State of Alaska
Department of Fish and Game
Division of Sport Fish

Nomination Form
Anadromous Waters Catalog

Region: Southwest

USGS Quad(s): Iliamna D-3, D-4, D-3SW

AWC Number of Water Body: 324-10-10150-2317 (additional listed below)

Name of Water body: Pedro Ponds

☒ USGS Name ☐ Local Name

☒ Addition ☐ Deletion ☐ Correction ☐ Backup Information

For Office Use

Nomination #	150093	James J Hasbrouck, Fisheries Scientist	10/26/2015 Date
Revision Year:	2016	Habitat Operations Manager	10/26/15 Date
Revision to: Atlas ____ Catalog ____ Both X		AWC Project Biologist	23 OCT 15 Date
Revision Code:	A-2	GIS Analyst	11/12/15 Date

OBSERVATION INFORMATION

Species	Date(s) Observed	Spawning	Rearing	Present	Anadromous
Sockeye	July-Sept 1995-2014	X		X	☒
Char	June-Sept " "		X		☐
pike	" " " "		X		☐
					☐
					☐

IMPORTANT: Provide all supporting documentation that this water body is important for the spawning, rearing or migration of anadromous fish, including: number of fish and life stages observed; sampling methods, sampling duration and area sampled; copies of field notes; etc. Attach a copy of a map showing location of mouth and observed upper extent of each species, as well as other information such as: specific stream reaches observed as spawning or rearing habitat; locations, types, and heights of any barriers; etc.

Comments Pedro Pond complex 59°47.555'N 154° 7.320' W

Add new waterbodies 324-10-10150-2317-3019, 3019-0010, 3019-0020, 324-10-10150-2317-3019-4020-4020-0010, 4020-0020, 4020-0030, 4020-0040, 324-10-10150-2317-3019-4030, -4030-0010 4030-0020, 3027, 3027-0010; 3035-3035-0010 3035-0020

Name of Observer (please print): Jackie Carter

Signature: Jackie Carter

Date: 1/26/15

Agency: ~~1122 NE Boat St~~ Univ. of WA.

Address: 1122 NE Boat St
Seattle WA 98105

This certifies that in my best professional judgment and belief the above information is evidence that this waterbody should be included in or deleted from the Anadromous Waters Catalog.

Signature of Area Biologist: _____ Date: _____

Name of Area Biologist (please print):

Revision 11/13

ALASKA DEPT. OF FISH & GAME
JAN 28 2015

Johnson, J D (DFG)

From: Thomas P. Quinn <tquinn@uw.edu>
Sent: Thursday, May 14, 2015 5:00 PM
To: Johnson, J D (DFG)
Subject: Re: Pedro ponds

J,
To answer your questions:

Was sockeye salmon spawning observed in ponds Big, Berg's Trail, P-1 – P4, Grass & Bear or pre-spawners?

Most definitely the sockeye salmon spawn in these ponds. There is no question that they are core spawning habitats.

Was spawning observed in creeks draining ponds downstream to Pedro Creek or pre-spawners?

We see spawning in the creeks draining these ponds (e.g., between Trail and Berg's ponds, between ponds 1-2, 2-3, etc. in some years. These are tiny creeks and when the run is low and bears are hungry I think few salmon successfully spawn there. However, in years with more salmon they definitely spawn in the streams, as well as using them as corridors to the ponds. We do not walk the whole system, and as one gets farther downstream the creek is more of a migration corridor. However, I have seen spawning well below our focal sampling sites.

Were spawning sockeye salmon observed in ponds or creeks draining them for ponds I've hand labeled as 1, 2, 3, 4, & 5 or pre-spawners?

To be honest I have not scouted these ponds, as we are busy keeping track of the ones we sample. I am pretty sure that there are other ponds with sockeye but cannot say which they are. However, we could make an effort to survey them this year if you were interested.

best wishes,
tom

On Thu, May 14, 2015 at 12:49 PM, Johnson, J D (DFG) <j.johnson@alaska.gov> wrote:

Johnson, J D (DFG)

From: Thomas P. Quinn <tquinn@uw.edu>
Sent: Thursday, May 14, 2015 9:09 AM
To: Jackie L. Carter; Johnson, J D (DFG)
Cc: Jason Ching
Subject: Re: Pedro ponds

J,
If I interpret this correctly, you are asking whether sockeye salmon (and other anadromous fishes) occupy waters outside this red line, yes? If so, then the answer is clearly yes. Indeed, the main ponds are much closer to the airstrip. I have attached a paper we did that reports sockeye numbers in a series of these ponds. The one we call Pond 1 is right next to the gravel road along the airstrip. You can throw a rock behind your back from the road into the pond. The one we call Grass Pond is within about 100 feet of the road, and the one we call Bear Pond is probably 50 feet from the road. As you can see from the paper, the sockeye runs vary greatly but densities can be very high. These ponds are also occupied by Dolly Varden and sculpins. I would need to check with the crew but I think we may have seen an occasional coho fry there but that species would likely be very rare compared to sockeye.

For what it is worth, I have wondered about the effects of the much-enlarged airstrip and associated road (with substantial berms) on the hydrology of these spring-fed ponds. I have seen (but cannot formally document) changes in water flow so that areas that used to have sockeye seem not to anymore and there seems to be lower flows.
Tom

On Thu, May 14, 2015 at 9:55 AM, Jackie L. Carter <jlcarter@uw.edu> wrote:
Here's the attachment. There's no rush, we can wait until Jason is back in town.
---------- Forwarded message ----------
From: **Johnson, J D (DFG)** <j.johnson@alaska.gov>
Date: Thu, May 14, 2015 at 9:02 AM
Subject: Pedro ponds
To: "Jackie L. Carter (jlcarter@uw.edu)" <jlcarter@uw.edu>

Jackie

Have a few questions, refer to the attached

District	USGS Quad	AWC #	Name	Mouth Lat	Mouth Long	Top Lat	Top Long	Notes
Southwest	Iliamna D-2	324-10-10150-2317	Pedro Ponds	59.792585	-154.12199			Currently nameless
Southwest	Dillingham B-8		Eagle Creek	59.316725	-158.69427	59.322679	-158.6623	
Southwest	Goodnews Bay C-1		Waterfall Creek	59.664732	-159.14673			
Southwest	Goodnews Bay C-1	325-30-10100-2031-3118-4125	Rainbow Creek	59.663636	-159.15304			Currently nameless, known as Rainbow Creek
Southwest	Dillingham C-8		Seventh (7th) Creek	59.579489	-158.91439	59.587526	-158.932	
Southwest	Dillingham C-8		Berm Creek	59.598544	-158.81459	59.603392	-158.83458	
Southwest	Dillingham C-7		Spider Creek	59.633205	-158.54604	59.644812	-158.48345	
Southwest	Dillingham C-8		B-12 Creek and Beach	59.664263	-158.80923			
Southwest	Dillingham C-8		Uno Creek (Unowhokkuit)	59.690623	-158.75429	59.71119	-158.75825	
Southwest	Goodnews Bay C-1	325-30-10100-2031-3118-4119-5004	C Creek/Beach	59.579054	-159.14109			Currently nameless
Southwest	Goodnews Bay C-1	325-30-10100-2031-3118-4119	A Creek/Beach	59.577371	-159.1309			Currently nameless
Southwest	Goodnews Bay C-1	325-30-10100-2031-3118-4117	Pick Creek	59.550785	-159.06422	59.526346	-159.08207	Currently named PIKE Creek (listed on USGS map as PIKE), but locally known as PICK. There is another Pike Creek on the South Arm of Nerka.
Southwest	Dillingham B-8		Midnight Creek	59.292377	-158.77166	59.289631	-158.77526	

