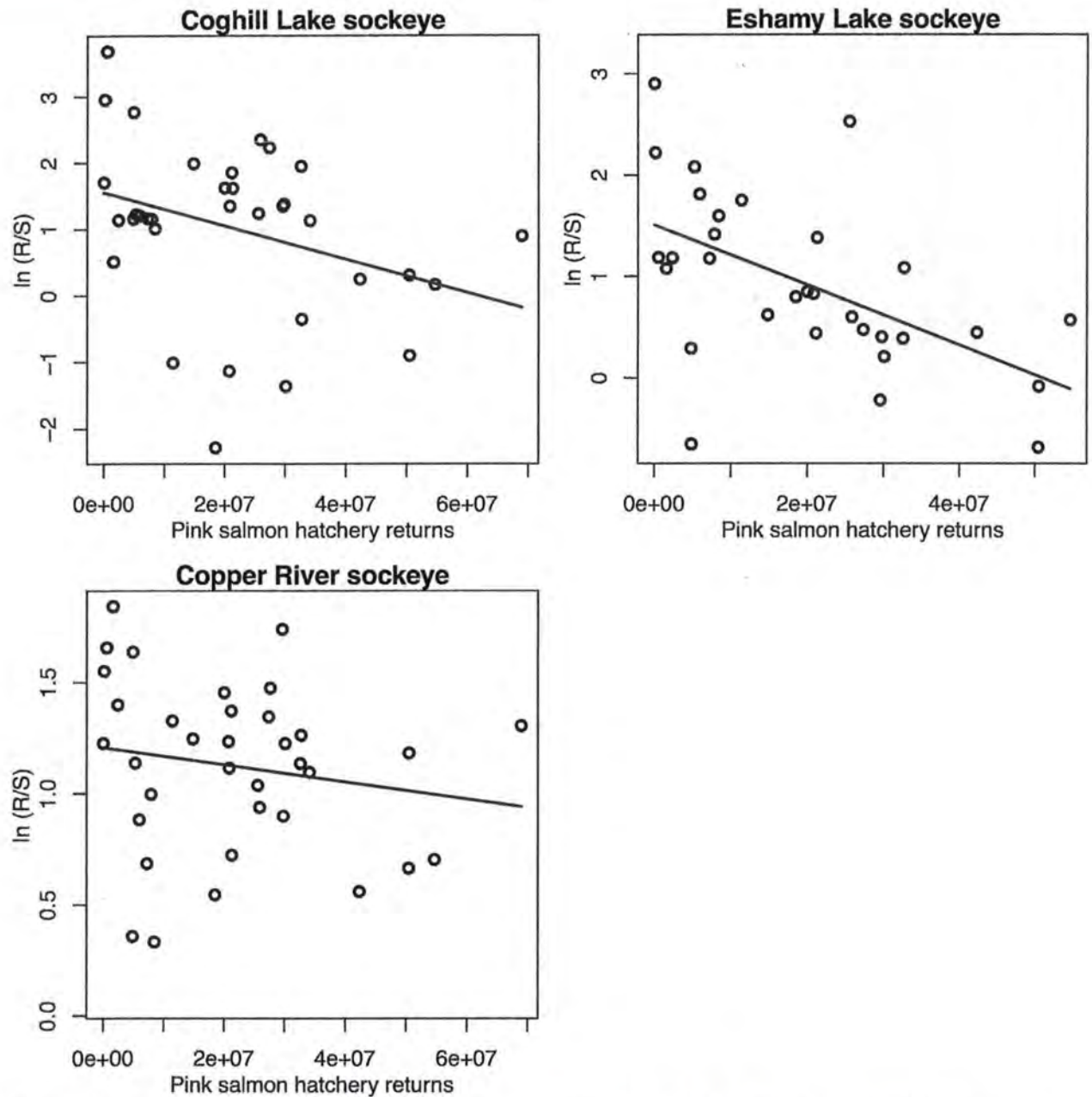


Fig 7. Sockeye salmon productivity, $\log(R/S)$, vs. total hatchery pink salmon returns to PWS. Black lines are best-fit lines from linear regressions fit separately to each time series. Note that the multivariate time-series method we used for the analysis is a different approach than the simple linear relationships shown here. Similar trends in the residuals also exist after the effect of spawning abundance is removed (see S3 Fig).

doi:10.1371/journal.pone.0172898.g007

Discussion

The short- and long-term impacts of the *Exxon Valdez* oil spill, and coincident changes in climate and the ecological community of Prince William Sound have remained controversial, even nearly three decades after EVOS [12,13,23]. Our results largely support the idea that

longer term changes in herring and salmon productivity in PWS have been affected by multiple processes, including negative effects of spawner density dependence (for herring, Chinook, and sockeye), changing environmental conditions (freshwater discharge for herring), and interspecific effects such as negative impact of adult hatchery pink salmon on wild sockeye salmon productivity. We also note that in order to accommodate the inclusion of multiple species, our analysis of productivity begins in 1981, several years after the onset of hatchery production in PWS [35] and the 1976–77 regime shift [28].

We found no evidence supporting a negative EVOS impact on herring, sockeye salmon, or pink salmon productivity, and weak evidence of a slightly positive EVOS signal (in the press-recovery model) on Copper River Chinook salmon productivity. It is unclear how EVOS may have impacted Chinook salmon positively. This result may be spurious, or Chinook salmon in particular may have benefitted from the substantial reduction in some predators; including the deaths of as many as several hundred thousand seabirds [72] and severe losses to pods of killer whales (*Orcinus orca*) [73] as a direct result of EVOS. Acute exposure to oil has known impacts on hatchery and wild fish [16], when measured at the individual level in a controlled environment. But when examining productivity at a population level, this may be much more difficult to detect, because the exposure of individual fish to oil is unknown, recruitment is highly variable, and recruitment and spawning numbers or biomass may change together. Further, the species included in our analysis exhibit life history variation that may help further buffer them from perturbations (as a ‘portfolio’ effect; [74]). For example, Chinook, sockeye, and chum salmon, have variation in age at maturity such that returns from a single brood year are dispersed across several years [75].

Though we found no evidence relating herring productivity to EVOS, or most climate drivers, we did find evidence of a strong negative correlation between herring productivity and freshwater discharge into the Gulf of Alaska. This finding suggests that herring survival may be vulnerable to changing climate conditions which may be affecting herring survival via multiple pathways. Over the past 40 years, the northern Gulf of Alaska has undergone a general warming and freshening in the upper 100 m of the water column, and an increase in salinity in depths between 100–200 m. This suggests that vertical stratification of the upper water column in the Gulf of Alaska has increased substantially over this time frame [30,33]. A second effect of warming conditions may be changing amounts of rain and snowpack melted, as well as the timing of the spring discharge [30]. Other studies have found support for increased freshwater discharge suppressing phytoplankton and favoring microbial production [76]. Though the relative importance of these pathways on plankton biomass is not known, the shift in timing and/or decreased primary production related to increasing water temperatures and water column stability, or increased freshwater inputs may be one of many factors that have kept herring abundances in the north-central Gulf of Alaska low over the past 25 years.

For the majority of the interspecific interactions we examined, including juvenile-juvenile competition, or adult competition and predation, we found little data support. All sockeye salmon stocks examined exhibited a downward trend in productivity with increasing PWS hatchery pink salmon returns (Fig 7, S3 Fig). While there was considerable variation in sockeye salmon productivity across the low- and mid-range of hatchery returns (0–30 million), productivity was particularly impacted at higher levels of hatchery returns. Pink salmon have been found to negatively affect sockeye salmon productivity and growth from British Columbia and Southeast Alaska [63,64], Bristol Bay [65], Kodiak [77,78], and Russia [79]. Pink and sockeye salmon compete in the marine environment due to a high degree of similarity in diets [40,80,81], including similarities in diets of adult pink salmon and juvenile sockeye salmon [82,83]. Our analysis was primarily designed to test drivers in the nearshore environment, which is why we stopped at a lag of 2 (brood) years—when the majority of juvenile sockeye

salmon outmigrate from the nearshore environment as adult pink salmon are returning to spawn. We do not know if possible deleterious interactions between hatchery pink salmon and wild sockeye salmon in this study are from predation or competition, or whether they occur in nearshore or offshore areas. Pink salmon feeding may cause a general depletion of prey availability [38] that could impact sockeye salmon without tight spatial overlap of these two species. In this regard, the apparent impact to sockeye productivity may reflect a general increase in pink salmon abundance across the NE Pacific rather than increased abundance of hatchery pink salmon to PWS in particular. However, adult pink salmon are known to feed on a broad diversity of prey items within PWS prior to spawning, including a variety of zooplankton [41]; and therefore have the potential to compete with juvenile sockeye salmon in PWS for the same prey. For example, Martinson et al. [77] showed decreased growth of sockeye salmon outmigrating from the Karluk River (Kodiak, AK) during years when large numbers of adult pink salmon returned to the same area. Competitive interactions in nearshore and offshore environments deserve greater attention in future research in the face of general increase in the abundance of pink salmon in the North Pacific [38,84,85].

Although our results did not show common drivers for salmon and herring productivity during the timespan of our analysis (1981–2014), it is possible that other drivers—rooted in the 1976–77 and 1989 regime shifts [28,29,86]—resulted in the similar trends in salmon and herring spawning populations in PWS during a relatively narrow timespan. For PWS herring, the large adult spawning biomass of the 1980s–early 1990s can be traced to strong recruitment from the 1976, 1984, and 1988 year classes, which has not occurred during more recent years [87–89]. The three salmon stocks located inside PWS (wild: pink salmon, Cogill Lake and Eshamy Lake sockeye) exhibited record high levels of productivity and increased abundance for brood years that entered the marine environment immediately following the 1976–77 regime shift (Fig 2). For wild pink salmon, record high return-per-spawner (R/S) and six of the top ten total returns occurred from the 1977–1988 brood years. For the Cogill Lake sockeye salmon population, the 1976 and 1977 brood years had by far the highest R/S on record and four of the top five total returns originated from brood years 1976–1984. For the Eshamy Lake sockeye salmon population, record R/S occurred for brood years 1974 and 1975 (first marine years 1976 and 1977) and all five of the largest historical brood-year returns occurred before 1988 (<https://github.com/NCEAS/pfx-covariation-pws>). Two stocks in the PWS region not included in our productivity analysis (wild PWS chum and Unakwik District sockeye salmon, S4 and S5 Figs) also experienced dramatic increases in abundance (wild chum salmon) and harvest (Unakwik sockeye) from brood years following the 1976–77 regime shift, but declined by the late 1980s. Thus, populations in PWS showed dramatic increases in abundance by 1979 (pink salmon) or early 1980s (herring, chum and sockeye salmon) with declines by the late 1980s (sockeye salmon) or early 1990s (wild pink and chum salmon, herring). As noted by others (e.g., [17]), declines in abundance for wild salmon occurred for cohorts of species (pink, sockeye, and chum salmon) that were not directly exposed to EVOS at either the adult or juvenile stages. For example, low returns of wild pink salmon in 1992 and 1993, Cogill and Eshamy sockeye salmon during 1990, and wild chum salmon beginning in 1991 (S4 Fig, <https://github.com/NCEAS/pfx-covariation-pws>).

Changes in herring and salmon populations in PWS between the late 1970s and early 1990s came about at a time of large-scale changes for other species groups in the Gulf of Alaska, including declines in populations of forage fish, birds, and marine mammals; and increased abundances of gadids—walleye pollock (*Gadus chalcogrammus*) in particular [25,57,90–93]. For PWS, a directed commercial trawl fishery for walleye pollock was initiated in 1995 after observations of substantial pollock biomass with acoustics [94], and annual harvests of pollock have ranged from approximately 1000–3000 metric tons since [94,95]. Studies conducted in

the late 1980s and early 1990s showed that walleye pollock and other gadids had become a significant component in the diets of birds in PWS and the Gulf of Alaska [72,93] that there is substantial dietary and spatial overlap between walleye pollock and herring [92,96]. Like other possible factors that may influence salmon and herring populations, walleye pollock were not considered in our analyses due to the absence of annual population-level estimates for PWS. However, given the dietary overlap and the increased abundance of walleye pollock around the time of the declining herring populations in PWS, we consider the interactions between walleye pollock and herring in PWS to be deserving of additional study.

In contrast to the PWS salmon and herring stocks described above, stocks of sockeye and Chinook salmon from the adjacent Copper River system did not experience a concomitant decline in abundance in the late 1980s or early 1990s (Fig 2). Total returns of Copper River sockeye have remained at historically high levels from the early 1980s to the time of this writing [54,55]; and only since 2008 have returns of Copper River Chinook declined, possibly in association with a broad-scale phenomena that have impacted this species across Alaska [97]. These differences in population trends indicate that, compared with PWS, alternate processes may influence salmon populations originating from the Copper River area.

Conclusions

The five major hypotheses examined here cover potentially important drivers for salmon and herring, but the lack of support for many of these predictors suggest that other factors may also be important (e.g., [17]). For example, we did not include covariates that only existed for portions of the time series, such as disease. Disease has been proposed as one mechanism for explaining declines in herring abundance in PWS [98–100]. The PWS herring disease data (1994–present) starts after EVOS and other climatic perturbations and therefore cannot be used to assess the decline of herring during 1992–93. We also did not evaluate support for long term effects of human resource use, including commercial fishing. Fishing practices may interact with climate variation [101], or make stocks more vulnerable to population collapse [102].

The contrast between recent studies that have demonstrated negative toxicity of oil on fishes and our results indicating little support for an effect at the population level also suggests a need for better data on the exposure of individual fish to oil after spills occur. Incardona et al. [16] suggested a mechanism by which detrimental effects could result from low toxicity 7–9 months after exposure, fine scale sampling of individual exposure rates immediately following a spill could be combined with intensive spatiotemporal histology sampling in the years that follow.

Better understanding the processes responsible for changing environmental drivers on marine fish like salmon and herring is essential, particularly when these processes link terrestrial and aquatic ecosystems, and are affected by variables like freshwater discharge, which is sensitive to effects of climate change [103]. Looking at the entire time series of freshwater discharge into the Gulf of Alaska (S2 Fig), the variability appears to be dampening over time. The mechanism responsible for this dampening is unknown, but it may be partially responsible for less common low discharge events (coincident with herring recruitment pulses). Though herring recruitment data aren't available for much of the 20th century, the mid-1930s may have been an extremely productive period for herring because of discharge patterns during that time (the most negative discharge anomaly in the mid-1930s, S2 Fig, was immediately followed by the highest herring landings ever recorded; [88]). Just as the previous analyses have evaluated synchrony in herring populations in the NE Pacific Ocean [104], it is important to understand how drivers like freshwater discharge vary spatially. Like many salmon populations in the NE Pacific, herring population dynamics may be synchronized through time and may be

shaped in part by external climate drivers. It remains unclear the degree to which asynchrony between herring in the Gulf of Alaska or elsewhere may exhibit a portfolio effect [105,106] and buffer the larger metapopulation from future perturbations.