SampleType	Lake	StationName	DateSampled	Sockeye Live Counts	Otoliths collected
CreekWalk	Aleknagik	Aleknagik Midnight Creek	8/3/1999	296	
CreekWalk	Aleknagik	Aleknagik Midnight Creek	8/11/2000	137	
CreekWalk	Aleknagik	Aleknagik Midnight Creek	8/10/2001	19	
CreekWalk	Aleknagik	Aleknagik Midnight Creek	8/7/2002	89	
CreekWalk	Aleknagik	Aleknagik Midnight Creek	8/9/2003	206	
CreekWalk	Aleknagik	Aleknagik Midnight Creek	8/7/2006	450	226
CreekWalk	Aleknagik	Aleknagik Midnight Creek	8/15/2006	330	
CreekWalk	Aleknagik	Aleknagik Midnight Creek	8/17/2012	3	
CreekWalk	Aleknagik	Aleknagik Midnight Creek	8/4/2014	28	
Creekwalk	Beverley	Beverley Spider Creek	8/12/1955	0	
Creekwalk	Beverley	Beverley Spider Creek	8/17/1955	0	
Creekwalk	Beverley	Beverley Spider Creek	8/8/1957	0	
Creekwalk	Beverley	Beverley Spider Creek	8/12/1958	50	
CreekWalk	Beverley	Beverley Uno Creek	8/13/2010	2645	228
CreekWalk	Beverley	Beverley Uno Creek	8/10/2011	2715	191
CreekWalk	Beverley	Beverley Uno Creek	8/9/2012	796	
CreekWalk	Beverley	Beverley Uno Creek	8/4/2013	2738	217
CreekWalk	Beverley	Beverley Uno Creek	8/14/2014	4571	212
CreekWalk	Iliamna	Iliamna Pedro Ponds	9/14/1963	21	
CreekWalk	Iliamna	Iliamna Pedro Ponds	8/29/1964	215	
CreekWalk	Iliamna	Iliamna Pedro Ponds	9/15/1964	525	
Ages	Iliamna	Iliamna Pedro Ponds	9/6/1968		40
Ages	Iliamna	Iliamna Pedro Ponds	9/15/1968		160
Ages	Iliamna	Iliamna Pedro Ponds	9/3/1969		200
Ages	Iliamna	Iliamna Pedro Ponds	9/15/1974		42
Ages	Iliamna	Iliamna Pedro Ponds	1/1/1900		110
Ages	Iliamna	Iliamna Pedro Ponds	8/16/1993		86
Ages	Iliamna	Iliamna Pedro Ponds	8/16/1994		196
Ages	Iliamna	Iliamna Pedro Ponds	8/27/1995		244
Ages	Iliamna	Iliamna Pedro Ponds	8/24/1997		2
Ages	Iliamna	Iliamna Pedro Ponds	8/27/1998		187
Ages	Iliamna	Iliamna Pedro Ponds	8/5/1999		144
Ages	Iliamna	Iliamna Pedro Ponds	8/15/1999		24
Ages	Iliamna	Iliamna Pedro Ponds	8/19/1999		25
Ages	Iliamna	Iliamna Pedro Ponds	8/21/1999		43
Ages	Iliamna	Iliamna Pedro Ponds	8/25/1999		38
Ages	Iliamna	Iliamna Pedro Ponds	1/1/1900		1
Ages	Iliamna	Iliamna Pedro Ponds	8/23/2002		1
Ages	Iliamna	Iliamna Pedro Ponds	8/17/2003		16
Ages	Iliamna	Iliamna Pedro Ponds	8/19/2003		11
Ages	Iliamna	Iliamna Pedro Ponds	8/21/2003		6
Ages	Iliamna	Iliamna Pedro Ponds	8/23/2003		1
Ages	Iliamna	Iliamna Pedro Ponds	8/27/2003		2
Ages	Iliamna	Iliamna Pedro Ponds	8/29/2003		4
CreekWalk	Iliamna	Iliamna Pedro Ponds	7/21/2008	0	
CreekWalk	Iliamna	Iliamna Pedro Ponds	7/24/2008	0	
CreekWalk	Iliamna	Iliamna Pedro Ponds	7/26/2008	81	
CreekWalk	Iliamna	Iliamna Pedro Ponds	7/29/2008	210	
CreekWalk	Iliamna	Iliamna Pedro Ponds	8/1/2008	614	
CreekWalk	Iliamna	Iliamna Pedro Ponds	8/4/2008	1477	
CreekWalk	Iliamna	Iliamna Pedro Ponds	8/7/2008	2126	
CreekWalk	Iliamna	Iliamna Pedro Ponds	8/10/2008	2490	
CreekWalk	Iliamna	Iliamna Pedro Ponds Bear Pond	8/13/2008	3190	43
CreekWalk	Iliamna	Iliamna Pedro Ponds Bear Pond	8/16/2008	4117	67
CreekWalk	Iliamna	Iliamna Pedro Ponds Bear Pond	8/19/2008	4301	59
CreekWalk	Iliamna	Iliamna Pedro Ponds Bear Pond	8/22/2008	3175	45
CreekWalk	Iliamna	Iliamna Pedro Ponds Bear Pond	8/25/2008	4736	63
CreekWalk	Iliamna	Iliamna Pedro Ponds Bear Pond	8/28/2008	4176	30
Ages	Iliamna	Iliamna Pedro Ponds Bear Pond	8/22/2009		1
Ages	Iliamna	Iliamna Pedro Ponds Bear Pond	8/19/2010		45

SampleType	Lake	StationName	DateSampled	Sockeye Live Counts	Otoliths collected
Ages	Iliamna	Iliamna Pedro Ponds Bear Pond	8/22/2010		55
Ages	Iliamna	Iliamna Pedro Ponds Berg's Pond	8/13/2004		2
Ages	Iliamna	Iliamna Pedro Ponds Berg's Pond	8/27/2005		1
Ages	Iliamna	Iliamna Pedro Ponds Berg's Pond	8/4/2006		1
Ages	Iliamna	Iliamna Pedro Ponds Big Pond	8/21/2005		22
Ages	Iliamna	Iliamna Pedro Ponds Big Pond	8/27/2005		71
Ages	Iliamna	Iliamna Pedro Ponds Big Pond	8/22/2009		44
Ages	Iliamna	Iliamna Pedro Ponds Big Pond	8/25/2009		21
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/13/2004		2
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/4/2006		4
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/14/2006		20
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/20/2006		10
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/24/2006		22
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/28/2006		24
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/13/2007		2
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/16/2007		7
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/19/2007		20
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/22/2007		16
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/25/2007		7
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/19/2009		1
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/16/2010		49
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/19/2010		50
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/16/2012		142
Ages	Iliamna	Iliamna Pedro Ponds Pond 1	8/4/2006		1
Ages	Iliamna	Iliamna Pedro Ponds Pond 1	8/8/2006		2
Ages	Iliamna	Iliamna Pedro Ponds Pond 1	8/17/2006		7
Ages	Iliamna	Iliamna Pedro Ponds Pond 1	8/13/2007		4
Ages	Iliamna	Iliamna Pedro Ponds Pond 1	8/16/2007		12
Ages	Iliamna	Iliamna Pedro Ponds Pond 1	8/19/2007		39
Ages	Iliamna	Iliamna Pedro Ponds Pond 1	8/22/2007		27
Ages	Iliamna	Iliamna Pedro Ponds Pond 1	8/22/2009		1
Ages	Iliamna	Iliamna Pedro Ponds Pond 1	8/16/2010		100
Ages	Iliamna	Iliamna Pedro Ponds Pond 1	8/17/2012		149
Ages	Iliamna	Iliamna Pedro Ponds Pond 1A	8/22/2009		1
Ages	Iliamna	Iliamna Pedro Ponds Pond 2	8/11/2006		1
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/15/1999		8
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/19/1999		16
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/21/1999		43
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/17/2003		57
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/19/2003		19
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/21/2003		35
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/23/2003		12
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/25/2003		3
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/27/2003		6
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/13/2004		28
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/16/2004		52
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/19/2004		85
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/23/2004		30
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/15/2005		2
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/18/2005		2
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/21/2005		2
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/24/2005		11
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/27/2005		9
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/4/2006		3
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/8/2006		17
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/11/2006		19
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/14/2006		20

SampleType	Lake	StationName	DateSampled	Sockeye Live Counts	Otoliths collected
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/17/2006		10
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/20/2006		11
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/24/2006		25
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/28/2006		6
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/3/2007		2
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/10/2007		18
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/16/2007		25
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/22/2007		20
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/7/2008		1
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/10/2009		6
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/13/2009		20
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/16/2009		30
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/19/2009		28
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/22/2009		27
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/25/2009		38
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/16/2010		37
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/19/2010		29
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/22/2010		31
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/25/2010		2
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/16/2012		65
Ages	Iliamna	Iliamna Pedro Ponds Bear Pond	8/30/2013		1
Ages	Iliamna	Iliamna Pedro Ponds Bear Pond	8/13/2014		2
Ages	Iliamna	Iliamna Pedro Ponds Big Pond	8/30/2013		3
Ages	Iliamna	Iliamna Pedro Ponds Big Pond	8/16/2014		3
Ages	Iliamna	Iliamna Pedro Ponds Big Pond	8/19/2014		9
Ages	Iliamna	Iliamna Pedro Ponds Big Pond	8/22/2014		29
Ages	Iliamna	Iliamna Pedro Ponds Big Pond	8/24/2014		1
Ages	Iliamna	Iliamna Pedro Ponds Grass Pond	8/13/2014		1
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/30/2013		2
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/13/2014		1
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/19/2014		3
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/22/2014		6
Ages	Iliamna	Iliamna Pedro Ponds Trail Pond	8/24/2014		7
CreekWalk	Nerka	Nerka Berm Creek	7/26/2006	602	
CreekWalk	Nerka	Nerka Berm Creek	7/30/2006	833	244
CreekWalk	Nerka	Nerka Berm Creek	8/7/2007	969	149
CreekWalk	Nerka	Nerka Berm Creek	8/8/2008	1902	224
CreekWalk	Nerka	Nerka Berm Creek	8/5/2009	370	50
CreekWalk	Nerka	Nerka Berm Creek	7/31/2010	226	
CreekWalk	Nerka	Nerka Berm Creek	8/4/2010	601	106
CreekWalk	Nerka	Nerka Berm Creek	8/5/2011	187	113
CreekWalk	Nerka	Nerka Berm Creek	8/4/2012	664	208
CreekWalk	Nerka	Nerka Berm Creek	7/31/2013	515	149
CreekWalk	Nerka	Nerka Berm Creek	7/24/2014	1665	
CreekWalk	Nerka	Nerka Berm Creek	8/2/2014	1041	113
CreekWalk	Nerka	Nerka Seventh Creek	8/10/2009	197	59
CreekWalk	Nerka	Nerka Seventh Creek	7/31/2010	1	
CreekWalk	Nerka	Nerka Seventh Creek	8/10/2010	18	
CreekWalk	Nerka	Nerka Seventh Creek	8/6/2011	31	
CreekWalk	Nerka	Nerka Seventh Creek	8/5/2012	614	161
CreekWalk	Nerka	Nerka Seventh Creek	8/2/2013	463	128
Ages	Beverley	Beverley B9-B12 Beaches	9/14/1951		201
Ages	Beverley	Beverley B9-B12 Beaches	9/16/1952		40
Ages	Beverley	Beverley B9-B12 Beaches	9/14/1954		80
Ages	Beverley	Beverley B9-B12 Beaches	9/16/1955		80
Ages	Beverley	Beverley B9-B12 Beaches	9/18/1958		120
Ages	Beverley	Beverley B9-B12 Beaches	9/10/1959		240
Ages	Beverley	Beverley B9-B12 Beaches	9/13/1960		379
Ages	Beverley	Beverley B9-B12 Beaches	9/17/1961		44
Ages	Beverley	Beverley B9-B12 Beaches	9/17/1963		200

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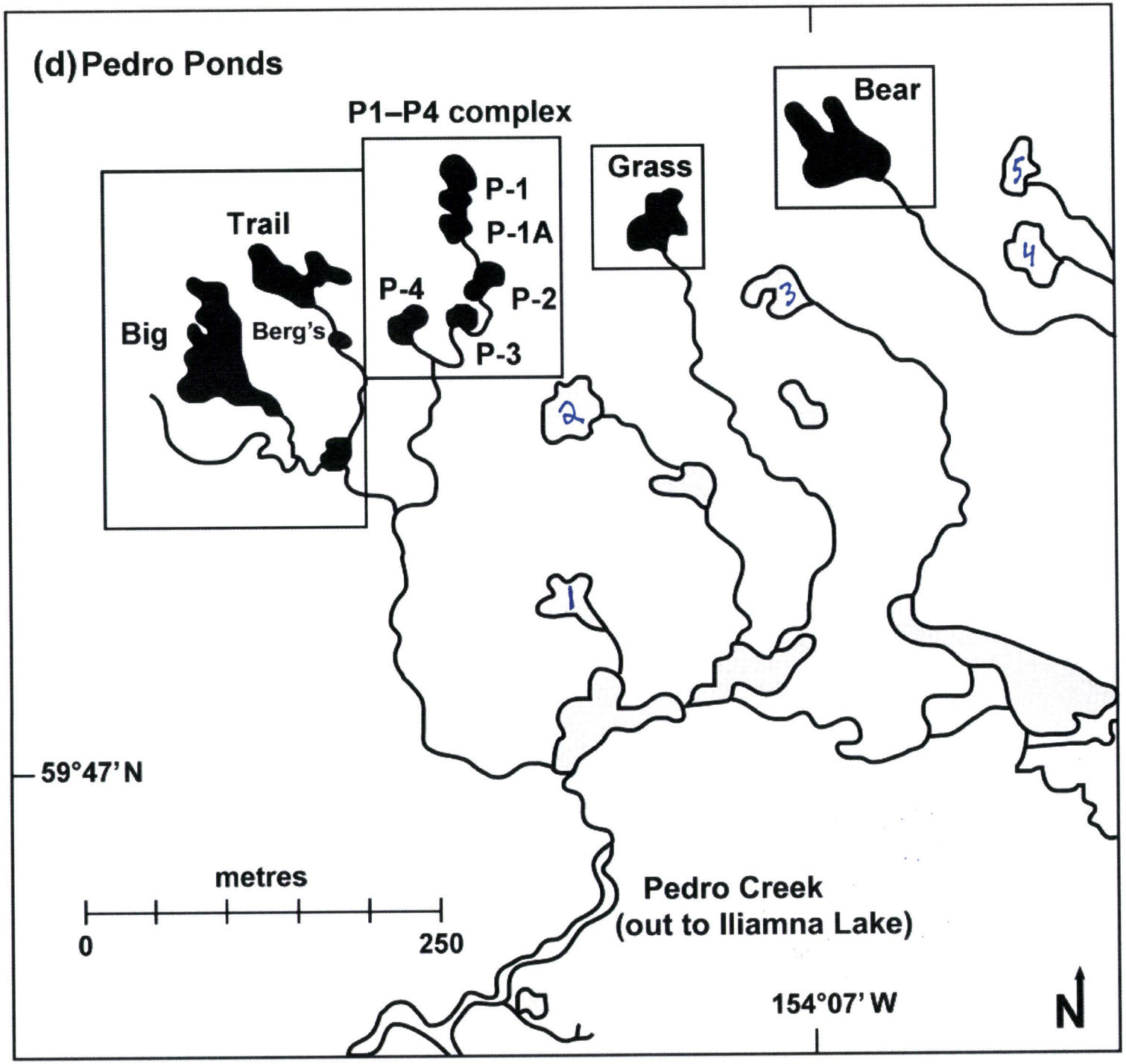
(d) Pedro Ponds
P1–P4 complex
Bear
Grass
Trail
P-1
P-1A
P-4
P-2
P-3
Big
Berg's
1
2
3
4
5
59°47' N
metres
0
250
Pedro Creek
(out to Iliamna Lake)
154°07' W
N

Population dynamics and asynchrony at fine spatial scales: a case history of sockeye salmon (*Oncorhynchus nerka*) population structure in Alaska, USA

Thomas P. Quinn, Harry B. Rich, Jr., Dido Gosse, and Nicolas Schtickzelle

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Abstract: Pacific salmon (*Oncorhynchus* spp.) exemplify the ways in which populations are structured by homing and the abiotic factors affecting their dynamics in discrete breeding and rearing habitats. What is the finest spatial scale of their population structure, and where do clusters of spatially proximate breeding groups lie along the continuum from isolated populations – metapopulation – patchy panmictic population? To investigate these questions, we monitored sockeye salmon, *Oncorhynchus nerka*, spawning in a complex of habitats ~1 km apart, joining to form a single stream flowing into Iliamna Lake, Alaska, USA. Annual surveys revealed levels of asynchrony in productivity that were comparable with values reported for sockeye salmon spawning in separate streams flowing into lakes elsewhere in Bristol Bay. A mark–recapture study revealed very little movement of spawning adults among habitats. The ponds occupied at highest density varied among years, and salmon consistently arrived and spawned later in one pond than the others. These results are consistent with the hypothesis that the salmon structured as a small-scale metapopulation rather than a single panmictic population.

Résumé : Les saumons du Pacifique (*Oncorhynchus* spp.) illustrent bien les façons dont les populations sont structurées par leur comportement de retour à la frayère natale et par les facteurs abiotiques qui affectent leur dynamique dans des habitats discontinus de reproduction et d'élevage. Quelle est donc l'échelle spatiale la plus fine de leur structure démographique? Où se placent les regroupements de peuplements de reproducteurs rapprochés dans l'espace le long du continuum formé par les populations isolées, la métapopulation et la population panmictique à répartition contagieuse? Afin de répondre à ces questions, nous avons suivi des saumons rouges, *Onchorhynchus nerka*, qui se reproduisent dans un complexe d'habitats, éloignés l'un de l'autre d'environ 1 km, puis réunis pour former un seul cours d'eau qui se jette dans le lac Iliamna, Alaska, É.-U. Des inventaires annuels révèlent des niveaux d'asynchronisme dans la productivité qui se comparent aux valeurs signalées chez les saumons rouges qui fraient dans des cours d'eau séparés, tributaires de lacs ailleurs dans la baie de Bristol. Une étude de marquage–recapture montre qu'il y a très peu de déplacements des adultes en fraie entre les habitats. Les étangs occupés aux densités maximales varient d'une année à l'autre et les saumons arrivent et fraient toujours plus tard dans l'un des étangs que dans les autres. Ces résultats concordent avec l'hypothèse qui veut que les saumons soient organisés en une métapopulation à petite échelle plutôt qu'en une seule population panmictique.

[Traduit par la Rédaction]

Introduction

Populations within species that are geographically isolated, exposed to different biotic and abiotic conditions, and with virtually no exchange of individuals should show little if any synchrony in dynamics, and extinction of one population would almost certainly be permanent without assisted re-establishment. However, even distant, isolated populations may show some synchrony if they are affected by common broad-scale influences (e.g., Lessios et al. 1984; Moran 1986; Guzmán et al. 1990). Proximate populations tend to be more synchronous because of the increased opportunity for exchange of individuals and the influence of common environmental factors (Liebhold et al. 2004; Ranta et al. 1995). With increasing proximity, extinct populations are more likely to be re-established, and declining populations "rescued" by dispersal. Such complexes of populations, showing (*i*) discrete habitat distribution, (*ii*) some level of

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asynchrony in population dynamics, and (*iii*) loose but important connections via dispersal events have been termed "metapopulations" (we use here the term metapopulation in a relatively broad sense, referring to any type of spatially structured set of populations displaying these three conditions: see Schtickzelle and Quinn (2007) and references therein).

Rates of dispersal vary as a function of the species' capacity for locomotion and the tendency to form home ranges or, if migratory, return to the natal site to breed. Anadromous fishes (e.g., Atlantic salmon (*Salmo salar*) and Pacific salmon (genus *Oncorhynchus*)) are a paradox in this regard because their migrations allow populations from widely separated breeding sites to experience common conditions while feeding at sea (Hansen and Quinn 1998) but then return and spawn in their natal rivers (Hendry et al. 2004; Quinn 1993). Even very proximate breeding populations may be discrete, as indicated by differences in selectively neutral genetic markers, persistent phenotypic differences, or both (Lin et al. 2008*a*, 2008*b*), and salmon can home to specific habitat units within a single small stream (Quinn et al. 2006).

Although famous for their homing tendency, salmon also display ecologically important dispersal. Most populations were established since the last glacial retreat, an on-going process in some areas (Milner et al. 2000; Milner and York 2001). Tagging studies also reveal small but persistent levels of "straying" from natal sites (Candy and Beacham 2000; Quinn et al. 1991). In addition to this capacity for exchange of individuals, the migratory life history of salmon causes correlations in abundance and survival over a range of spatial scales resulting from common environmental conditions (e.g., Mueter et al. 2005; Pyper et al. 2005; Rogers and Schindler 2008). Anadromous fishes show less synchrony in recruitment patterns, at a given spatial scale, than marine fishes but more than freshwater fishes, consistent with the roles of dispersal, shared environmental conditions, and population structure (Lande et al. 1999; Myers et al. 1997).