Supporting information

S1 Fig. Hatchery release trends for coho, sockeye, chum, and pink salmon, 1979–2014.
(TIFF)

S2 Fig. Historic freshwater discharge into Prince William Sound, 1931–2010 (Royer 1982, IMS 2016). The dashed horizontal line represents the mean, and the dashed vertical lines represent the time period included in our analyses.
(TIFF)

S3 Fig. Residuals from a simple Ricker stock-recruit model fit separately to each population. Sockeye time series versus year and total pink salmon hatchery returns (neither covariate included in this model). Using the model selection described in main text and a model that integrates all three time series in the same analysis, the model with the inclusion of pink salmon returns is supported because of the negative trend in residuals (particularly for Eshamy and Coghill).
(TIFF)

S4 Fig. Total estimated run size of wild chum in Prince William Sound.
(TIFF)

S5 Fig. Total harvest of Unakwik District sockeye salmon.
(TIFF)

S1 Table. Detailed results for models that only include density dependence. Table of model selection values (AICc) comparing null models (constant productivity, or $\log(R/S)$ independent of spawners) to models that estimated density dependence via the Ricker stock-recruitment relationship. For each species, the best model and all models within 1 log-likelihood unit are highlighted in bold (the best model only being defined for this particular table—all results are included in Table 1).
(DOCX)

S2 Table. Detailed results for models that only include effects of EVOS. Table of model selection values (AICc) comparing models without covariates (i.e. models presented in S1 Table) to models that also estimate an impact of the EVOS event (pulse, press, pulse/recovery with various lags). All models that include an EVOS impact also include density dependence (the sockeye models with EVOS allowed density dependence to vary by population). For each species, the best model and all models within 1 log-likelihood unit are highlighted in bold (the best model only being defined for this particular table—all results are included in Table 1). Lag-1 impacts were not considered on Chinook and sockeye, as these species generally migrate to the ocean in their second year of life.
(DOCX)

S3 Table. Detailed results for models that only include environmental covariates. Table of model selection values (AICc) comparing models without covariates (i.e. models presented in S1 Table) to models that also estimate an impact of environmental effects. All models that include environmental predictors also include density dependence (the sockeye models with environmental effects allowed density dependence to vary by population). For each species, the best model and all models within 1 log-likelihood unit are highlighted in bold (the best

model only being defined for this particular table—all results are included in Table 1). Additional details included online, <https://github.com/NCEAS/pfx-covariation-pws>.
(DOCX)

S4 Table. Detailed results for models that only include effects of juvenile competition.

Table of model selection values (AICc) comparing models without covariates (i.e. models presented in S1 Table) to models that also estimate an impact of juvenile competition. All models with juvenile competition included also include density dependence (the sockeye models with juvenile competition allowed density dependence to vary by population). For each species, the best model and all models within 1 log-likelihood unit are highlighted in bold (the best model only being defined for this particular table—all results are included in Table 1).

(DOCX)

S5 Table. Detailed results for models that only include effects of predation and adult competition.

Table of model selection values (AICc) comparing models without covariates (i.e. models presented in S1 Table) to models that also estimate an impact of predation or adult competition on wild salmon productivity. All models with predation or adult competition included also include density dependence (the sockeye models with predation or adult competition allowed density dependence to vary by population). For each species, the best model and all models within 1 log-likelihood unit are highlighted in bold (the best model only being defined for this particular table—all results are included in Table 1). All salmon models used the estimated total run size of adult salmon.

(DOCX)

Acknowledgments

This project was conducted as part of a NCEAS working group, "Applying Portfolio Effects to the Gulf of Alaska Ecosystem" (led by K. Marshall). Data sets included in our analysis have been provided by agencies (ADF&G, NOAA) and have been made available on the EVOS Data Portal, <http://gulfwatch.nceas.ucsb.edu/#data/page/0>. ADF&G retains intellectual property rights to data collected by or for ADF&G. Any dissemination of the data must credit ADF&G as the source, with a disclaimer that exonerates the department for errors or deficiencies in reproduction, subsequent analysis, or interpretation

The authors thank staff at NCEAS, and additional post-docs for support (R. Blake, C. Ward). We also thank A. Beaudreau, R. Gustafson, C. Jordan, A. Munro, S. Rice, C. Siddon, and B. Templin for providing helpful reviews that greatly improved this manuscript.

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Measuring the net biological impact of fisheries enhancement: pink salmon hatcheries can increase yield, but with apparent costs to wild populations

Ricardo O. Amoroso, Michael D. Tillotson, and Ray Hilborn

Abstract: Hatchery production of juvenile fish for release into the wild has been practiced for well over a century in an effort to increase the number of salmon available to harvest. In this study, we evaluate the net impact of the largest such program in North America, the hatchery program for pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound (PWS), Alaska. At the same time the hatchery program was increasing in output, there was a major change in productivity in the North Pacific so that throughout Alaska pink salmon increased dramatically in abundance between the 1970s and the 2000s. Using other regions of Alaska as reference sites, we estimate that the PWS hatchery program has increased the total catch by an average of 17 million fish, of which 8 million have been allocated to pay hatchery operating expenses. We estimate that the maximum sustainable yield (MSY) of wild spawning fish in PWS has increased slightly (28%), while in regions of Alaska without pink salmon hatchery programs the MSY has tripled. Our results support the use of a precautionary approach to future large-scale stock enhancement efforts.

Résumé: La production en alevinières de poissons juvéniles destinés à être relâchés dans la nature est pratiquée depuis plus d'un siècle dans le but d'accroître le nombre de saumons disponibles pour la pêche. Nous évaluons l'incidence nette du plus grand programme du genre en Amérique du Nord, le programme de production en alevinières de saumons roses (*Oncorhynchus gorbuscha*) dans le golfe du Prince William (GPW), en Alaska. Au même moment où la production de ce programme augmentait, un changement majeur de la productivité dans le Pacifique Nord s'est produit, de sorte que l'abondance des saumons roses à la grandeur de l'Alaska a connu une augmentation très marquée entre les années 1970 et 2000. En utilisant d'autres régions de l'Alaska comme sites de référence, nous estimons que le programme de production en alevinières du GPW s'est traduit par une augmentation moyenne des prises totales de 17 millions de poissons, dont 8 millions ont été alloués pour payer les dépenses d'exploitation des alevinières. Nous estimons que le rendement équilibré maximum (REM) des poissons se reproduisant à l'état sauvage dans le GPW a augmenté légèrement (28 %), alors que dans des régions de l'Alaska sans programme de production de saumons roses en alevinières, le REM a triplé. Nos résultats appuient l'adoption d'une approche prudente dans les efforts futurs de mise en valeur des stocks à grande échelle. [Traduit par la Rédaction]

Introduction

Despite increasing global demand for seafood, the production of marine capture fisheries has remained essentially stable over the past three decades (FAO 2014). Although there remains the potential for some increase by improved management (Worm and Branch 2012; Watson et al. 2013), the plateau in capture fisheries is generally believed to reflect a fundamental limitation in the capacity of the world's oceans to generate food (Worm et al. 2009; Chassot et al. 2010; Worm and Branch 2012). Intensive aquaculture appears to offer an opportunity to circumvent this limitation, and indeed, the rapid expansion of the industry has allowed continued growth in fish production in recent decades (FAO 2014). However, in many cases intensive culture of marine species is infeasible for technical, economic, or political reasons (Bostock et al. 2010). The enhancement of wild populations through release of hatchery-reared juveniles is an intermediate approach that has been practiced in a variety of marine fish and invertebrate species for over a century (Hilborn 1998; Bell et al. 2006; Lorenzen et al. 2013). Also known as stock enhancement or ocean ranching, this type of aquaculture generally involves the rearing of juveniles in a hatch-

ery past some critical stage before release into the wild, thereby circumventing high levels of mortality or habitat limitations associated with early life-history stages (Leber et al. 2004). Surviving individuals are then expected to be available for capture after several years of ocean growth. These methods may also be suitable for hastening the recovery from historical overfishing (Molony et al. 2003). As such, there is a great deal of interest in the use of fisheries enhancement to rebuild depleted fisheries and to bolster the productivity of healthy stocks. However, despite a long history of experimentation, successful enhancement of marine species is rare, and most efforts remain in a research and development phase (Lorenzen et al. 2013; Trushenski et al. 2014).

In contrast with the limited success of marine stock enhancement, large-scale hatchery programs for anadromous salmonids — especially Pacific salmon (*Oncorhynchus* spp.) — have been operating for decades, and today it is estimated that nearly one in four salmon in the Pacific Ocean are of hatchery origin (Larkin 1974; Ruggerone et al. 2010) and overall abundance of Pacific salmon in the ocean has increased greatly (Wertheimer et al. 2005; Ruggerone et al. 2010; Peterman et al. 2012). Despite the long history and massive scale of hatchery salmon production, the

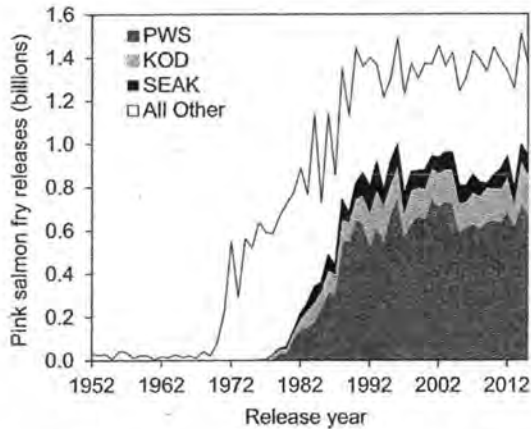
Received 26 July 2016. Accepted 10 January 2017.

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Fig. 1. Annual releases of pink salmon fry to the North Pacific Ocean between 1952 and 2015. PWS, Prince William Sound; KOD, Kodiak; SEAK, Southeast Alaska. Data from North Pacific Anadromous Fish Commission (NPAFC 2016).



efficacy of salmon enhancement programs as a tool for increasing fisheries productivity has rarely been rigorously demonstrated (Larkin 1974; Lorenzen 2005; Naish et al. 2007; Paquet et al. 2011). It has been repeatedly suggested over the past 30 years that to improve enhancement efforts it is necessary to specify clear, measurable goals and monitor outcomes relative to these goals (Peterman 1991; Hilborn 1998; Naish et al. 2007; Paquet et al. 2011). Nevertheless, monitoring and evaluation of salmon hatchery programs remains largely insufficient (Naish et al. 2007). To ensure that expected enhancement effects are being achieved, evaluation of hatchery programs must consider all relevant risks and benefits (Hilborn 1998).

Much of the difficulty in evaluating salmon hatchery programs results from a lack of suitable controls that would allow for isolation of any enhancement effect. Manipulation of stocking rates provides one avenue for distinguishing environmental and hatchery influences on fisheries production (Buhle et al. 2009), but experimental reductions in hatchery production are typically precluded by legal, political, or economic considerations (Naish et al. 2007). Retrospective analyses that attempt to explain trends in abundance using time series of environmental variables and stocking rates have become more common as data on enhanced populations is increasingly available (Wertheimer et al. 2004; Morita et al. 2006; Scheuerell et al. 2015). Alaska's pink salmon (*Oncorhynchus gorbuscha*) enhancement programs provide a unique opportunity to examine the net biological impact of large-scale stock enhancement both because of its scale and the quality of available data. Compared with other salmon-producing regions in the Pacific, Alaska's hatchery programs are relatively young, and as a result reliable catch and abundance data exist for both pre- and posthatchery periods (Olsen 1993). Additionally, since 1995 most hatchery pink salmon have been thermally marked, which allows for reliable attribution in the catch (Hilborn and Eggers 2000). Hatchery releases began during the mid-1970s (Olsen 1993) and combined releases from the two largest programs have been stable around 750 million since about 1990 (Brenner et al. 2012). These programs constitute around 10% of the total number of salmon juveniles released to the North Pacific and more than half the total pink salmon (NPAFC 2016; Fig. 1; Table 1).

Four regions account for the majority of the pink salmon catch in Alaska. Prior to hatchery supplementation, pink salmon were most abundant in Southeast Alaska (SEAK; ~20 million annual run), followed by Kodiak (KOD; ~10 million), Prince William Sound (PWS; ~7 million), and the south Alaska Peninsula (SPEN; ~3 million). Enhancement occurs in three of the regions, though

Table 1. The ten largest Pacific salmon hatchery-producing regions, ranked by average juvenile releases for the 10 years ending in 2015.

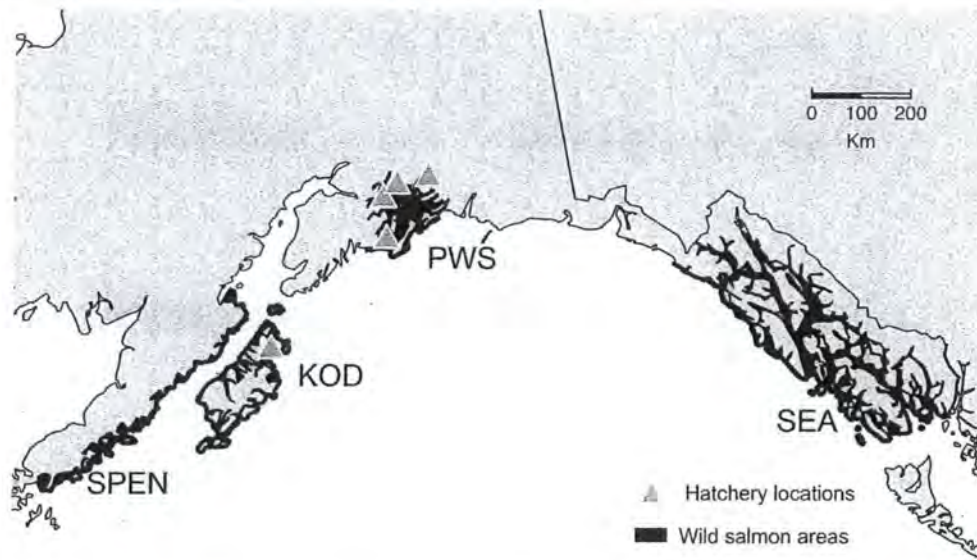
Country	Region	Species	Juvenile releases (millions)	
			2006–2015 (mean)	1952–2015 (total)
USA	Alaska — PWS	Pink	649.1	19 546.8
Japan	Hokkaido — Pacific	Chum	613.7	30 059.7
Japan	Honshu — Pacific	Chum	531.7	24 742.6
USA	Alaska — SEAK	Chum	443.4	11 104.9
Japan	Hokkaido — West	Chum	427.1	18 427.4
Russia	Sakhalin Coast	Chum	222.9	7 140.9
USA	Wash., Ore., Calif., Idaho	Chinook	202.7	10 335.2
Russia	Sakhalin Coast	Pink	200.1	9 491.0
Japan	Honshu — West	Chum	150.3	9 230.0
USA	Alaska — KOD	Pink	147.8	4 456.6

Note: Programs addressed in this study are bolded. PWS, Prince William Sound; SEAK, Southeast Alaska; KOD, Kodiak. Data summarized from North Pacific Anadromous Fish Commission (NPAFC 2016).

the scale of operations varies by orders of magnitude. PWS pink salmon is currently the largest hatchery program in the world by annual number of releases (NPAFC 2016). Since 1990, on average, 77 (SD = 48) hatchery fry have been released for each returning wild adult fish in PWS, while in KOD this ratio is about 8:1 (SD = 3.6) and in SEAK close to 1:1 (SD = 0.5). Unlike many other regions where hatcheries are intended to mitigate declines in salmon populations resulting from habitat degradation, Alaska's hatcheries are designed to produce harvestable fish to supplement relatively healthy wild populations (Naish et al. 2007). Since the inception of the hatchery programs, pink salmon catches have increased dramatically, especially in PWS where hatchery returns now average over 35 million fish and peaked at 76 million in 2013. The majority of these fish are harvested in common-property commercial fisheries, though hatchery operators also harvest on average 30% of returning fish to cover production costs (Botz et al. 2013). Despite the ostensible success of enhancement, uncertainties regarding impacts of hatchery-origin fish on wild salmon and other species continue to cause concern among many stakeholders (Pearson et al. 2012; Brenner et al. 2012; Jasper et al. 2013). Since 2012 these concerns have contributed to delays in the recertification of Alaska salmon by the Marine Stewardship Council, resulted in a "Category C" grade for PWS salmon from the Fisheries Sustainability Partnership, and motivated an intensive research program by the Alaska Department of Fish and Game.

Recent analysis of hatchery programs from around the Pacific have found limited evidence of a large enhancement effect and in many cases identified concerns about negative impacts on wild populations. For example, Morita et al. (2006) modeled pink salmon catch in relation to hatchery output and climate factors and found that intensive stocking contributed little to a dramatic increase in abundance after 1990. Ohnuki et al. (2015) used tagging data to confirm the minor contribution hatchery-origin fish to commercial pink salmon catches in Japan and suggest that the costs of hatchery production likely outweigh the benefits. Kaev (2012) examined the population dynamics of chum (*Oncorhynchus keta*) and pink salmon in the Sakhalin-Kuril region of Russia and found evidence of an enhancement effect in hatchery-supplemented chum populations, but not in pink salmon populations. Sahashi et al. (2015) found that hatchery stocking of masu salmon (*Oncorhynchus masou*) in the Shari River tended to displace rather than supplement natural production. Similarly, Scheuerell et al. (2015) compared supplemented and natural populations of Snake River Chinook salmon (*Oncorhynchus tshawytscha*) and identified only minor increases (~3% on average) in adult density attributable to enhancement efforts. Buhle et al. (2009) identified negative im-

Fig. 2. Study area map showing the four Gulf of Alaska pink salmon-producing regions. Triangles indicate the location of major pink salmon hatcheries. PWS, Prince William Sound; KOD, Kodiak; SEAK, Southeast Alaska; SPEN, south Alaska Peninsula. Basemap created from TM World Borders 0.3 (<https://koordinates.com/layer/7354-tm-world-borders-03/>).



pacts of hatchery coho (*Oncorhynchus kisutch*) on wild Oregon coast populations and documented increased wild productivity following large reductions in hatchery supplementation. Finally, Zhivotovsky et al. (2012) used genetic and demographic analyses to show that rapid expansion of a chum hatchery program on Iturup Island led to the extirpation of a distinct beach-spawning ecotype by abundant hatchery strays.

Given the limited success demonstrated by these recent hatchery studies, it is not surprising that the net biological impact of Alaska's pink salmon hatchery programs have been a matter of considerable debate. Consistent with reports of limited benefits of hatchery programs, several previous studies have concluded that improved ocean survival associated with a large-scale shift in marine environmental conditions would have led to increased pink salmon catch even in the absence of hatchery production (Eggers et al. 1991; Tarbox and Bendock 1996; Hilborn and Eggers 2000, 2001). Others have argued that hatchery production is primarily responsible for increasing catches and conclude that the enhancement program is highly successful (Smoker and Linley 1997; Wertheimer et al. 2001; Heard 2003; Wertheimer et al. 2004). Hilborn and Eggers (2001) describe these two hypotheses as "augmentation" and "replacement". Under the augmentation hypothesis, hatchery production adds additional productivity to the fishery without impacting existing wild stocks. Alternatively, the replacement hypothesis asserts that hatchery production reduces wild stock productivity, and thus hatchery fish effectively replace wild fish in the catch. In practice these hypotheses define the ends of a gradient; under complete replacement the net value of one hatchery fish approaches zero, while under complete augmentation each hatchery fish could be considered equal to one additional wild fish.

To make predictions about the trajectory of the PWS pink salmon fishery in the absence of the hatchery program, we rely on two key patterns of productivity in salmon populations. First, oscillation between North Pacific climate regimes has been shown to predictably influence salmon abundance (Hare et al. 1999; Beamish et al. 1999, 2004). Second, covariation in the productivity of salmon stocks has been shown to be highest in geographically proximate populations (Pyper et al. 2001; Wertheimer et al. 2001), and indeed Alaskan salmon populations have shown strong spatial coherence in decadal-scale patterns of productivity (Hare et al.

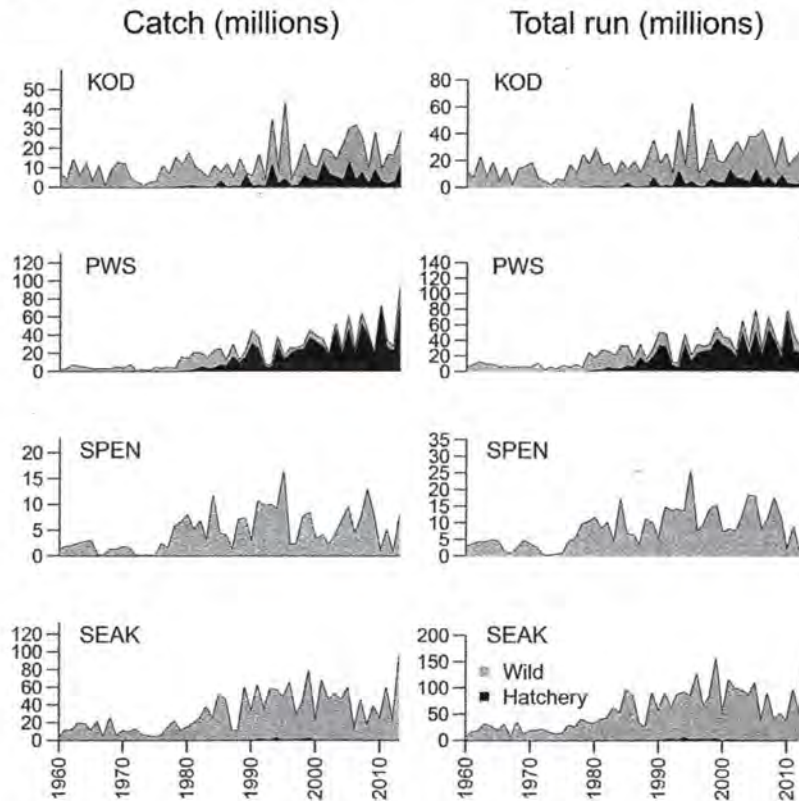
1999). Thus, to establish an empirical estimate of net biological benefit, we examine over 50 years of catch and abundance data from four pink salmon-producing regions in Alaska (Fig. 2) to predict catch and wild stock productivity in the absence of enhancement efforts. The present study builds on previous reviews of Alaska's pink salmon hatcheries, including Eggers et al. (1991), Hilborn and Eggers (2000), and Wertheimer et al. (2001), and benefits from over 15 recent years of data, a period of consistently intense hatchery stocking (Fig. 1). With this extended data set, we are also able to compare spawner–recruit relationships for wild pink salmon populations before and after the implementation of hatchery programs. In addition, we consider the impact of hatchery production on interannual variability in pink salmon abundance.

Methods

The data set

Data on wild escapement, total catch, hatchery fry releases, wild catch, and cost recovery catch were obtained from annual Management and Fisheries Enhancement reports published by Alaska Department of Fish and Game (e.g., Botz et al. 2013). We followed the conventions described in Hilborn and Eggers (2000) for classifying hatchery and wild fish in the catch and escapement. In short, for stock identification purposes, hatchery salmon in PWS have been monitored with tagging programs since 1987 and with 100% thermal otolith marking since 1996. In the KOD region, hatchery pink salmon return to and are harvested in several bays with little natural production and are therefore distinguished from wild fish based on reported harvest location. In SEAK, the vast majority of hatchery pink salmon are harvested for cost recovery in terminal areas and are therefore distinguished by harvest location. No hatchery production occurs in the South Peninsula (SPEN) region. Thermal otolith marking and intensive catch sampling provide reliable estimates of hatchery contribution to harvest, but despite widespread marking of hatchery pink salmon there is no systematic effort to evaluate the proportion of wild stock escapement made up by hatchery strays (Brenner et al. 2012). As such, we assume all naturally spawning fish to be wild, though straying is likely common. In total we analyzed data on catch and escapement beginning with calendar year 1960 and

Fig. 3. Stacked area plot showing catch and total abundance (catch + escapement/broodstock) of hatchery and wild pink salmon in four management areas of Alaska, 1960–2013.



ending with the wild return in 2013 and, given the 2-year life cycle of pink salmon, were thus able to construct spawner–recruit data for brood years 1960 to 2011.

For the purposes of our analyses, we identified three distinct periods in the abundance and catch data and compared four adjacent areas of Alaska with major pink salmon production. Brood years 1960–1976 represent preregime shift natural productivity; 1977–1987 is a period of transition when the productivity of wild stocks throughout Alaska had increased, but hatchery production was not yet at its current capacity; and 1988–2011 represents when catch was generally higher in all areas and total hatchery releases were relatively stable at around 750 million (Fig. 3). Rapid change in the climate, ecology, and fisheries productivity of the North Pacific occurred in 1977 (Mantua et al. 1997; Hare et al. 1999), and we used this well-documented phenomenon to define the first period assuming that the 1977 brood year would be the first pink salmon to be fully impacted by changes in marine conditions. These fish returned 2 years later, and for the catch analysis the break between periods therefore occurs between 1978 and 1979.

Magnitude and drivers of increased catch

Because releases of hatchery pink salmon began in PWS at the same time as a large shift in natural salmon productivity in Alaska, it is difficult to separate the influence of these two factors on the observed increase in catch that has occurred since the late 1970s. Although there is no perfect control for the influence of hatcheries, the spatial coherence of Alaskan salmon productivity trends on a decadal scale allows nearby pink salmon-producing regions to serve as pseudo-controls (Hilborn and Eggers 2000). Thus, to assess the relative contribution of the environment and fry release on the temporal changes observed in catches, we fit two models to catch data for the four harvest areas: one that

included hatchery releases as a predictor variable and one that did not:

Model (1) $\log(\text{catch}_{s,t}) = p_1 + p_2S + p_3P + \varepsilon$

Model (2) $\log(\text{catch}_{s,t}) = p_1 + p_2S + p_3P + p_4H_{s,t} + \varepsilon$

where S is a fixed area effect, P is a fixed period effect (before and after the regime shift), H is the number of fry released in area S in the year t , p_i are estimated coefficients, and ε is a normally distributed random error term. The Akaike information criterion (AIC) was computed for each model and used to compare their relative support. The difference between observed mean catch and mean catch predicted by Model 1 in the postregime shift period can be interpreted as the contribution of hatchery production to catch after accounting for the shift in natural productivity. Subtracting mean cost-recovery catch from this value gives the net contribution of hatchery production to the common-property fisheries.

Hatchery impacts on wild stock productivity

To evaluate the impact of hatchery production to wild stock productivity for the four management areas during two periods — the preregime shift period (1960–1976) and the most recent period (1988–2011) — we fit the Ricker spawner–recruit curve by period and area.

$R = Se^{\alpha - \beta S + \varepsilon}$

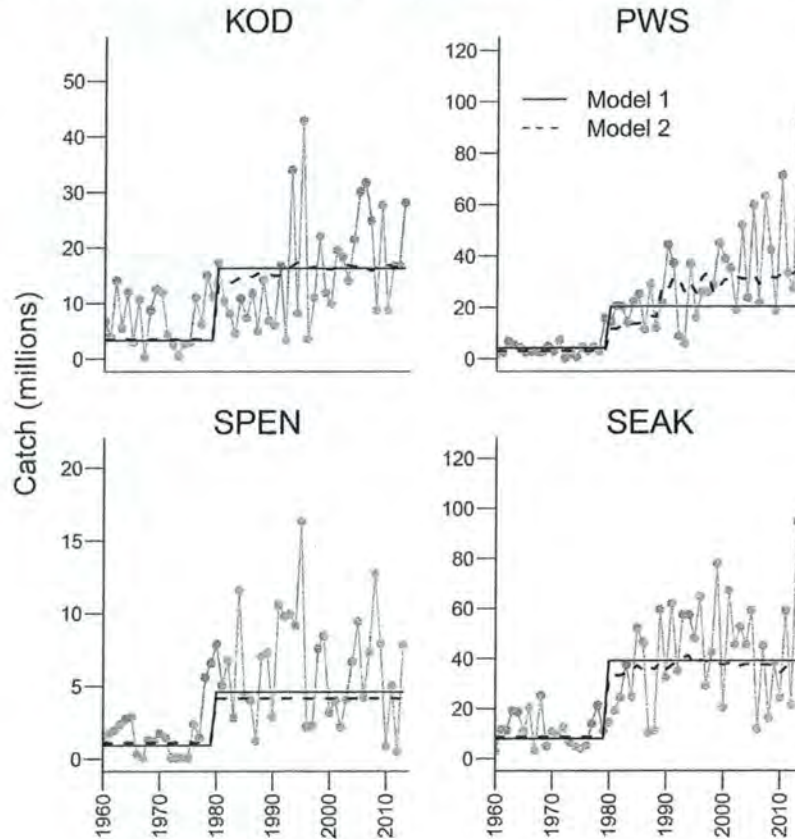
where R is the number of returns (catch plus escapement) produced by spawners, S , in a brood year, α and β are the estimated

Table 2. Pink salmon catch and variability for the preregime shift (period 1: 1960–1976) and post-regime shift, full hatchery production (period 3: 1988–2013) periods in four management areas in Alaska.