The metapopulation concept is important for understanding salmon population dynamics and for conservation (Cooper and Mangel 1999; Rieman and Dunham 2000; Schtickzelle and Quinn 2007). Complex population structure can buffer the effects of changing conditions, providing a "portfolio effect", and stabilizing overall abundance (e.g., Hilborn et al. 2003; Greene et al. 2010; Schindler et al. 2010). At finer spatial scales, research on Chinook salmon (*Oncorhynchus tshawytscha*) breeding within a large basin indicated that as adult abundance decreased, the counts became more synchronous among different sites, and fewer breeding sites were used (Isaak and Thurow 2006; Isaak et al. 2003). As the authors noted, both of these features would tend to increase extinction risk.

We report here an investigation into the spatial structure and dynamics of sockeye salmon (*Oncorhynchus nerka*) spawning in a series of small, interconnected ponds that flow into Iliamna Lake, Alaska, via a single stream. In contrast to the work on Chinook salmon in Idaho, where the spawning sites were ~10–200 km apart, these sites are ~1 km apart. The habitat is essentially unaltered by human activity, and the populations are entirely natural and native. Well-managed, sustainable fisheries are the only significant human factor affecting their dynamics at present (Hilborn et al. 2003). The purpose of the study was to determine where the breeding aggregations of sockeye salmon in the Pedro Bay pond system habitats fall on the continuum between fully independent populations, a metapopulation, and a single, freely interbreeding patchy population (Schtickzelle and Quinn 2007).

There is no single "litmus paper test" to determine whether or not the salmon breeding aggregations are independent populations or parts of a single panmictic population, so our approach was to examine a number of attributes of the populations to estimate, by weight of evidence, their level of interaction. We combined annual counts of adult fish (ranging from 0 to >1000 in individual ponds) with age composition data and fishery exploitation rates to generate spawner–recruit relationships for four habitat units within the complex. A tagging experiment with adult salmon indicated very limited movement among ponds within the season. With this validation of the counts (i.e., individual fish are not counted in multiple ponds in a season), we constructed a correlation matrix of spawner–recruit estimates to assess the extent to which the salmon breeding in these ponds function as one or a series of independent populations. We then integrated the data on salmon in these ponds with data at three progressively larger spatial scales: (*i*) annual returns to the entire Kvichak River system; (*ii*) the commercial fishing district that includes this river system and two other proximate, large river systems; and (*iii*) the other districts that comprise the Bristol Bay sockeye salmon complex. The Kvichak River system is noteworthy because it has had very large (>47 million adults in 1965) but variable sockeye salmon runs (Eggers and Rogers 1987; Hilborn et al. 2003). The pond system is interesting because its spring-fed nature results in relatively stable physical attributes but there are strong biotic controls from density-dependent competition for breeding space and predation from brown bears (*Ursus arctos*) (Quinn and Kinnison 1999).

Materials and methods

Site description and survey methods

The study was conducted on sockeye salmon spawning near the village of Pedro Bay, Alaska, in a series of small ponds and streams that flow into the northeastern part of Iliamna Lake, in the Bristol Bay region of Southwest Alaska (outlet: 59°47′38″N, 154°7′20″W; Fig. 1). The spring-fed ponds (~100 to ~2000 m^2) are relatively uniform in depth (ca. 0.2–0.4 m), with low (at ~5 °C) and stable temperatures throughout the summer (Quinn and Kinnison 1999; Quinn et al. 1999). The substrate is dominated by fine granite sand ~1 mm in diameter over a bed of medium-sized cobble (Quinn et al. 1995). Very small streams ~1–2 m wide and 10–20 cm deep connect the ponds, which collect and flow into the lake via a single outlet. Upon emergence in spring, the juveniles migrate from the pond system to the lake, where they feed in common with juveniles from many other populations before migrating to sea 1 or 2 years later.

We recorded the locations of all fish in discrete ponds and streams, including three large ponds (Bear Pond, 1820 m^2 and 41.6 cm deep; Trail Pond, 1135 m^2 and 38.5 cm deep; Grass Pond, 1070 m^2 and 19.9 cm deep); the ponds do not have official names but those that we used previously (Quinn

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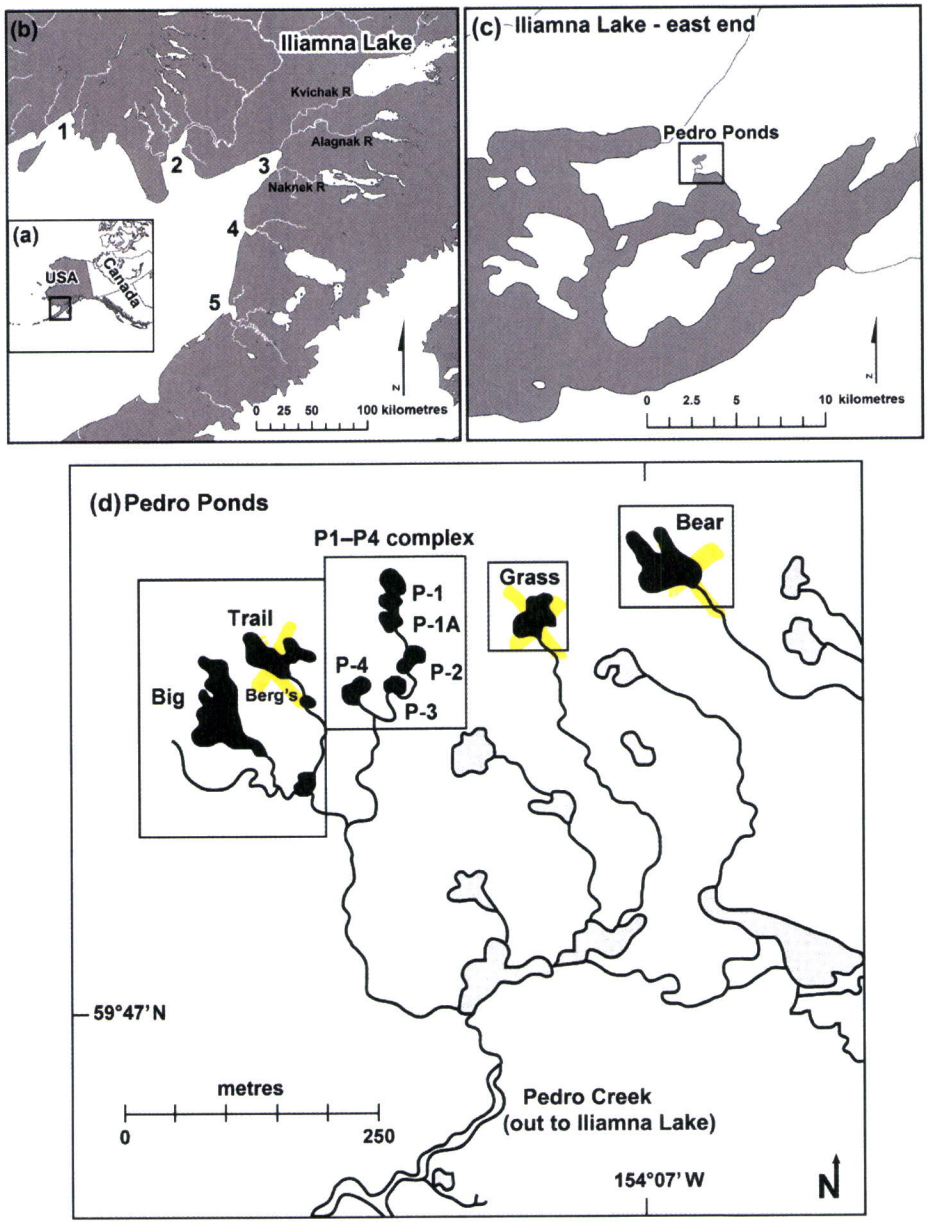
Fig. 1. Map of western Alaska, USA, showing the location of Iliamna Lake and the suite of ponds and streams near Pedro Bay where sockeye salmon were studied. In panel (*b*), the numbers correspond to the commercial fishing districts: (1) Togiak, (2) Nushagak, (3) Naknek–Kvichak, (4) Egegik, and (5) Ugashik.



and Kinnison 1999) are retained here. We also recorded fish in a series of smaller ponds and the streams between them, dominated by Pond 1 (695 m^2 and 26.0 cm deep) but including other ponds 165–355 m^2 and streams 17–90 m long. This group, which we refer to as the P1–P4 complex, had a total area of 2368 m^2.

Adult sockeye salmon (the only salmonid other than small Dolly Varden (*Salvelinus malma*) regularly seen in the ponds) were counted during annual surveys. Two or more people walked through the ponds and streams, counting live sockeye salmon and dead salmon in the water and adjacent riparian areas. Carcasses were identified to sex, mode of death (senescent or bear killed), measured for length (mid-eye to hypural plate) unless the condition (e.g., from partial consumption by a bear) or sheer number of carcasses necessitated subsampling, and then moved sufficiently far into the riparian zone that they would not be counted again. In some years, the salmon were so scarce that only small scraps of tissue were found that the bears had not consumed, notably pyloric caeca and pieces of liver, and we were able to identify the presence or absence of the conspicuous nests of salmon in the substrate. In the absence of live fish, these were taken as evidence that salmon had been present.