District	Period	Mean catch (millions)	Standard deviation	Variance	Coefficient of variation	Normality (Shapiro test <i>p</i> value)	Homogeneity of variance (F test <i>p</i> value)
KOD	1	7.3	4.8	22.4	0.65	0.13	
	3	18.2	10.4	108.2	0.57	0.44	9.7E-04
PWS	1	3.9	3.3	10.9	0.84	2.1E-03	
	3	36.3	20.4	416.2	0.56	0.16	3.7E-11
SPEN	1	1.7	1.7	3.0	0.99	2.0E-02	
	3	6.4	4.0	15.9	0.61	0.37	5.7E-04
SEAK	1	11.3	6.6	43.8	0.58	0.14	
	3	46.0	20.4	416.6	0.44	0.85	6.2E-06

Note: KOD, Kodiak; PWS, Prince William Sound; SPEN, south Alaska Peninsula; SEAK, Southeast Alaska.

Fig. 4. Observed (grey lines and points) and model-predicted (black solid and dashed lines) pink salmon catch for four management areas in Alaska, 1960–2013. Model 1 includes period and area effects, while Model 2 adds hatchery releases as a predictor.



Ricker maximum recruits per spawner and density-dependence parameters, respectively, and ε is a normally distributed random error term. For each area we assessed eight hypotheses that could account for changes in wild productivity between periods: a null hypothesis of no change (α , β , and ε remain equal), and all possible combinations of changes in growth rate, density dependence, and error variance between periods. We calculated the AIC and AIC weights for each model. AIC model averaging (Burnham and Anderson 2002) was used to calculate the magnitude of change and standard deviation of the parameters across models.

The estimated parameters were used to compute the biological reference points maximum sustainable yield (MSY), biomass producing MSY (BMSY), and the optimal harvest rate for achieving MSY (Hilborn 1985):

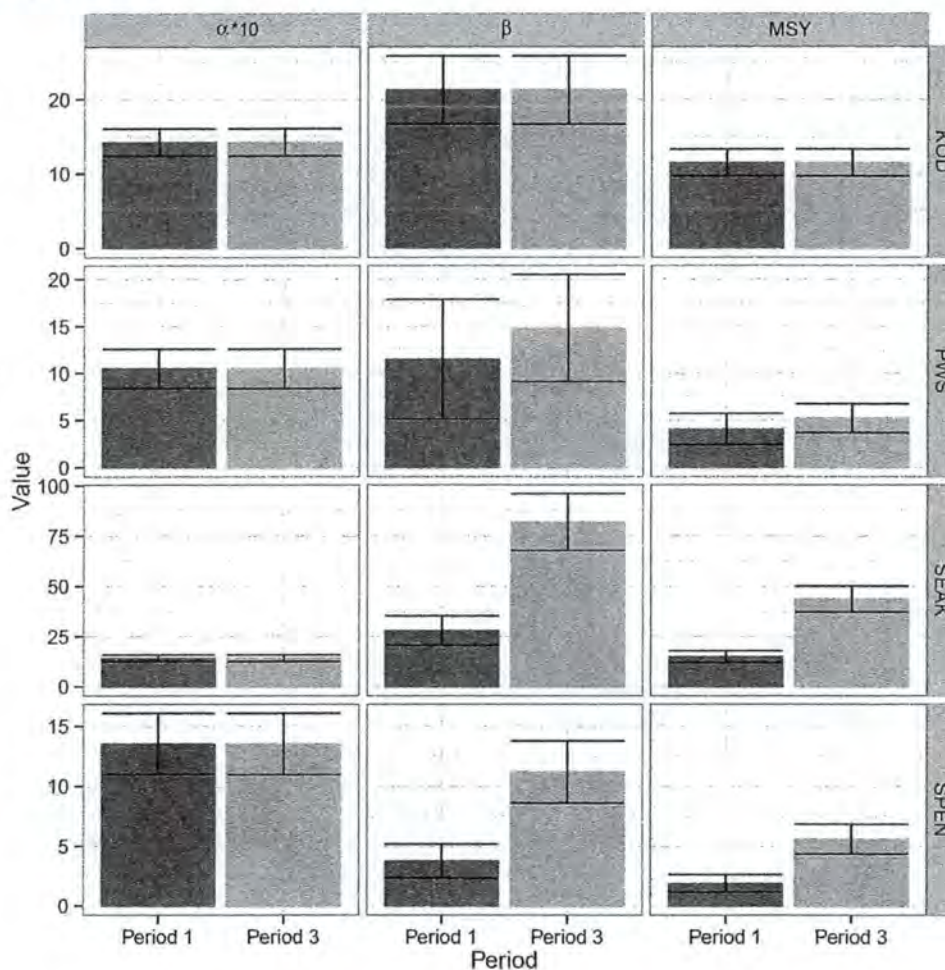
$$BMSY = (0.5 - 0.07\alpha)\beta$$

$$MSY = BMSY e^{\alpha(1-BMSY/\beta)} - BMSY$$

Hatchery influence on variability of catch

Two indicators of catch variability were computed for each area and time period: the variance and the coefficient of variation ($CV = \sigma^2/\mu$). Variance tends to increase with increasing mean, which can confound a comparison of variances. The CV is a normalized measure of variability that accounts for differences in mean and therefore removes the influence of differences in means between time periods. After testing for normality (Shapiro test), an F test was conducted to test the hypothesis that the variances observed in each area during the first (1960–1976) and last

Fig. 5. Lowest AIC Ricker model parameter estimates for preregime shift (period 1: 1960–1976) and postregime shift, full hatchery production (period 3: 1988–2011) periods in four pink salmon management areas in Alaska. α values have been multiplied by 10 to aid in visualization. Error bars show standard errors as calculated using the delta method.



(1988–2011) periods were different. The modified Bennet’s test was used to test the hypothesis that all the CVs (one for each combination of period and area) belong to the same population of CVs.

Results

Magnitude and drivers of increased catch

In all management areas examined, pink salmon catch increased following a regime shift in the late 1970s (Fig. 3; Table 2). However, in PWS, catch increased nearly tenfold between the low-productivity, prehatchery period (period 1) and the high-productivity, full hatchery production period (period 3). Meanwhile, in all other management areas (KOD, SEAK, and SPEN) catch increased approximately threefold. The disproportionate increase in catch observed in PWS compared with the other areas suggests a considerable contribution by the PWS hatchery program, even after accounting for potentially increased wild stock productivity following the shift to improved environmental conditions. We compared a model that explains changes in catch as only affected by the productivity change from periods 1 to 3 (Model 1) and a model that also uses hatchery releases as a covariate (Model 2). Including hatchery releases as a covariate improves model performance substantially compared with an environment-area only model (Model 1 AIC = 553; Model 2 AIC = 540; Fig. 4). In particular, for PWS the model that ignores hatchery releases failed to explain the large catches observed after 1990 (period 3);

the model using only regime changes predicts a mean catch of 19 million fish (Fig. 4), while the mean observed catch for that period was 36 million, a difference of 17 million. Since 1990, an average of 8 million fish per year have been harvested by the hatcheries to pay their operating expenses, suggesting that the hatcheries in PWS had an average net contribution to the commercial fleet of 9 million fish. Meanwhile, there is very little difference between predicted catch in the absence hatcheries and observed catch for KOD and SEAK, which suggests a negligible effect of enhancement in these areas.

Hatchery impacts on wild stock productivity

The estimated parameters α and β of the Ricker stock–recruitment function represent intrinsic population growth rate and carrying capacity, respectively. Thus, changes in either value reflect altered productivity for salmon stocks. Following from the notion of spatial coherence in trends of salmon productivity (Beamish et al. 1999; Finney et al. 2002), it is reasonable to assume that in the absence of region-specific factors, the productivity of wild pink salmon stocks would show similar trends in productivity. However, following the climate regime shift in the late 1970s, the period-specific stock–recruit relationships appear to show a commensurate shift in productivity in the SEAK and SPEN management areas, but not in KOD or PWS (Fig. 5; Table 3). The two regions without major hatchery programs experienced increases

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Table 3. Candidate models assessed to explain changes in production between periods and the respective AIC and AIC weights.

District	Model specification	Best model	ΔAIC	AIC weight
KOD	$\alpha_1 = \alpha_2, \beta_1 = \beta_2, \sigma_1 = \sigma_2$	0	5.01	0.02
	$\alpha_1 \neq \alpha_2, \beta_1 \neq \beta_2, \sigma_1 \neq \sigma_2$	0	2.44	0.07
	$\alpha_1 \neq \alpha_2, \beta_1 \neq \beta_2, \sigma_1 = \sigma_2$	0	2.41	0.08
	$\alpha_1 = \alpha_2, \beta_1 = \beta_2, \sigma_1 \neq \sigma_2$	1	0.00	0.25
	$\alpha_1 \neq \alpha_2, \beta_1 = \beta_2, \sigma_1 = \sigma_2$	0	0.68	0.18
	$\alpha_1 = \alpha_2, \beta_1 \neq \beta_2, \sigma_1 \neq \sigma_2$	0	1.78	0.10
	$\alpha_1 = \alpha_2, \beta_1 \neq \beta_2, \sigma_1 = \sigma_2$	0	1.70	0.11
PWS	$\alpha_1 \neq \alpha_2, \beta_1 = \beta_2, \sigma_1 \neq \sigma_2$	0	0.65	0.18
	$\alpha_1 = \alpha_2, \beta_1 = \beta_2, \sigma_1 = \sigma_2$	0	0.37	0.15
	$\alpha_1 \neq \alpha_2, \beta_1 \neq \beta_2, \sigma_1 \neq \sigma_2$	0	2.54	0.05
	$\alpha_1 \neq \alpha_2, \beta_1 \neq \beta_2, \sigma_1 = \sigma_2$	0	0.54	0.14
	$\alpha_1 = \alpha_2, \beta_1 = \beta_2, \sigma_1 \neq \sigma_2$	0	0.16	0.17
	$\alpha_1 \neq \alpha_2, \beta_1 = \beta_2, \sigma_1 = \sigma_2$	0	0.09	0.17
	$\alpha_1 = \alpha_2, \beta_1 \neq \beta_2, \sigma_1 \neq \sigma_2$	0	1.99	0.07
	$\alpha_1 = \alpha_2, \beta_1 \neq \beta_2, \sigma_1 = \sigma_2$	1	0.00	0.18
	$\alpha_1 \neq \alpha_2, \beta_1 = \beta_2, \sigma_1 \neq \sigma_2$	0	2.06	0.07
	$\alpha_1 = \alpha_2, \beta_1 = \beta_2, \sigma_1 = \sigma_2$	0	2.67	0.01
SPEN	$\alpha_1 \neq \alpha_2, \beta_1 \neq \beta_2, \sigma_1 \neq \sigma_2$	0	3.06	0.14
	$\alpha_1 \neq \alpha_2, \beta_1 \neq \beta_2, \sigma_1 = \sigma_2$	0	1.63	0.01
	$\alpha_1 = \alpha_2, \beta_1 = \beta_2, \sigma_1 \neq \sigma_2$	0	3.26	0.25
	$\alpha_1 \neq \alpha_2, \beta_1 = \beta_2, \sigma_1 = \sigma_2$	0	3.92	0.01
	$\alpha_1 = \alpha_2, \beta_1 \neq \beta_2, \sigma_1 \neq \sigma_2$	1	1.44	0.32
	$\alpha_1 = \alpha_2, \beta_1 \neq \beta_2, \sigma_1 = \sigma_2$	0	0.00	0.01
	$\alpha_1 \neq \alpha_2, \beta_1 = \beta_2, \sigma_1 \neq \sigma_2$	0	4.58	0.27
SEAK	$\alpha_1 = \alpha_2, \beta_1 = \beta_2, \sigma_1 = \sigma_2$	0	8.08	0.09
	$\alpha_1 \neq \alpha_2, \beta_1 \neq \beta_2, \sigma_1 \neq \sigma_2$	0	1.69	0.08
	$\alpha_1 \neq \alpha_2, \beta_1 \neq \beta_2, \sigma_1 = \sigma_2$	0	7.86	0.16
	$\alpha_1 = \alpha_2, \beta_1 = \beta_2, \sigma_1 \neq \sigma_2$	0	0.50	0.07
	$\alpha_1 \neq \alpha_2, \beta_1 = \beta_2, \sigma_1 = \sigma_2$	0	6.91	0.05
	$\alpha_1 = \alpha_2, \beta_1 \neq \beta_2, \sigma_1 \neq \sigma_2$	0	0.00	0.17
	$\alpha_1 = \alpha_2, \beta_1 \neq \beta_2, \sigma_1 = \sigma_2$	1	6.14	0.35
	$\alpha_1 \neq \alpha_2, \beta_1 = \beta_2, \sigma_1 \neq \sigma_2$	0	0.34	0.04

in MSY of nearly 200%, while in KOD and PWS no significant change in productivity parameters or MSY was detected (Table 4).

In SEAK and SPEN, a large increase in the β parameter of the Ricker model best explains the differences between periods. Although several candidate models have similar weights (Table 3), when averaged across models the general pattern still holds; large increases in MSY are observed in SEA and SPEN, while little or no increase in productivity is observed in PWS and KOD. That these regions could have experienced similar productivity increases in the absence of hatcheries seems plausible given that during the early 1980s, a period in which environmental conditions had improved but hatchery production averaged less than 20% of its current level, the mean return of wild pink salmon to PWS was 22.3 million fish, and wild catch averaged over 15 million. Since 1988 when hatchery releases stabilized around 600 million fish, the mean wild return and catch have been 10.7 and 5.4 million fish, respectively, less than 50% of the pre-hatchery peak for returns and 35% for catch.

Hatchery influence on variability of catch

The four areas showed a similar general pattern in the temporal evolution of catch variability; as the mean catches increased, the variability tended to be larger. However, the increase in variability appeared to be sharper in PWS and KOD after 1990 (Fig. 3). Statistical tests comparing the variance between periods 1 and 3 showed a significant increase in all management areas (Table 2). Although the absolute variability increased between periods, the CV decreased from period 1 to period 3 (note that in SEAK the reduction was markedly larger). Despite this apparent trend, the Bennet's test failed to reject the hypothesis that all the CVs were equal (value = 5.42; $p = 0.12$; $df = 7$). These findings suggest that hatchery

production has not had a stabilizing effect on pink salmon catch over time.

Discussion

Enhancement of pink salmon in Alaska — particularly in the PWS management area — has succeeded in producing a substantial and sustained enhancement effect and contributed to an order of magnitude increase in catch since the 1960s. At the same time, local wild populations have remained “sustainable” insofar as their abundances remain stable and they appear at no immediate risk of collapse. While increased variability in catch resulting from high abundances may be problematic from a fisheries and processing perspective, overall the hatchery program appears to provide a net contribution to harvest. However, our results also demonstrate that if reduced wild productivity and the costs of hatchery production are not accounted for, the benefits of enhancement may be considerably overestimated. The magnitude of increased catch in PWS has been at least twice as great as nearby areas, implying a large contribution from hatchery production, but comparisons with adjacent regions also suggest that favorable ocean conditions would have resulted in an increasing abundance trend even in the absence of an enhancement program. Therefore, in the case of PWS, although the mean catch of hatchery fish since 1990 has been 30 million, our best estimate of the net enhancement effect to the commercial fishery (9 million) is less than one-third of the apparent contribution when impacts on wild production and cost-recovery are ignored. In regions with smaller hatchery programs — KOD and SEAK — our models suggest a negligible contribution of hatcheries to increased catches. Thus, overall our results are consistent with previous studies that find enhancement effects of salmon hatcheries to be relatively minor (Morita et al. 2006; Scheuerell et al. 2015) and context-dependent (Kaev 2012).

The utilization of adjacent management areas as pseudo-replicates leaves the possibility that some local phenomenon has caused the atypical trajectory of wild pink salmon productivity in PWS and KOD. At a larger spatial scale, wild pink salmon populations from throughout the species range have increased in abundance by an average of 90% since the 1976–1977 ocean regime shift, further suggesting some unique factor at play in PWS and KOD (Morita et al. 2006; Ruggerone et al. 2010). A continued upward trend in hatchery returns despite relatively steady release levels since 1990 demonstrate that local marine conditions are not limiting productivity in hatchery pink salmon. Some persistent change in the productivity of the freshwater life-history phase would therefore be required to explain constant productivity despite improved marine conditions. Wertheimer et al. (2001) posited that the 1989 Exxon Valdez oil spill could account for the divergent pattern of abundance in PWS wild pink salmon. However, recent estimates of the impact of the spill on PWS pink salmon are modest, and the populations have been considered fully recovered from spill impacts since 2002 (Quinn et al. 2002; Brannon et al. 2012; EVOSTC 2014).

Based on our analysis of wild pink salmon productivity in Alaska, we conclude that the release of hatchery pink salmon has likely reduced productivity of the wild populations that interact substantially with hatchery salmon. While wild stocks in the SPEN and SEAK regions experienced dramatic increases in MSY (~200%) — apparently as a result of increased carrying capacity (Fig. 5) — no such increases were observed in PWS or KOD. This pattern suggests that natural carrying capacity may have also increased in PWS and KOD, but is utilized by hatchery fish and thus no change is apparent for the wild stocks, essentially the pattern predicted by the replacement hypothesis (Hilborn and Eggers 2001). Our analyses do not, however, implicate any particular mechanism for negative impacts of hatchery-wild interaction. Understanding the mechanism or mechanisms by which

Table 4. Parameters of the lowest AIC Ricker model, optimum escapement, maximum sustainable yield (MSY), and harvest rate (HR) producing MSY for each stock in for the preregime shift (1: 1960–1976) and postregime shift, full hatchery production (3: 1988–2013) periods.

	KOD 1	KOD 3	PWS 1	PWS 3	SEAK 1	SEAK 3	SPEN 1	SPEN 3
α	1.42	1.42	1.04	1.04	1.39	1.39	1.25	1.25
β	21.22	21.22	11.46	14.77	28.36	82.76	3.92	11.87
σ	0.67	0.49	0.57	0.57	0.47	0.39	0.88	0.88
BMSY	8.49	8.49	4.89	6.30	11.17	33.30	1.61	4.89
MSY	11.42	11.42	4.03	5.19	14.85	43.33	1.76	5.33
Δ MSY		0%		28%		202.7%		191.8%
Optimal HR	57%	57%	45%	45%	56%	56%	52%	52%

Note: α , intrinsic population growth rate; β , density dependence; σ , standard deviation; BMSY, biomass producing MSY.

hatchery production reduces wild stock productivity is critical for quantifying the long-term risk to wild stocks and identifying appropriate management responses. If reduced productivity is primarily a result of ecological interactions that reduce wild pink salmon survival or spawning success, then wild stocks would presumably recover quickly in response to reduced hatchery releases. Although salmon are well known for their ability to reliably return to their natal streams, some proportion of a population will enter and spawn in other streams, a phenomenon known as straying (Westley et al. 2013). Hatchery salmon commonly stray and often interbreed with wild conspecifics, but generally produce fewer successful offspring than their wild counterparts (Naish et al. 2007; Christie et al. 2014). The long-term effects of regular hatchery introgression are uncertain, but in any case genetic impacts on productivity would be expected to persist for multiple generations (Grant 2011; Baskett and Waples 2013; Harbicht et al. 2014).

Previous studies have identified the potential for both ecological and genetic interaction between hatchery and wild pink salmon in Alaska. As noted previously, despite widespread marking of hatchery pink salmon in Alaska, there is no systematic effort to quantify rates of straying by hatchery fish. However, recent studies have provided evidence that straying rates by PWS hatchery pink salmon may be significant. Brenner et al. (2012) found that in some PWS streams up to 98% of fish on spawning grounds were of hatchery origin. The degree to which these fish successfully breed with wild individuals is unknown, but recent genetic analyses have found significant hatchery introgression in PWS and SEAK wild chum salmon (Jasper et al. 2013). Notwithstanding breeding success, high rates of straying reduce the validity of escapement estimates and can therefore diminish the effectiveness of wild stock management.

High straying rates indicate large potential for ecological or genetic interaction between hatchery and wild fish and also confound efforts to estimate wild escapement. With hundreds of millions of hatchery releases occurring in PWS, even low absolute straying rates can result in high proportions of hatchery fish on some wild spawning grounds. Further research on the prevalence of straying and the genetic contribution of hatchery strays to the wild gene pool should be a priority. Though high stray rates implicate reproductive interaction as a likely mechanism for hatchery impacts, interactions at other life-history stages should not be ignored. The period immediately following ocean entry is thought to be very important to lifetime survival of anadromous salmon, and localized resource depletion by large numbers of hatchery fry may potentially impact growth and survival of wild fish (Cross et al. 2008). Increased abundance is also thought to be driving a downward trend in adult body size in PWS hatchery and wild pink salmon, which suggests competition during ocean rearing and homeward migration (Wertheimer et al. 2005). Taken together, these various interactions between hatchery and wild pink salmon demonstrate that a variety of plausible mechanisms exist for hatchery program impacts on wild productivity. It seems fea-

sible that with improved understanding of these mechanisms, an effective accounting of the benefits and risks of hatchery operations for Alaska salmon enhancement could be accomplished. However, because pink salmon migrate long distances and potentially interact with many other salmon populations and species, the net benefits of enhancement will ultimately be sensitive to the geographic scope of analysis.

There is accumulating evidence that pink salmon have far-reaching impacts on ocean ecosystems. Patterns of alternating abundance in species that share ocean habitat with pink salmon strongly suggest impacts of competition (Ruggerone and Nielsen 2004). Such patterns have been observed in other salmon species, including comparatively valuable Bristol Bay sockeye salmon (*Oncorhynchus nerka*) (Ruggerone et al. 2003) and threatened Puget Sound Chinook salmon populations (Ruggerone and Goetz 2004). Recent analysis of long-term data on seabird populations in the North Pacific demonstrated similar patterns in reproductive success, implying that pink salmon also compete directly or indirectly with higher trophic levels (Springer and van Vliet 2014). There is also growing concern that large hatchery releases from around the North Pacific may be resulting in density-dependent declines in growth and survival for all salmon species as oceanic carrying capacity is approached (Cooney and Brodeur 1998; Kaeriyama et al. 2009). When considered in this broader ecosystem context, the analysis of stock enhancement becomes much more complex. With an increasing focus on ecosystem-based management of the oceans, the broader impacts of future enhancement efforts are likely to be heavily scrutinized (Pikitch et al. 2004; Samhuri et al. 2014). Ultimately, if these efforts are to be compatible with ecosystem-based principles, it will be critical to understand the biological capacity for enhancement and the potential unintended consequences of large-scale hatchery releases.

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MORE REFERENCES NOAA CONSIDERATIONS

General effects of salmon hatcheries on wild salmon and the aquatic environment

According to NOAA (2011), hatcheries affect wild salmonids in various ways:

- Facility effects
- Fish removal
- Genetics
- Ecological interactions
- Harvest
- Monitoring and evaluation

Obviously, the effects of any particular hatchery on wild salmonids and the larger ecology of the region is dependent on a number of factors including 1) the physical location of the hatchery facilities, 2) the proximate effects caused by the various physical structures of the hatchery, 3) the operational practices of the hatchery, 4) the proximity of acclimation points to those of wild salmonid stocks, 5) the nature of the fishery facilitated by the hatchery programs, and 6) the sensitivity of the receiving waters and surrounding area. The following discussion is drawn from NOAA (2011), augmented with additional information, primarily from recent literature.

1. Facility Effects. Facility effects include 1) water withdrawals, 2) wastewater and other discharges, 3) effects from the hatchery's physical structures, and 4) risk from spills or other extraordinary incidents occurring at the hatchery.

Production salmon hatcheries must have a reliable source of freshwater, and local streams may be adversely affected if large water withdrawals occur during low flow periods. If intake structures are unscreened, wild salmonids and other aquatic life may be injured or killed after entrainment. Improper screening may lead to injury or death after impingement.

Wastewater discharges along with discharges of ground fish waste are the subject of this general permit. Effluent from hatcheries can include dissolved nutrients (nitrogen and phosphorus) and solids from fish waste and uneaten fish food. Nutrient pollution can cause excess plant growth in receiving waters (both fresh and estuarine), resulting in pH and dissolved oxygen fluctuations outside that of the normal diel cycle (Smith et al. 1999). Solids negatively affect all life history stages of salmonids, including effects on physiology and behavior, and can cause adverse modifications to habitat (Bash et al. 2001). Hatchery effluent can also contain fish disease control chemicals and cleaning agents, as well as cause changes in the temperature and pH of the receiving water. Any treatment of wastewater before discharge will minimize the adverse effects but many hatcheries do not treat the majority of their wastewater.

Discharged ground fish waste can form deposits that displace aquatic life and can affect water quality parameters, if loading rates and receiving water characteristics are not carefully considered (Mazik et al. 2005).

If weirs or other barriers are not removed after broodstock collection, returning wild salmonids may be blocked from spawning areas. If barriers are removed or opened to allow wild salmonid migration, the structures must be properly maintained to ensure fish passage.

Hatcheries often keep quantities of chemicals, fuels, lubricants, fish food, and other materials on hand. The hatchery must have emergency response plans and sufficient equipment on hand to contain or minimize the effects of spills as municipal emergency responders may be distant. Hatchery staff must be properly trained and familiar with the emergency response plans and equipment.

2. Fish Removal. If hatcheries rely on local wild stocks for their broodstock, local wild populations may be depressed. Broodstock collection, regardless of the origin of the broodstock, may affect wild fish if they are held in weirs, traps, or collection ponds, where the fish may be injured, die, or delay their own migration to the spawning areas.

3. Genetics. The effect of hatchery-origin salmon on the genetics of wild salmon has been increasingly studied, both in relation to the effects on Endangered Species Act-listed salmon (in Washington, Oregon, and Idaho), and the effects on pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon in Alaska where large hatchery programs have been in operation (Josephson 2017). NOAA (2011) presents a comprehensive review of the genetic effects of salmon hatcheries.

Genetic effects can occur through hatchery fish mating with other hatchery fish or with wild fish and producing offspring that are less fit, and a diminishment of the genetic diversity of the wild stock. Wild salmon are equipped with sufficient genetic material to be successful in a range of natural environmental conditions. Hatchery salmon, on the other hand, are not subject to natural conditions. Recent research has shown that salmon raised in a hatchery environment become “domesticated” (i.e., adapted to captivity) in as little as one generation (Christie et al. 2012a; 2016; Le Luyer et al. 2017); therefore, even periodic supplements of wild fish into the hatchery broodstock cannot prevent the domestication of the hatchery stock. Hatchery fish, if they escape to the spawning grounds in sufficient numbers, can depress the overall fitness of a wild salmon population (Christie et al. 2012b). Salmon produced from hatchery x hatchery matings or hatchery x wild matings will be less fit and less likely to return, and thus represent a “waste” of the spawning habitat (and the reproductive potential of the wild fish in a hatchery x wild mating).

One notable characteristic of salmonids, so notable that it can likely be identified by most of the general public, is homing, that is, the return of adults to their natal waters to spawn. This trait has the advantages of, among other things, matching adapted individuals with the local environmental conditions and increasing the probability of finding suitable mates and spawning habitat (Westley et al. 2013). The homing trait has led to the development of hundreds of ecotypes of salmon in the north Pacific. Straying, or the ascension of non-natal waters to spawn, is an adaptive trait in that it allows for

colonization of underutilized habitat. Straying in hatchery-origin salmon, however, is detrimental from a human standpoint because individuals may escape to the wild-salmon spawning grounds and occupy spawning habitat and wild mates, thus representing a “waste” of wild salmon reproductive potential (as well as the fact that the hatchery fish avoids being harvested, the primary purpose of hatchery salmon).