Analysis of abundance patterns

The surveys always began by early to mid-August when salmon abundance was increasing and included a survey on 24 or 25 August. The cumulative count of dead salmon to

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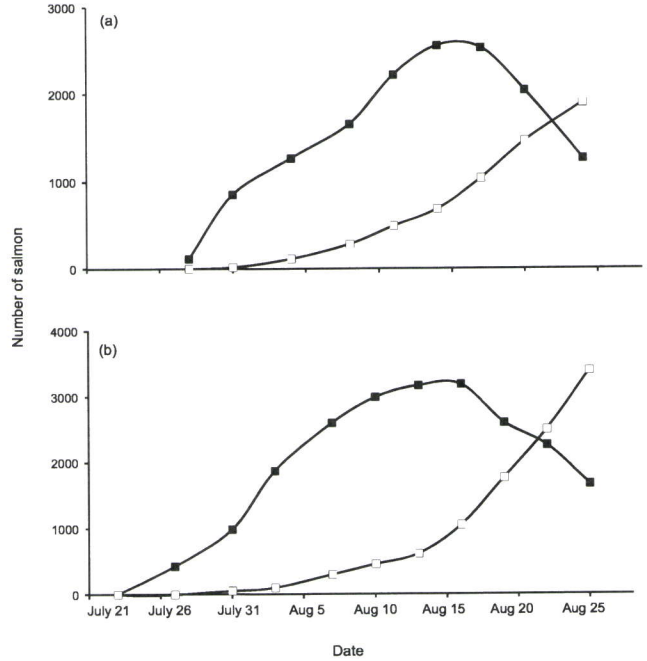
that date (24 or 25 August) plus that day's live count was used as the annual index of abundance in each pond and stream. This value underestimates the total number of salmon because some probably arrived after that date and some were probably taken by bears farther from the ponds than we routinely searched (Quinn et al. 2009) and so were missed. However, the number of live salmon was declining and the cumulative number of dead salmon rapidly increasing (Fig. 2), so the 24–25 August counts are a reliable index of abundance. We grouped ponds 1–4 and the streams between them into one complex (P1–P4 complex) and compared their total counts (transformed to density to facilitate comparison) with those from Bear, Grass, and Trail ponds. Pooling the data from the streams and ponds in the P1–P4 complex precluded detection of some fine-scale patterns (e.g., comparisons of dynamics between streams and ponds within this complex), but in some cases, it was difficult to determine the habitat to which the fish should be assigned if the carcass was on the downstream or upstream edge of the pond or deposited on land by a bear at a point equidistant between two units. In addition, many of the fish in the lower habitats and especially the streams were killed, likely on their way to habitats farther upstream.

To place the abundance levels of salmon in the ponds in the context of broader spatial and population scales, we used abundance data provided by the Alaska Department of Fish and Game (ADF&G) from 1956 to 2010. First, there were aerial counts of sockeye salmon in the pond complex, treated as a single unit, on one day each year, except that surveys were not carried out in 1977, 1984, 1986, 1988–1990, 2001, and 2003. These counts were expanded for the exploitation rate on the complex of populations in the Kvichak River system, including Iliamna Lake and its tributaries, and so are estimates of the total run to the ponds each year. Second, the annual counts of sockeye salmon ascending the Kvichak River, made visually from towers overlooking the river, were combined with the catch to estimate the total run to this system each year. Third, we obtained data on the total run (catch plus escapement) to the other rivers in the Naknek–Kvichak district that drain together into Kvichak Bay: the Naknek and Alagnak rivers. All these rivers are also dominated numerically by sockeye salmon and experience similar climate regimes, and the juveniles enter marine waters very close to each other, but the adults spawn in different rivers, and the juveniles rear in different lakes prior to seaward migration. We then examined data on the combined runs of sockeye salmon to all of Bristol Bay (the Naknek–Kvichak district plus the Egegik, Ugashik, Nushagak, and Togiak districts; Fig. 1). With these data sets we (*i*) compared coefficients of variation at the Pedro Bay pond system, Kvichak River, Naknek–Kvichak district, and Bristol Bay scales, (*ii*) correlated the runs to the pond system with those to the Kvichak River system, Naknek–Kvichak district, and Bristol Bay, and (*iii*) correlated the runs among the three rivers within the Naknek–Kvichak district.

Synchrony of local population dynamics

In a metapopulation context, synchrony refers to the level of correlation between dynamics of the local populations, so counts are illustrative but less useful than population growth rate (i.e., the number of recruits produced per spawner).

Fig. 2. Counts of live (solid squares) and cumulative dead (open squares) sockeye salmon in (*a*) 2006 and (*b*) 2007 in the Pedro Bay pond system, illustrating that surveys through 25 August include most of the salmon present in each year.



Sockeye salmon in this system commonly mature at ages 4, 5, and 6 years, and in years when sufficient carcasses were present, we removed the otoliths (ear bones) for age determination. These age data allowed us to allocate fish seen in a given year to the years in which they had been spawned and thus to construct brood tables. We pooled age composition data from the entire pond complex in years when sufficient samples could be obtained, but a combination of low returns and intense bear predation made it impossible to obtain adequate samples in 1996, 1997, 2000, 2001, and 2002. For these years, we used the average age composition based on pooled samples from all years (n = 3093, age 4 = 61.4%, age 5 = 37.1%, age 6 = 1.5%) to estimate spawner–recruit relationships. We also expanded the observed numbers of salmon to account for the fish that were caught using age-specific catch and escapement data provided by ADF&G (Rogers and Schindler 2008). The use of common ages assumes that the ponds do not differ in average age, and this is supported by the similarity in long-term average lengths of salmon (T.P. Quinn, unpublished data).

The dynamics of salmon populations are affected by density-dependent processes because competition for breeding space depresses production of juveniles (Essington et al. 2000). The ponds are used for spawning but the juveniles migrate to Iliamna Lake to grow, so only density dependence related to spawning habitat use was considered. To compare patterns of productivity among populations, we first fit a Ricker spawner–recruit model to the data from the four populations. After eliminating cases with zero values and recent years for which recruits have not returned yet, we had 40 values. The following model was fitted using linear regression:

$$(1) \qquad \ln(R_{it}/S_{it}) = \beta_0 + \beta_1(S_{it}/A_i) + \varepsilon_{it}$$

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where R_{it} recruits (expanded for catch) were spawned in population i in year t as the progeny of S_{it} spawners reproducing in this population occupying a habitat of area A_i. We then computed the correlations between dynamics of each pair of populations through Pearson's correlation coefficient of pairwise residuals ε_{it}, considered as indices of higher (or lower) productivity compared with what was expected given local density, as in previous studies (Peterman et al. 1998; Rogers and Schindler 2008).

Tagging

The use of data from the annual surveys to assess the functional independence of the populations depends on the assumption that the fish do not routinely and frequently move among sites (i.e., that fish counted in a pond on one day do not get counted elsewhere on subsequent surveys). In addition, we wanted to validate our other assumption that the ponds we surveyed support the great majority of sockeye salmon in this system. To test these assumptions, we captured salmon with a beach seine net in Iliamna Lake at the mouth of Pedro Creek as they schooled prior to entering the pond system and tagged them on 29 July (n = 210) and 7 August (n = 142) in 2007 and 28 July (n = 128) and 5 August (n = 109) in 2008. Each fish was marked with a pair of uniquely lettered plastic disk tags, attached below the dorsal fin, and released on site. We surveyed the ponds every three days until 4 September in 2007 and 28 August in 2008, noting the locations of tagged salmon and their status when they were dead. For this purpose, we report the data at the level of the individual streams and ponds within the P1–P4 complex and also counted salmon in two other ponds: Big Pond (3072 m^2 and 54.5 cm deep) and Berg's Pond (185 m^2 and 26.7 cm deep). These are both situated downstream of Trail Pond and had not been surveyed consistently and so could not be included in the analysis of population dynamics.

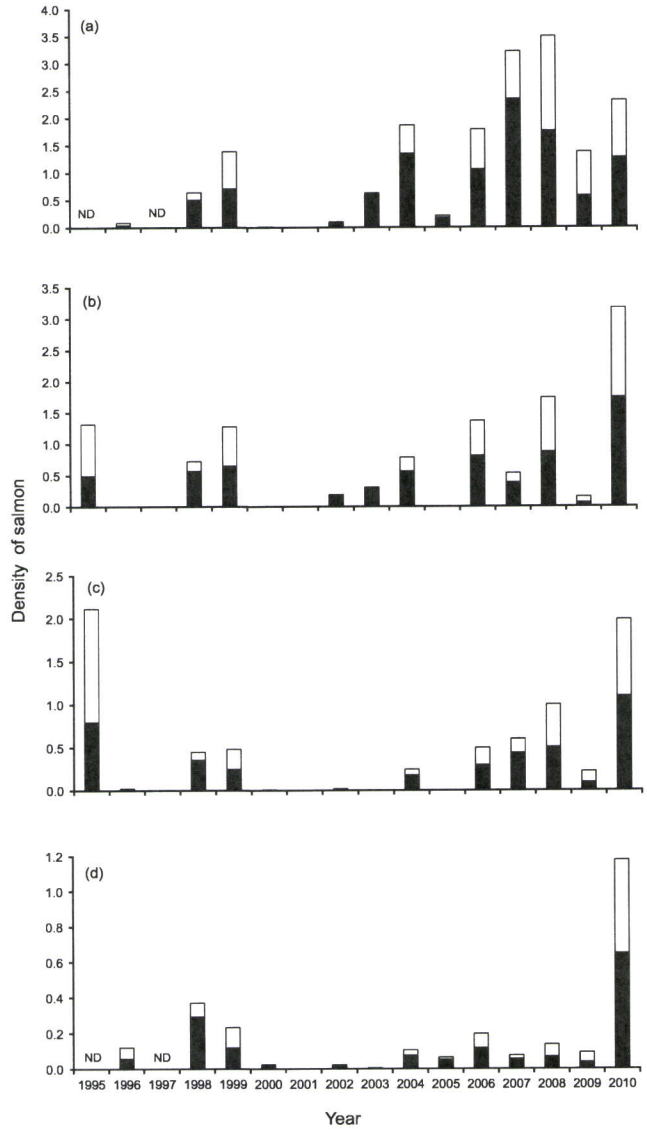
Most salmon were recovered as carcasses but some were still alive when the surveys ended, and others were seen repeatedly but then went missing, apparently transported by bears from the areas that we surveyed (Quinn et al. 2009). Salmon were categorized as having remained in one location within the pond system if they were seen there on at least three surveys (i.e., 9+ days). It is possible that some of the fish that were killed by bears might have moved later in their lives, but analysis indicated that most moves were early in the period of residence (see Results), so this is probably a small source of error. Salmon seen only once or twice were excluded from analysis.

Results

Patterns of abundance and density

Combined raw index counts in the ponds and creeks regularly surveyed (Bear, Grass, Trail, and the P1–P4 complex) from 1995 to 2010 ranged from 9 in 2001 to 7076 in 2010. Individual habitats had counts of zero on four occasions and counts <10 on six other occasions. In general, the habitats with the highest average density (fish·m^{-2}) were less variable (Trail Pond, average = 1.23 fish·m^{-2}, coefficient of variation (CV) = 97%; Grass Pond, 0.74 fish·m^{-2}, CV = 123%; P1–P4 complex, 0.40 fish·m^{-2}, CV = 139%; Bear Pond, 0.19 fish·m^{-2}, CV = 160%; Fig. 3). These data might suggest that Trail Pond

Fig. 3. Annual index densities (salmon·m^{-2}) of adult sockeye salmon in ponds (*a*, Trail Pond; *b*, Grass Pond; *c*, P1–P4 complex; *d*, Bear Pond) within the Pedro Bay system (solid bars) with expansion for fishery interceptions based on age-specific catch rates (open bars). ND, no data collected; other zero values indicate the absence of salmon. Note differences in *y*-axis scales.



was always occupied at high density and that the other ponds were filled only as the overall density increased, but this was not the case. Trail Pond had the highest density in eight years, but density was the highest in Grass Pond in three years, and Bear Pond (where average density was lowest) had the highest density in three years. Moreover, the proportion of salmon seen in Trail Pond was not highest when overall density was low, as would be the case if it was consistently occupied preferentially. In four of five years with low overall abundance (<500 salmon in all ponds), the percent in Trail Pond was below the overall average of 39.9%. Furthermore, regression analysis revealed no relationship between the total abundance of spawning salmon and the percent of all spawning salmon in Trail Pond (R^2 = 0.003, P = 0.84).

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Table 1. Matrix of movement data from the sockeye salmon tagged in 2007 and 2008, indicating the numbers of salmon that were initially observed in one pond and moved to other ponds or that died in the pond in which they were first seen (in bold).

	To						
From	Big	Berg's	Trail	P1–P4 complex	Grass	Bear	Total
Big Pond	**98**	3	26	2	2	0	131
Berg's Pond	0	**2**	8	0	0	0	10
Trail Pond	7	2	**108**	0	1	0	118
P1–P4 complex	0	0	1	**43**	0	0	44
Grass Pond	0	0	0	1	**38**	0	39
Bear Pond	0	0	0	0	0	**5**	5
Total	105	7	143	46	41	5	347

Note: The ponds are ordered from left to right in approximate west–east order.

As an additional way to assess possible differentiation among the breeding groups, we calculated the percent of salmon alive at the end of the survey period (24 or 25 August) in each year. Populations spawning earlier in the season would have more salmon dead on a fixed date than those spawning later. The averages, based on 56 estimates among the four ponds, were 27% alive in Grass Pond, 29% in the P1–P4 complex, 42% in Trail Pond, and 89% in Bear Pond. Analysis of variance (ANOVA) on the data after arcsine square root transformation indicated significant differences ($F_{[3,50]} = 17.06$, $P < 0.001$). Based on Tukey's post hoc test, a higher percent of salmon were alive in Bear Pond than any other pond ($p < 0.001$), but the other ponds were similar (Grass to Trail, $P = 0.26$; Grass to P1–P4 complex, $P = 0.99$; Trail to P1–P4 complex, $P = 0.44$).

Movements of tagged salmon

Of the 589 tagged salmon, 455 (77%) were seen at least once, supporting the assumption that our surveys included most of the habitats supporting sockeye salmon in this system. In 2007 and 2008, we observed 186 and 161 sockeye salmon, respectively, with sufficient frequency to meet our criteria for determining movement patterns. Females showed a slightly greater tendency to remain rather than move (88% vs. 82% for males), but the difference was not significant ($\chi^2 = 1.83$, 1 df, $p = 0.18$) so the sexes were pooled for subsequent analyses. Of the 347 fish whose movements could be examined, 294 (85%) were only seen in a single pond or within the P1–P4 complex, and 53 were observed in more than one pond (Table 1). The movements among the other ponds showed close correspondence to their geography. Of the 53 detected movements, 48 (91%) were within three ponds in close proximity to each other: Big, Berg's, and Trail. These movements were primarily in an upstream direction; 26 fish first seen in Big Pond subsequently settled in Trail Pond but only seven fish moved from Trail Pond down to Big Pond. The more isolated ponds (Bear, Grass, and the P1–P4 complex) showed limited movement to and from other ponds (Table 1). In part because of the tendency to move upstream, analysis of the number of fish moving between sites as a function of their distance was not informative ($R^2 = 0.08$, $n = 30$, for a logarithmic fit with distance between sites as the independent variable and number of salmon moving as the dependent variable). Removal of one outlier (the 26 fish that moved from Big Pond to Trail Pond) improved the fit but still explained little of the variation ($R^2 = 0.15$). The distances between sites fell into two categories and so analyses were conducted to compare the movements between nearby sites (140–365 m apart, $n = 12$) and distant sites (1100–1780 m apart, $n = 18$). The pairs of nearby sites had more exchange (mean = 4.1 fish vs. 0.03 between distant sites, $t = 1.77$, df = 11, $P = 0.05$, one-tailed test), and more of the pairs of nearby sites had at least one fish move than between the distant sites (7 of 12 vs. 4 of 18, $\chi^2 = 4.04$, 1 df, $P = 0.044$).

Synchrony of population dynamics at local and broader spatial scales

As expected, due to density dependence, productivity (number of recruits per spawner) decreased with spawner density (Spearman correlation on ln-transformed *R/S*: $r = -0.40$, $n = 40$, $P = 0.01$). The small sample size and measurement errors associated with very small populations and intense bear predation reduced the power to test the functional form of this decrease; an exponential decrease of *R/S* with density as modeled by the Ricker equation was not significant ($R^2 = 0.064$, $P = 0.117$). However, density dependence at breeding sites is well established for sockeye salmon (e.g., Essington et al. 2000). We therefore corrected productivity estimates for this density dependence by computing residuals of the Ricker equation as fitted on the data: $\ln(R_{it}/S_{it}) = 1.254 - 1.251(S_{it}/A_i) + \varepsilon_{it}$. Correlations of these residuals between pairs of populations within the Pedro Pond system averaged 0.72 but ranged from 0.46 to 0.97 (Table 2). As an additional comparison, we computed a matrix of correlations based on the raw estimates of recruits per spawner without adjustment for density dependence. The mean correlation was 0.26 with a range from –0.23 between Bear and Grass ponds to 0.70 between Bear Pond and the P1–P4 complex.

To determine whether the correlations in recruitment among the ponds within years varied with density, we took the total number of spawning salmon in the four major ponds in the 10 years for which all were surveyed and calculated the CV of the *R/S* values. This analysis revealed no relationship between CV(*R/S*) and density ($R^2 = 0.05$).

The ponds have been surveyed from airplanes in all but eight of the years from 1956 and 2010. During these years, the estimates for the pond complex, expanded for the catch, averaged 7924 sockeye salmon (standard deviation (SD) = 15538). Decreasing levels of variation, as indicated by the CV, were seen among years at increasing spatial scales: Pedro Ponds system = 196%, Kvichak River system = 99%,

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Table 2. Matrix of Pearson's correlation coefficients (r), with associated sample sizes (n) and P values, between time series of residuals from a Ricker spawner–recruit model (below diagonal) and between time series of raw spawner–recruit data (above diagonal) for sockeye salmon spawning in a series of pond habitats.

		Bear	Grass	Trail	P1–P4 complex
Bear	r		-0.23	0.08	0.70
	n		9	9	8
	P		0.545	0.831	0.05
Grass	r	0.46		0.29	0.26
	n	9		9	9
	P	0.211		0.444	0.505
Trail	r	0.76	0.46		0.46
	n	9	9		7
	P	0.017	0.215		0.297
P1–P4 complex	r	0.97	0.86	0.78	
	n	8	9	7	
	P	<0.0001	0.003	0.039	

Naknek–Kvichak District = 69%, Bristol Bay = 53%. The runs to the ponds were only 0.076% of the average run to the whole Kvichak River system (10 404 137, SD = 10 292 225), but there was a significant correlation between the counts (r = 0.678, n = 47, P < 0.001). The Kvichak River produced, on average, 68% of the sockeye salmon in the Naknek–Kvichak district (15 303 773, SD = 10 489 363) and 34% of the total run to Bristol Bay (30 610 193, SD = 16 259 860). The runs to the Pedro Bay pond system were significantly correlated with those in the district (r = 0.638, n = 47, P < 0.001) and Bristol Bay as a whole (r = 0.356, n = 47, P < 0.01). Interestingly, although the Kvichak River system dominated the Naknek–Kvichak district numerically, the Kvichak River runs were not correlated with those to the other watersheds, despite their proximity (Kvichak vs. Alagnak, r = –0.126, n = 55, P = 0.36; Kvichak vs. Naknek, r = –0.045, n = 55, P = 0.75). However, the runs to the other two watersheds were correlated with each other (Naknek vs. Alagnak, r = 0.432, n = 55, P < 0.01).