If straying would occur in sufficient numbers to a system with a low wild salmon population, then the fitness of that wild salmon population could be adversely affected. Brenner et al. (2012) found very high stray rates in hatchery-origin pink, chum, and sockeye (*O. nerka*) in Prince William Sound (PWS), and fear that such stray rates may have adverse effects on productivity as well as genetic diversity and fitness of the corresponding wild stocks in PWS. Preliminary results from an ADF&G-led study (Josephson 2017) indicate lower stray rates in pink and chum salmon in PWS than those found by Brenner et al (2012). Piston and Heintz (2012) report stray rates of hatchery chum of over 13% in one of two studied sub-regions of Southeast Alaska, with stray rates in some index streams of over 40%. Jasper et al. (2013) determined that some wild PWS chum populations were introgressed by hatchery chum. Grant’s review (2012) concentrates on the adaptive consequences of the interactions of hatchery and wild Alaska salmon and concludes that 1) hatchery fish are less fit than wild fish and 2) hatchery straying leads to reduced fitness of wild salmon populations.

4. Ecological Interactions. Releases of hatchery-origin juvenile fish can result in ecological interactions that are detrimental to wild salmon and other aquatic life. NOAA (2011) lists that disease, competition (density dependence), predation (both predation by the hatchery-origin fish, as well as that the large numbers of released hatchery fish attract predators on wild fish), and marine-derived nutrients.

Hatchery fish may harbor more disease organisms than wild fish due to the rearing densities of hatcheries. Once wild fish come in contact with released hatchery fish (if hatchery releases coincide with migration of wild juveniles), the wild fish may be exposed, especially if local conditions (post-hatchery release) result in higher densities than would be naturally found. Pathogens may be found in higher concentrations near net pens where hatchery salmon juveniles are acclimated. Pathogens may also be released in hatchery wastewater effluent and affect wild salmon.

Competition between hatchery juveniles and wild salmon juveniles for food and rearing habitat can have many components. Factors that determine if competition is a significant factor in a hatchery program include 1) timing of the hatchery releases, 2) size of the hatchery fish compared to wild juveniles, 3) the time that the juveniles would be occupying the habitat before migrating to the ocean, and 4) the species involved. If hatchery fish are released before conspecific wild fry emerge, the hatchery fish may occupy the prime rearing habitat. Similarly, if hatchery fish are larger or in better condition, they may out-compete conspecific wild fish for available food sources. The magnitude of either effect will be increased as the time that the hatchery and wild fish rear together increases. Investigating a decline in wild chum harvests, Sturdevant et al

(2012) found little evidence for competition between wild and hatchery chum salmon in Taku Inlet, southeast Alaska, unless it was occurring in the littoral zone before both wild and hatchery fish made the transition to epipelagic waters. Taking a wider view, Ruggerone et al. (2011) found multiple lines of evidence that competition at sea between Alaska (Norton Sound) wild chum and chum released from Asian hatcheries resulted in lower productivity of the Alaskan wild chum.

Interspecies competition can also affect wild salmon but because different species will generally have different habitat and food preferences, it is generally less problematic for wild salmon than intraspecies competition. Peterman et al. (2012) called for international cooperation to limit northern Pacific hatchery salmon releases, citing oceanic competition between wild fish and hatchery fish. Over the last thirty years, approximately 5 billion hatchery salmon fish have been released annually in the north Pacific (NPAFC 2017).

Competition between adult hatchery fish and adult wild fish for mates and spawning space was discussed above in the genetics section.

Predation effects of hatchery origin-fish has two components, namely predation *by* hatchery-origin juvenile fish and increased predation of juvenile salmon (both hatchery and wild). Both types of predation effects can be minimized by thoughtful hatchery practices regarding fish size and timing of releases.

Hatchery-origin fish prey on fish 1/3 to 1/2 their own length, so timing of releases and size of hatchery fish when released can be major factors in the effect of predation by hatchery fish. Predation on fry is generally greater than predation on smolts or sub-adults.

The release of large numbers of hatchery fish can attract bird, fish, or pinniped predators that can adversely impact juvenile wild salmon numbers if comingled.

Local nutrient budgets may be altered if large numbers of hatchery fish return to a watershed. Alaska watersheds have not experienced the precipitous decline in wild salmon populations that have occurred in British Columbia and the US states of the Pacific Northwest, so hatchery fish returns represent an absolute increase over historical returns of marine-derived nutrients in Alaska watersheds. Of course, harvested fish (hatchery and wild) are generally exported from the ecosystem, and Alaska watersheds may in fact be suffering from a net deficit of marine-derived nutrients compared to the era before industrial-scale commercial fishing. Today, in some cases disposal of carcasses (e.g. pink salmon used only for roe stripping) may cause local water quality issues.

5. Harvest. Because the purpose of hatchery fish is to raise fish for harvest, the fisheries may disproportionately impact wild populations. Careful management is required to ensure that wild fish are not disproportionately harvested in the fishery so that adequate escapement of wild fish is ensured.

Hillborn and Eggers (2000) analyzed Prince William Sound pink salmon harvest data and concluded that hatchery production replaced rather than augmented wild pink production. Amoroso et al. (2016) analyzed pink salmon harvest data from 1960 to 2011 in the various regions of Alaska and found that after accounting for reductions in wild fish populations and cost recovery harvest, most Alaska regions did not see appreciable increases in harvest that was attributable to hatchery programs.

6. Monitoring and evaluation. Generally, these activities are only a problem when attempting to assess stocks that are severely depressed. Nearly all Alaska hatchery fish are marked (Stopha 2017), so hatchery and wild fish can be easily differentiated in monitoring and evaluation activities.

#6 is not true.

- ① Kitoi Hatchery release of 150,000,000 has no marked otoliths.
- ② Tutka Bay Hatchery otoliths are very hard to differentiate between wild stocks due to salt water influence confounding a clear mark on the otolith, skewing results.
- ③ Monitoring and evaluation happens rarely and sporadically. Revenues are not there to perform needed oversight.

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HYPOXIA - SUFFOCATION REFERENCES

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ECOSPHERE

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

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Citation: Sergeant, C. J., J. R. Bellmore, C. McConnell, and J. W. Moore. 2017. High salmon density and low discharge create periodic hypoxia in coastal rivers. *Ecosphere* 8(6):e01846. 10.1002/ecs2.1846

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.

Received 16 March 2017; revised 28 April 2017; accepted 5 May 2017. Corresponding Editor: Debra P. C. Peters.

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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. 2010b, Campbell et al. 2011, Bellmore et al. 2014, Benjamin et al. 2016).

In small watersheds (<30 km²), 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 km²) to large watersheds (>200 km²) with high annual average discharge (>10 m³/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 Heirl 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

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 km²)," 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 km² 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 m³/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 m³/s and reached a maximum of 0.45 m³/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,

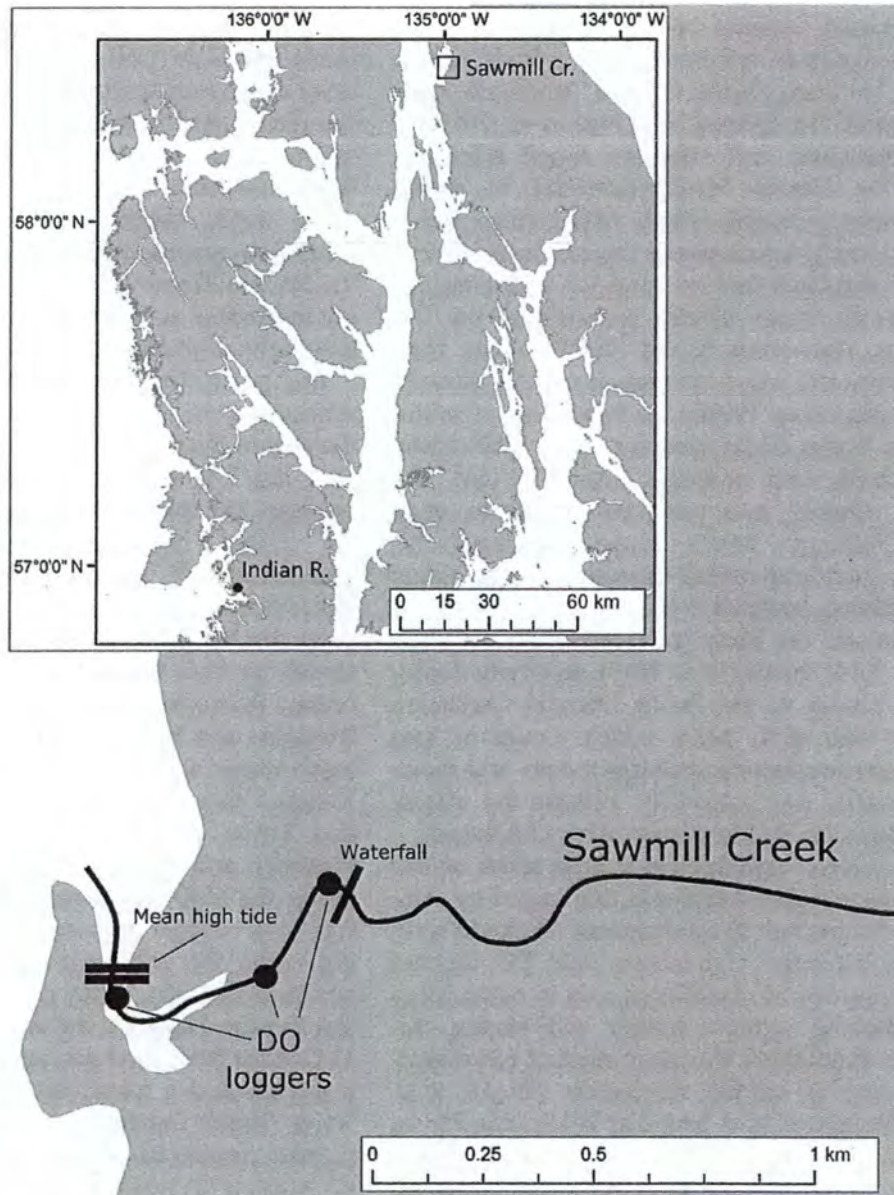


Fig. 1. Map of study area and Sawmill Creek dissolved oxygen (DO) logger locations in relation to anadromous barrier (waterfall) and mean high tide.

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,

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 $\mu\text{S}/\text{cm}$ 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 ($^{\circ}\text{C}$) 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 ($^{\circ}\text{C}$) 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>).

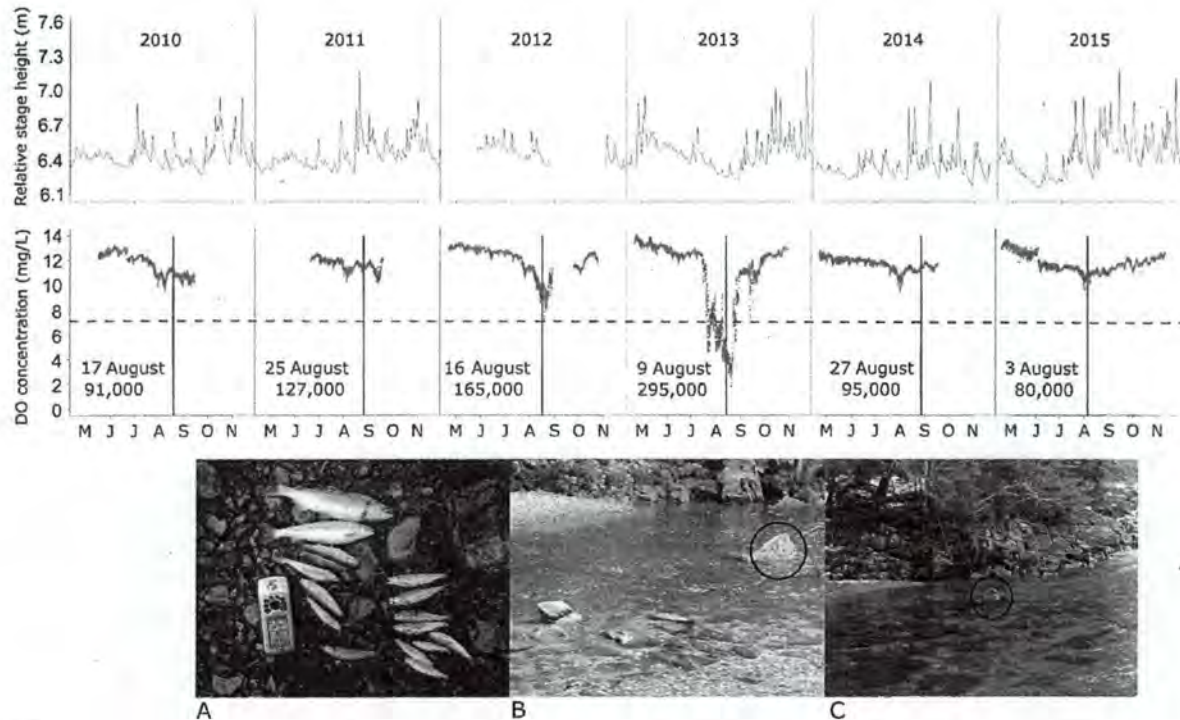


Fig. 2. Inter-annual patterns of Indian River dissolved oxygen (DO) concentration and saturation in comparison with relative river stage and salmon presence. In the lower panel, colored points represent DO saturation levels (green > 70%, blue 50–70%, and red < 50%). The horizontal dashed line represents 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

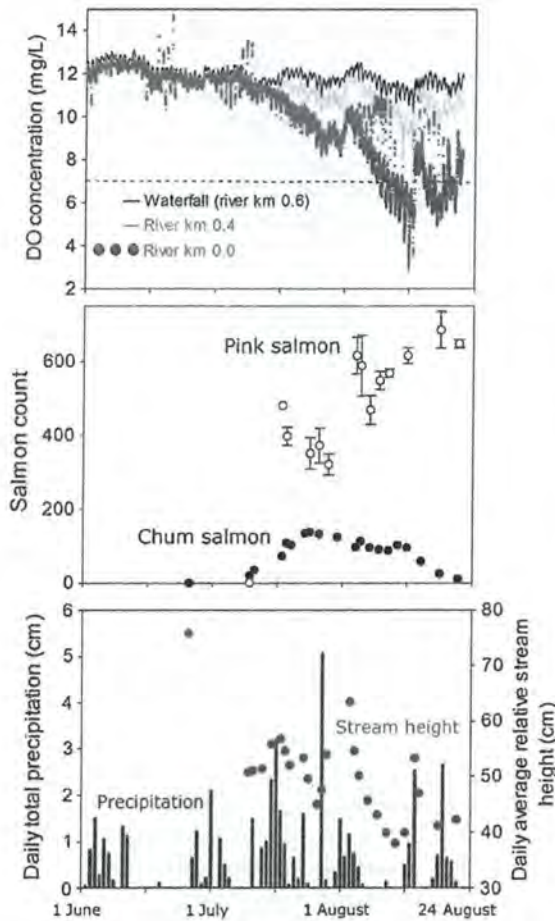


Fig. 3. Intra-annual patterns of Sawmill Creek dissolved oxygen (DO) concentration and saturation at three stream locations in comparison with stream height and salmon abundance. In the upper panel, colored points represent DO saturation levels at river km 0.0 (green > 70%, blue 50–70%, and red < 50%). 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:

$$\frac{d[O_2]}{dt} = k([O_2]_{sat} - [O_2]) - R_{sal}$$

where $[O_2]$ is DO concentration (mg/L), $[O_{2sat}]$ 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 O_2 $L^{-1} h^{-1}$). 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):

$$k_{20^\circ C} = \frac{50.8 v^{0.67} d^{0.85}}{d}$$

where $k_{20^\circ C}$ 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):

$$k_T = k_{20^\circ C} \left(\frac{T}{20} \right)^{\theta}$$

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:

$$R_{sal} = N_{sal} \alpha W^\beta e^{\phi T} U^\nu$$

where R_{sal} is the amount of oxygen respired by spawning salmon (mg O_2 $L^{-1} h^{-1}$); N_{sal} is the number of spawning salmon per liter of water (salmon/L = salmon/m² × 1/depth (m) × m³/1000 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).

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. 2010a) were not included in our model. Ecosystem metabolism can strongly influence DO dynamics in some rivers (Holtgrieve et al. 2010a), 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 $\pm 20\%$ 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/m² by dividing by the wetted area of the spawning

reach (wetted length 9 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 m³/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/m²), 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 pre-spawn 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

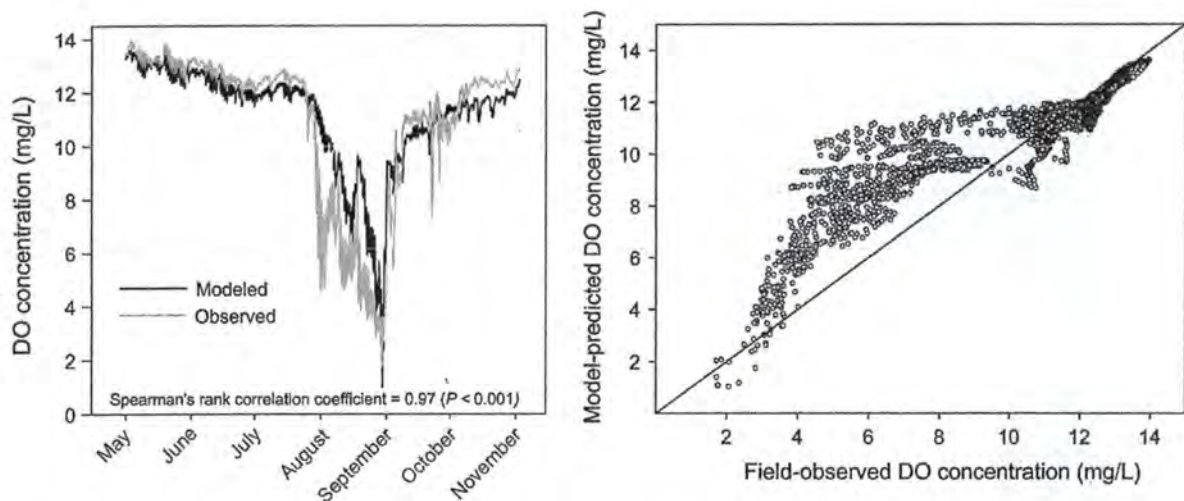


Fig. 4. Dissolved oxygen (DO) model vs. field DO measurements. Left panel compares modeled (black line) DO time series to field observations (gray line) during 2013. Right panel is a scatter plot of modeled vs. field DO measurements; black line represents 1:1 values.

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 $\pm 20\%$ 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 $\pm 20\%$ 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 ($<0.01 \text{ m}^3/\text{s}$) and water temperature ($>12^\circ\text{C}$) 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 $0.6 \text{ m}^3/\text{s}$ (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 ($<0.2 \text{ m}^3/\text{s}$) and water temperature ($>6^\circ\text{C}$; Fig. 5). At high salmon spawning densities (70 spawners/m), the range of discharge ($<0.7 \text{ m}^3/\text{s}$) and water temperature ($>6^\circ\text{C}$) 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,

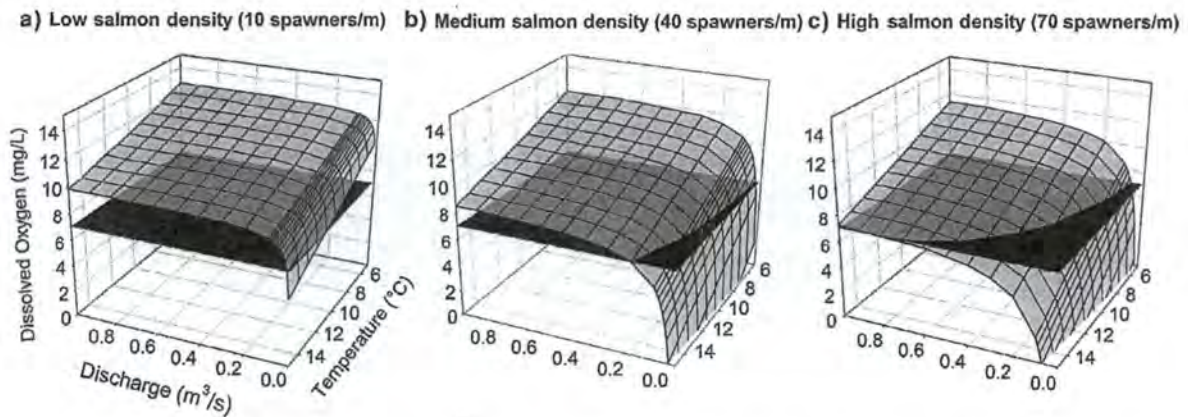


Fig. 5. Three-dimensional model representation of Indian River dissolved oxygen dynamics (mg/L) based on varying discharge (m^3/s) and water temperature ($^{\circ}\text{C}$) across three pink salmon spawning densities (spawners/m). The flat black plane represents our defined hypoxic level of 7 mg/L.

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 Heisl 2012). Even though stray rates tend to decrease as the distance from hatchery release sites increases (Brenner et al. 2012, Piston and Heisl 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 m³/s, and during August 1999 and 2000, it ranged from 0.42 to 0.85 m³/s (USGS gage 15087730, <http://waterdata.usgs.gov/nwis>). During August in years 2013–2016, the mean diversion rate was 0.25 m³/s, while the maximum was 0.45 m³/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 m³/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.

ACKNOWLEDGMENTS

The views expressed in this article do not necessarily represent the views of the authors' respective agencies and institutions. The use of firm, trade, or brand names is for identification purposes only and does not constitute endorsement by the federal government. Indian River water quality monitoring is funded by the National Park Service Inventory and Monitoring Program and Water Resources Division. T. Kucerovy, S. Paustian, and T. Schwarz assisted with Indian River wading discharge measurements. C. McConnell's Sawmill Creek field research was supported by the Northern Gulf of Alaska Applied Research Award and the Ladd Macauley Graduate Fellowship. We thank E. Coonradt at the Alaska Department of Fish and Game (ADFG) for providing aerial salmon count data. C. Shanley of The Nature Conservancy provided

summaries of southeastern Alaska watershed size and annual average discharge originally used in Shanley and Albert (2014). J. Nichols (ADFG) and E. Tucker (United States Forest Service) provided valuable input and stream habitat data for the salmon respiration model. We thank M. Bower, R. Brenner, B. Carter, S. Gende, J. Hard, J. Hughes, E. Ward, L. Welling, and one anonymous reviewer for preliminary manuscript reviews. Two anonymous referees provided thoughtful peer reviews.

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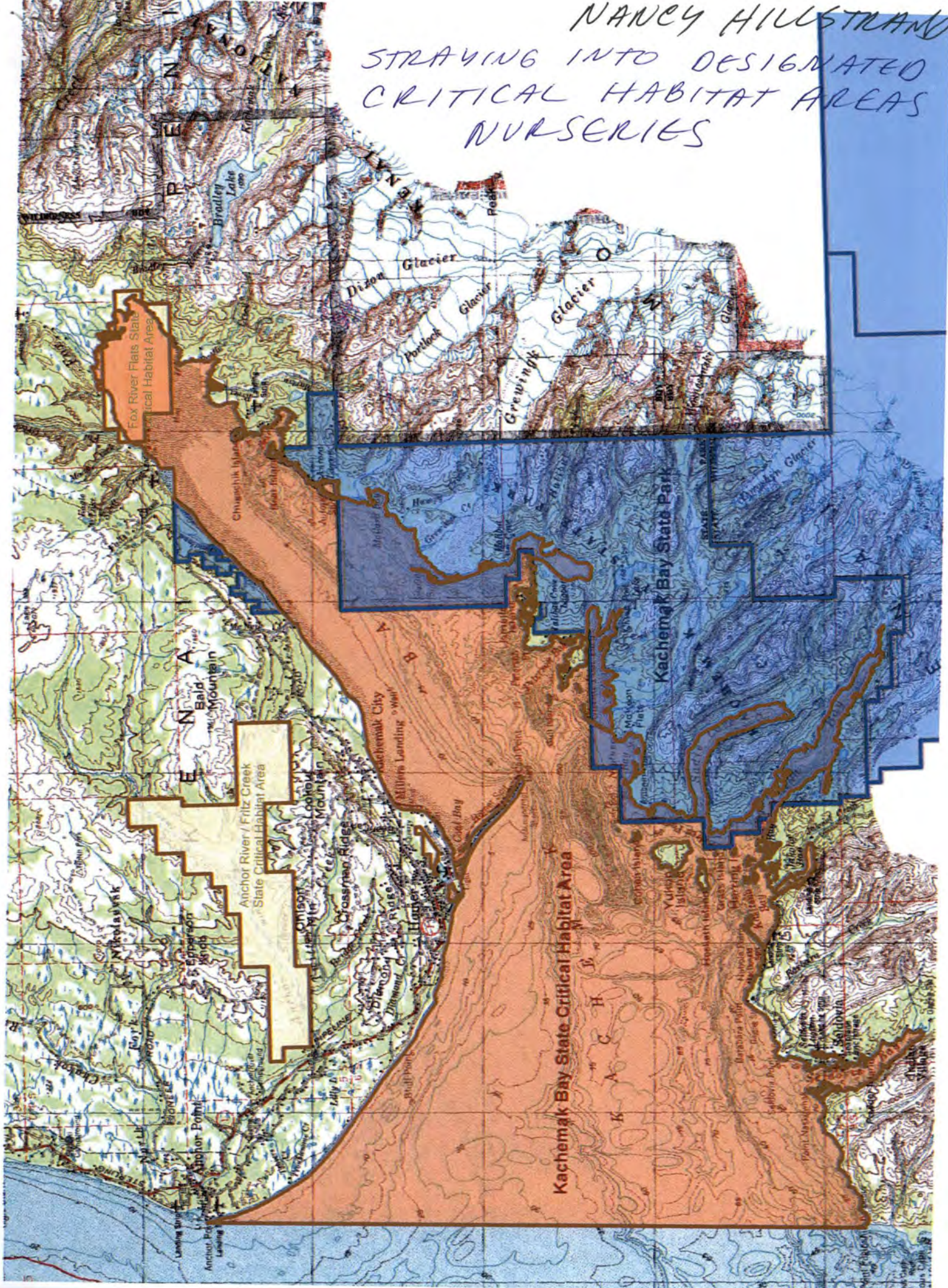
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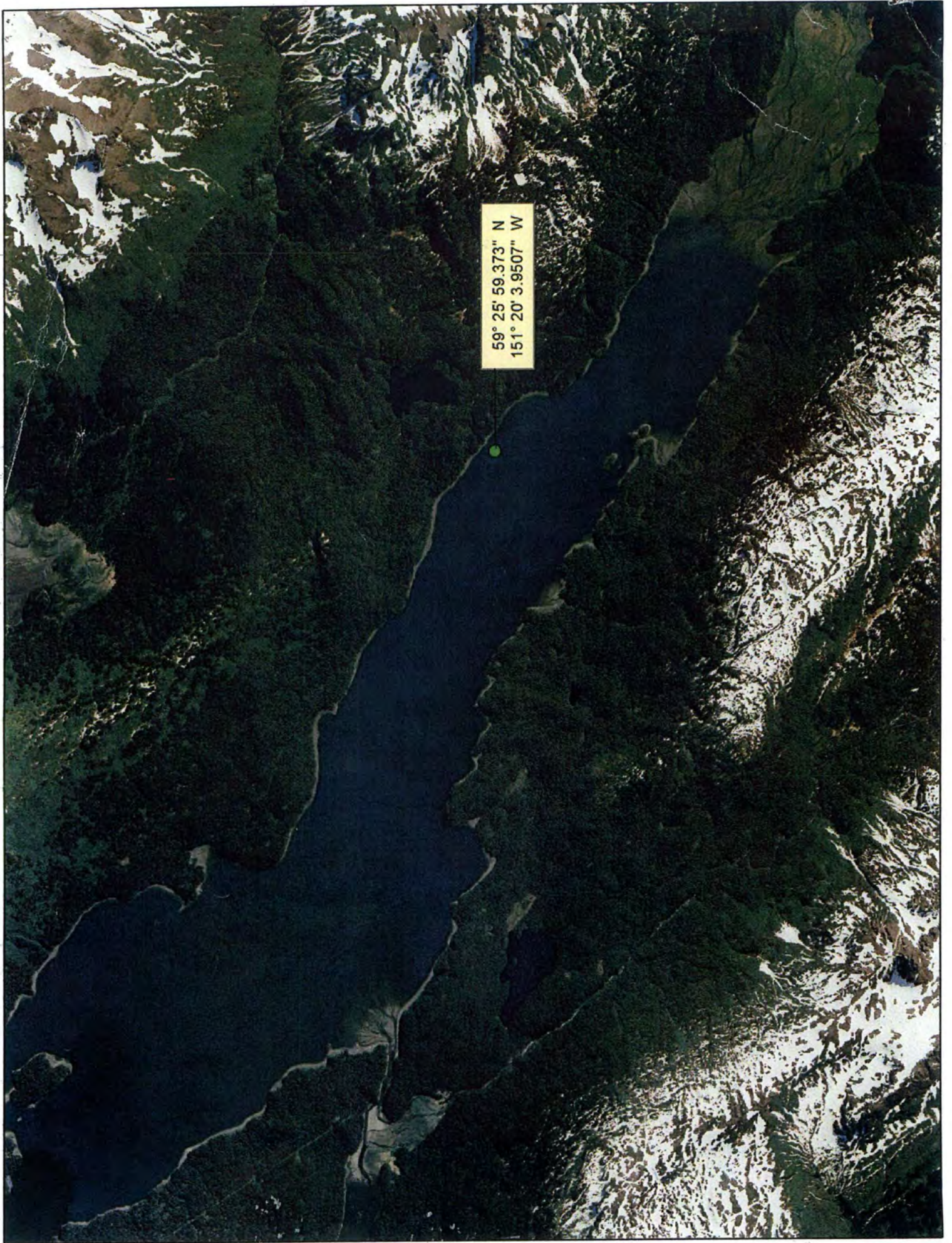
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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1846/full>