Discussion

The specific goal of this study was to determine where salmon breeding in a series of ponds falls along the continuum from fully independent populations to a metapopulation to a single panmictic population. Our analysis was based on the premise that independent, multiple populations should be characterized by (*i*) correlations in abundance or productivity that converge on values seen in other independent populations, (*ii*) limited in-season movement by adults among habitats, (*iii*) consistent differences in breeding date among sites, as this is characteristic of salmon populations (Brannon 1987; Stewart et al. 2002) and breeding timing is a highly heritable trait (Quinn et al. (2011) and references therein), and (*iv*) inconsistency in the habitat that is occupied at highest density among years. Given the imprecision in field-survey data and the continuum of possibilities from discrete populations to a single panmictic population, the nature of the analysis relies more on the weight of evidence rather than falsification of a null hypothesis. Our broader goal was to then place these breeding aggregations in the context of variability in sockeye salmon at progressively larger spatial scales to illustrate how population-level correlations change with scale.

The salient findings of this study were the considerable asynchrony in abundance and productivity and the very limited movements by adult sockeye salmon breeding in this complex of physically very proximate breeding sites. Other studies on much broader spatial scales have found comparable or even higher correlations in productivity. For example, Phelps et al. (2008) studied recruitment of common carp in 18 lakes in South Dakota and found pairwise correlation coefficients ranging from 0.74 to 0.99, even though no movement among lakes was possible. These high correlations were attributed to physical controls over recruitment, specifically temperature, precipitation, and wind, operating in common on all populations. Elsewhere in Bristol Bay, Rogers and Schindler (2008) reported correlations in productivity between pairs of sockeye salmon populations breeding in separate streams in two lakes in the same watershed. The correlations between pairs of populations averaged 0.68 in the smaller lake and 0.54 in the larger lake, only slightly lower than those that we observed (average = 0.72, including two values of 0.46). The populations reported by Rogers and Schindler (2008) can be assumed to be almost exclusively self-recruiting (i.e., very nearly complete homing by adults), based on persistent differences in life history traits and genetic analyses (e.g., Quinn et al. 2001; Lin et al. 2008*a*, 2008*b*; McGlauflin et al. 2011). The progeny would experience common biotic and abiotic conditions in the lake and at sea, so the extent of asynchrony presumably results from differences in survival by embryos in the gravel related to differences in the ways that the streams respond to common environmental conditions. For example, spring-fed streams might be less affected than those dominated by surface runoff during exceptionally cold winters.

The ponds and streams that we studied are much closer than those reported by Rogers and Schindler (2008), only two of which were <1 km apart, and the ponds are all spring

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fed, so they should experience more common conditions. The productivity results thus indicated a rather high degree of dynamical independence for such proximate breeding groups. It should be noted that errors in population assessment will tend to result in apparent asynchrony, and none of the assessments in this or similar studies is without error. Some fish likely entered after the last survey, and some were probably removed from the area by bears and not counted. However, the pond system was surveyed very carefully every three days and carcasses were removed to avoid multiple counting, so the counts are probably more accurate than most at this fine spatial scale. In comparison, the data examined by Rogers and Schindler (2008) included much longer time series but only a single survey in each year at each site. The gain in precision due to longer time series to estimate correlation coefficients is likely counterbalanced by the lower precision on individual counts.

The tagging data also supported the hypothesis that the populations are largely discrete, at least in terms of the breeding sites used by adults. Most detected movements were fish that briefly entered ponds while moving upstream, but once they reached their primary breeding site, they seldom moved elsewhere. This is consistent with other tagging studies on sockeye salmon showing limited movement within breeding areas in a single small stream (Rich et al. 2006) or beach (Hendry et al. 1995). The site fidelity of adults does not prove that they returned to the site where they were bred, but homing to the natal site at comparable spatial scales has been shown elsewhere (Quinn et al. 2006).

Given the extreme variation in recruitment, one might wonder whether the changes in abundance might have resulted from straying by salmon from other locations. For example, in 2001, we counted only nine salmon and they produced 149 recruits. This level of productivity (16:1) is exceptional but by no means impossible, as major components of the Bristol Bay sockeye salmon complex have produced over 10 recruits per spawner on many occasions (Hilborn et al. 2003). The analysis of timing was also consistent with some level of population structure. Specifically, Bear Pond was occupied later than the other ponds, and timing differences characterize many salmon populations as this is a highly heritable trait in salmonids (e.g., Quinn et al. 2011). Bear Pond also had the lowest and most variable densities, so one might infer that it was simply less desirable as habitat and only used by late-arriving salmon when the other ponds were fully occupied. However, in three years, it had the highest densities, and in general, the habitat seems to be comparable with the other ponds. If anything, the greater area and depth make the salmon somewhat less vulnerable to predation by bears. The variation in rank order of occupancy (i.e., which pond had the most fish in a given year) was inconsistent with a model in which salmon seek the highest quality habitat and use other habitats only when crowding takes place. The ponds are spring fed and so highly stable, and there were no detectable changes in characteristics of the major ponds among years, so the highest quality habitats should have been consistently used year after year. The tagging data indicated that the vast majority of the fish went to one pond and remained there rather than moving from pond to pond as might be expected if they were comparing habitats.

Do these populations or other salmon population complexes qualify as metapopulations? Application of the metapopulation concept to salmon hinges on three criteria (Schtickzelle and Quinn 2007): (*i*) discreteness of the breeding habitat patches; if variation in habitat quality is gradual, the populations are poorly defined and the metapopulation theory does not apply; (*ii*) some asynchrony in the dynamics of local populations, reducing the likelihood of simultaneous stochastic extinction of all populations; and (*iii*) sufficient proximity among the breeding habitat patches to allow for dispersal and rescue events. Stewart et al. (2003*b*) presented evidence indicating some level of dynamical independence in sockeye salmon spawning on beaches in discrete islands in Iliamna Lake, despite genetic similarity and also high correlations in abundance among years (Stewart et al. 2003*a*). These beach populations might qualify as a metapopulation because the breeding sites are discrete, separated by entirely unsuitable deep water, and show the mix of independence and connection that characterizes metapopulations. The ponds and streams that we studied, on the other hand, present a more continuous range in breeding habitat quality. Salmon can spawn in all ponds and the streams between them, though substrate size, water depth, and bear predation make some sites less desirable than others. Without the data on limited movement and asynchrony in the abundance and productivity among ponds, it would have been easy to characterize it as a single population with some spatial variation in breeding habitat quality.

The interannual fluctuations in abundance of populations spawning in the Iliamna Lake system, as indicated by aerial surveys, were correlated but the extent varied among habitat types (Stewart et al. 2003*a*). Those spawning on island beaches were most closely correlated with other island beaches, and those spawning in rivers were less correlated with beaches and with other rivers. These patterns of correlations are consistent with common environmental influences; lake level, ice, and temperature would affect all beaches in common, whereas rivers would have more discrete processes affecting the salmon during spawning and embryo incubation. However, all juveniles rear in common in the lake, migrate to sea, and then return at the same time. Thus the total return to the ponds was significantly correlated with that to the entire Kvichak River system ($r = 0.678$, $n = 47$, $P < 0.001$). However, the returns to the Kvichak River system were not correlated with those to either of the nearby watersheds in the district, the Naknek and Alagnak river systems, though the Naknek and Alagnak returns were significantly correlated with each other. None of the watersheds has had any substantial shifts in habitat quality, as might affect recruitment and abundance in more developed regions (Moore et al. 2010). Rather, the Kvichak River system showed a pronounced cycle with a 5-year period for several decades (Eggers and Rogers 1987), whereas the other watersheds did not. The precise reasons why some populations or complexes of populations respond differently to common environmental changes are not clear but the implication, from conservation perspectives, is the importance of keeping a wide range of life history types and populations to maximize long-term success (Greene et al. 2010; Schindler et al. 2010).

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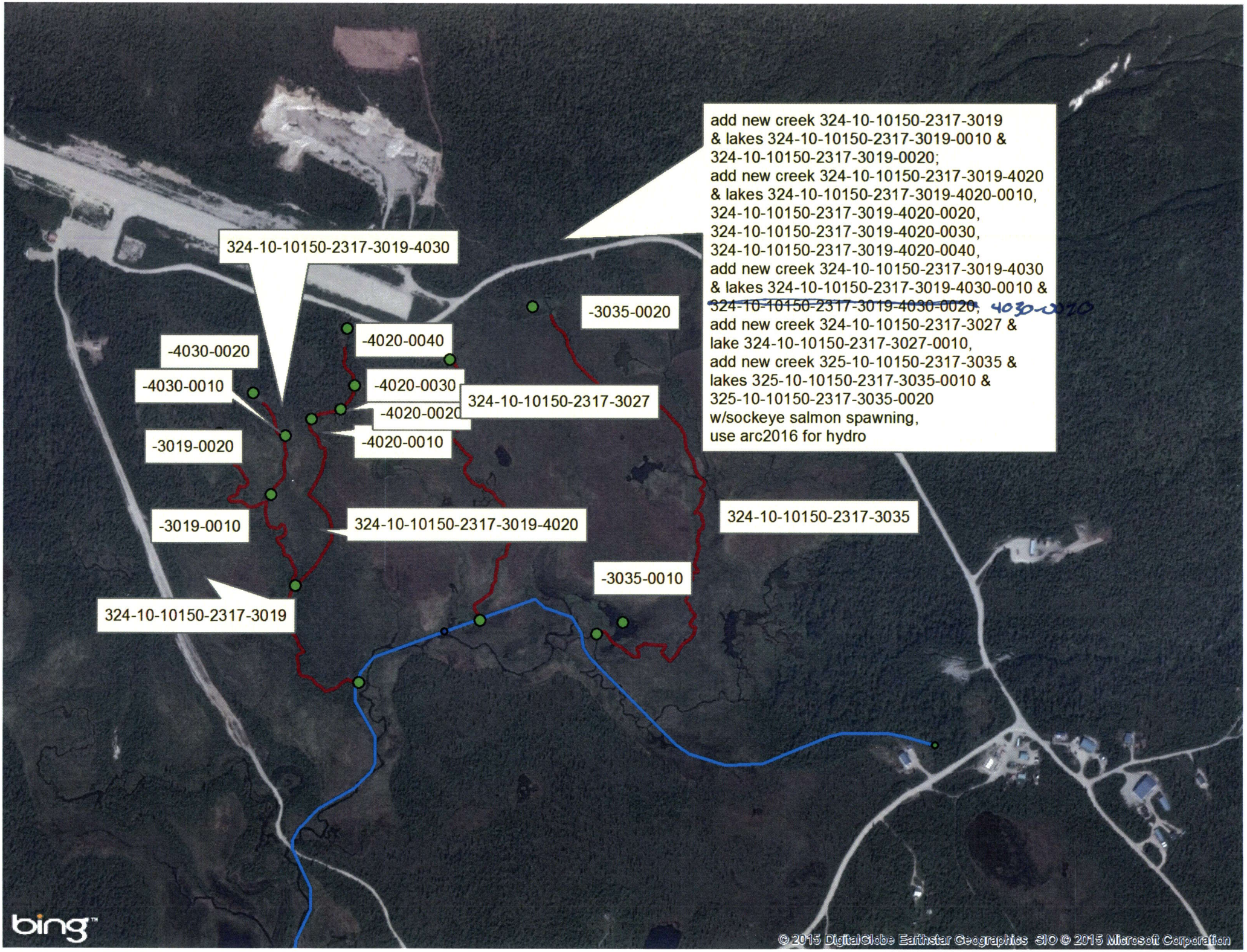
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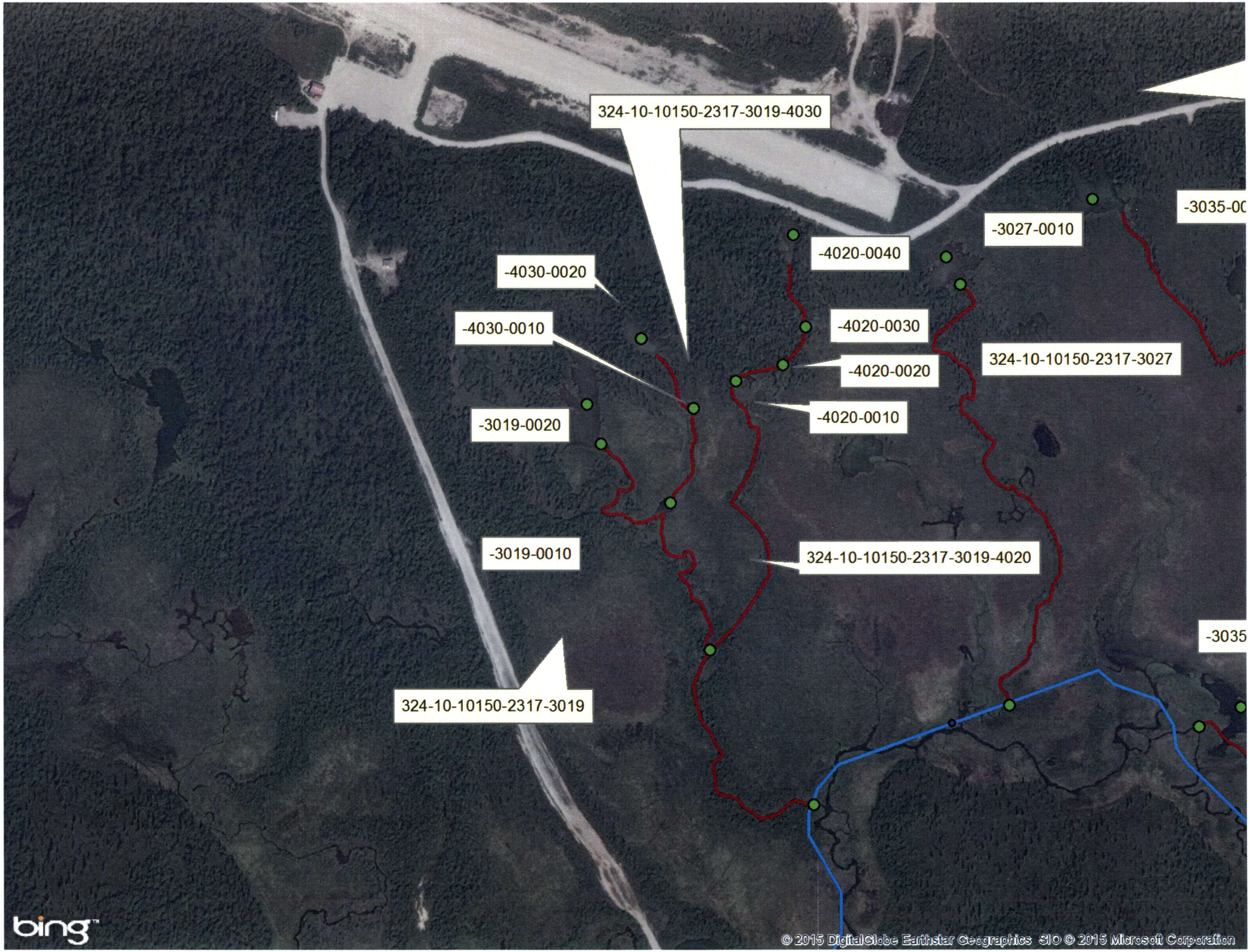
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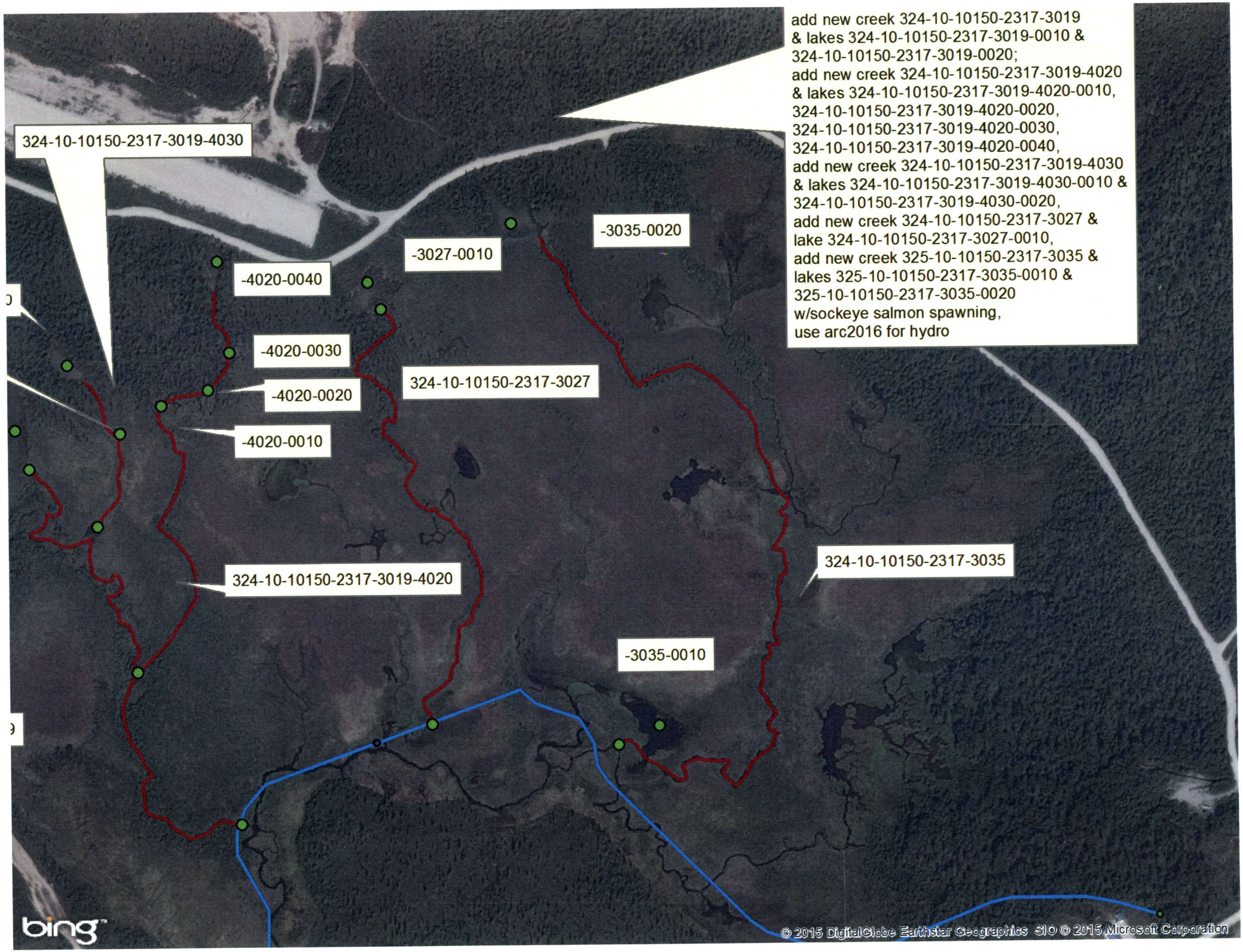
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