NANCY HILLSTRAND
STRAYING INTO DESIGNATED
CRITICAL HABITAT AREAS
NURSERIES





59° 25' 59.373" N
151° 20' 3.9507" W

SHRIMP



General Distribution



Known Concentration Areas



Known Spawning Concentration Areas

DUNGNESS CRAB



General Distribution



Known Concentration - Reproduction Areas

RAZOR CLAMS



Known Concentration Areas



Southcentral Regional Boundary

CRUSTACEAN LARVAL BIOLOGICAL TIMING
 AT RELEASE OF HATCHERY PINKS TO
 PREY ON THEM AND ADULT RETURN
 PREDATION.

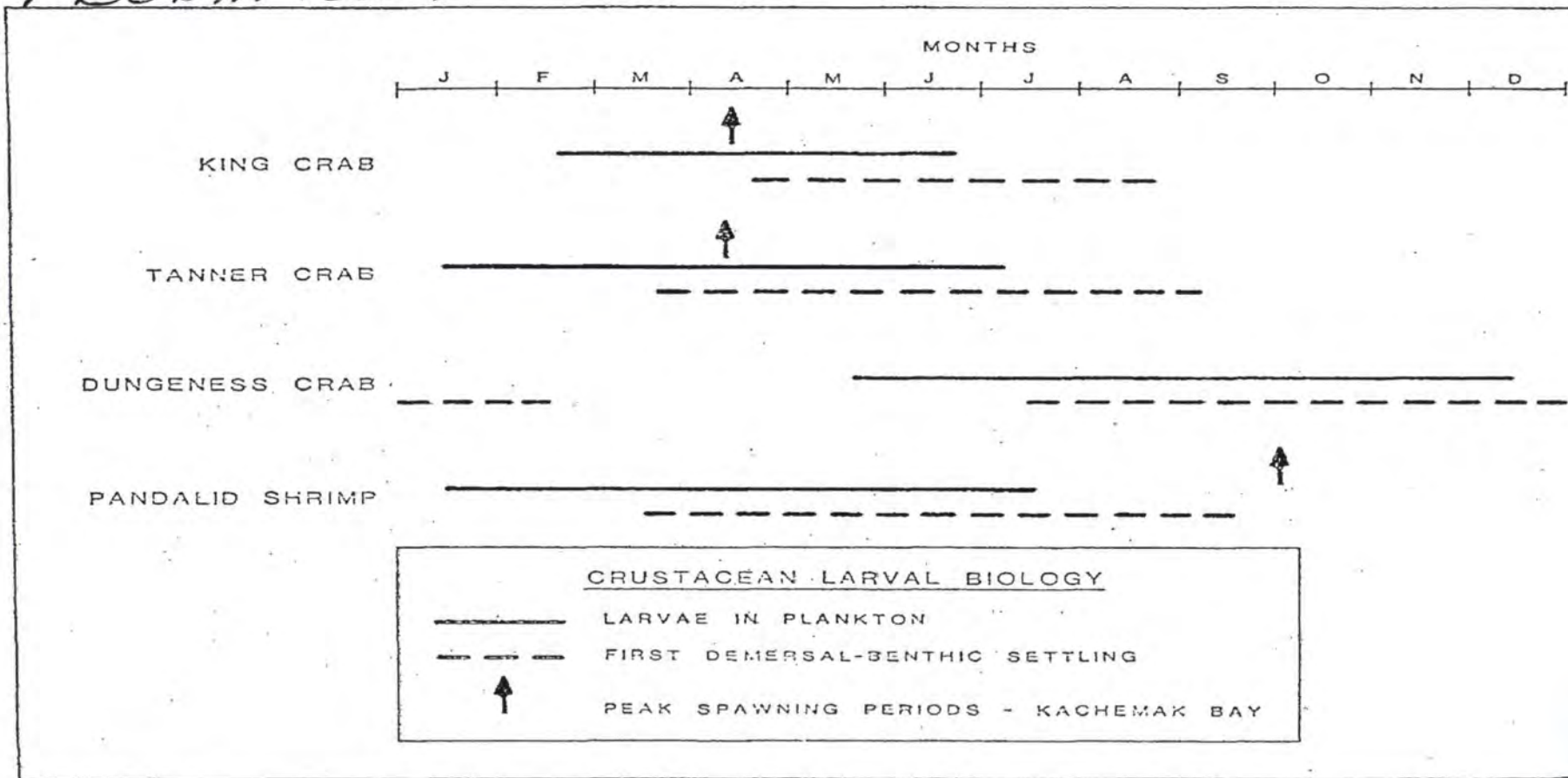


Figure 2-6 Lower Cook Inlet, crustacean larval biology (ADF&G, Vol. 2, 1976)

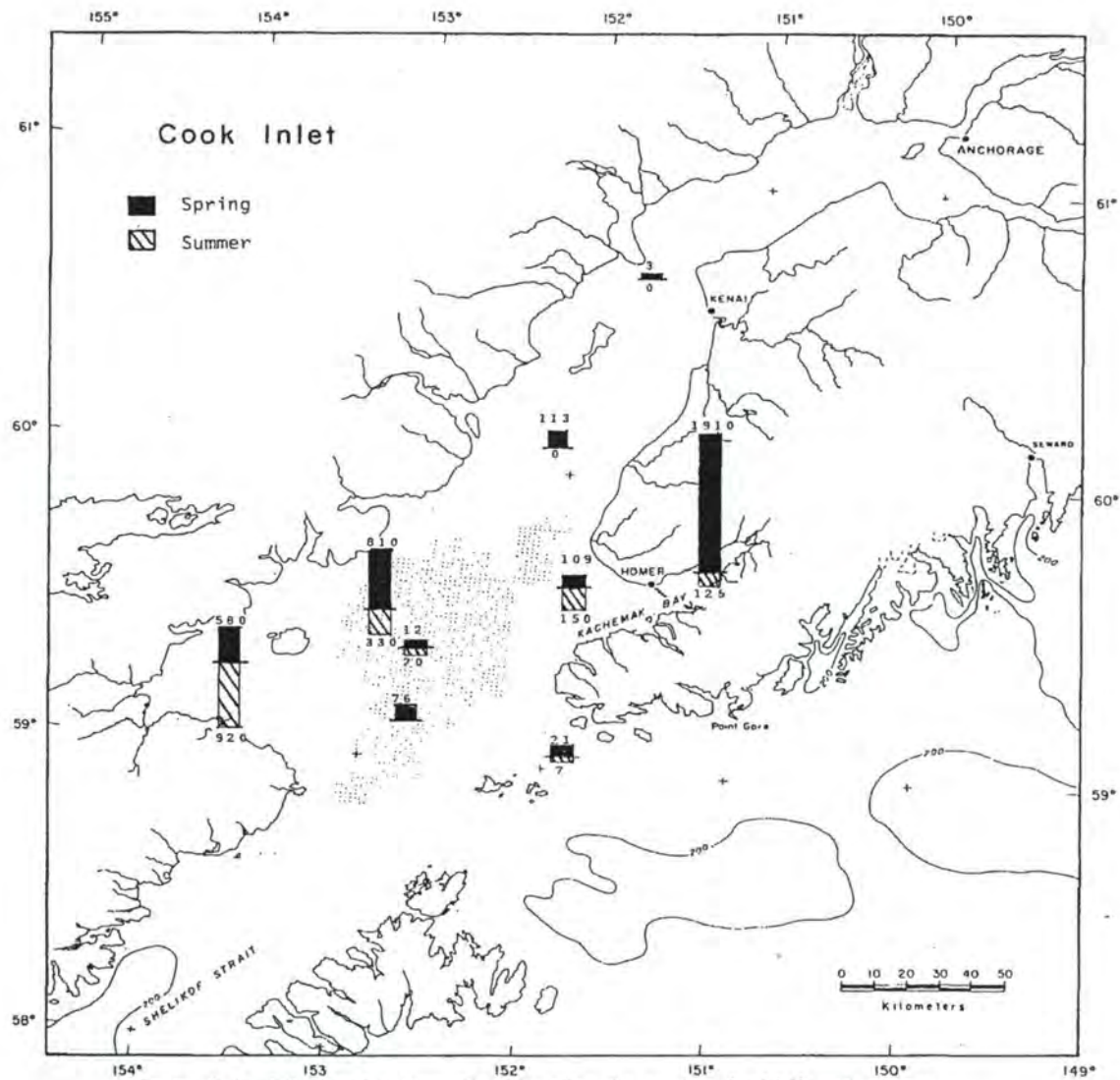
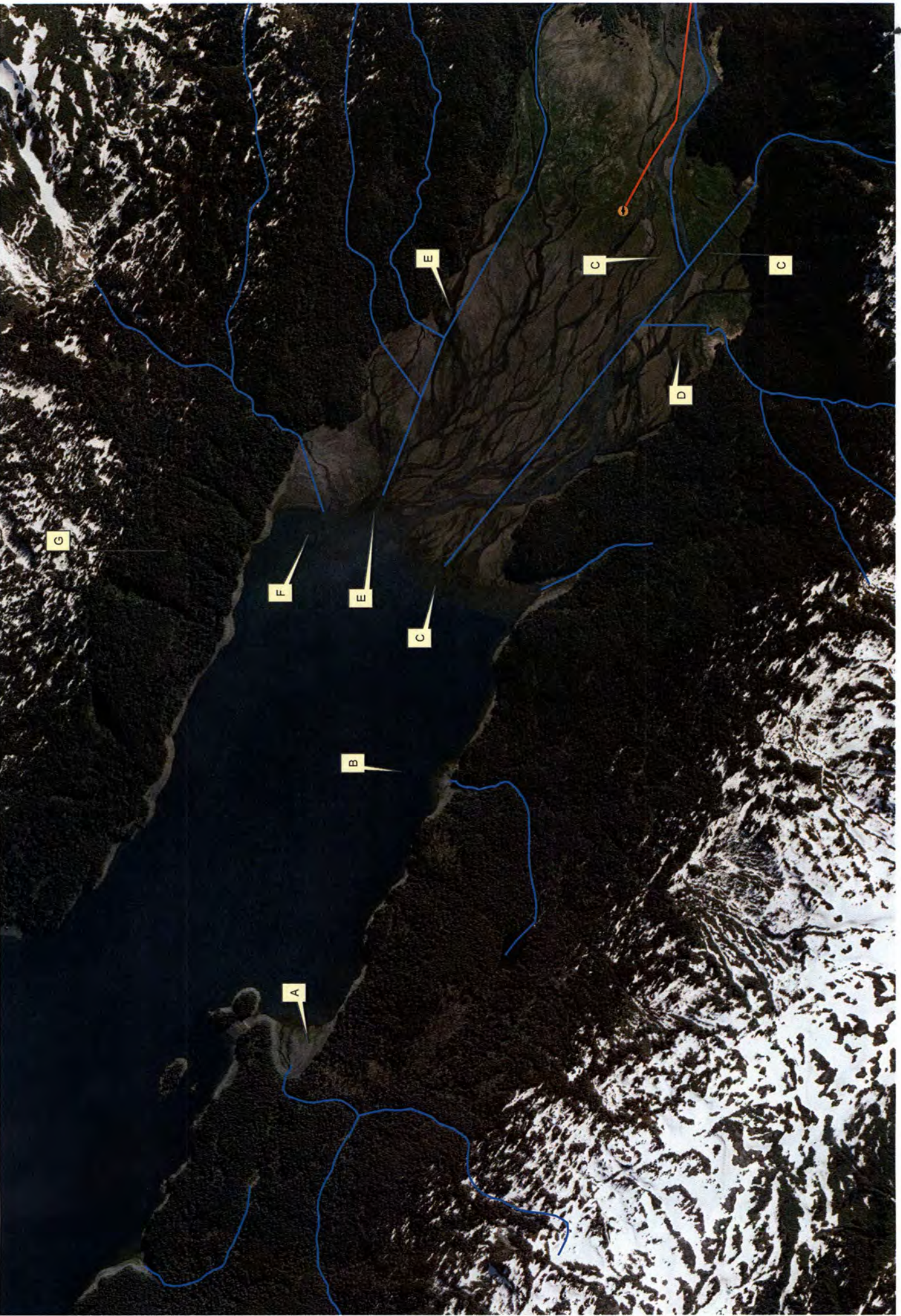


Figure 2-3 Ichthyoplankton distribution in spring (solid) and summer (hachured). Horizontal line indicates sample location; length of bar above/below line proportional to numbers of fish eggs collected per bongo net tow, using standard MARMAP methods. (Adapted from unpublished data provided by T. English, University of Washington, Seattle)

WILD PORTFOLIO STOCKS AT RISK



DUNGENESS SHELF HABITAT AT RISK WHEN CLOSED WATERS
- OPENED TO CATCH HATCHERY FISH

