State of Alaska
Department of Fish and Game
Sportfish Division

Nomination Form
Anadromous Waters Catalog

ME

Taku R.

Region: Southeastern

USGS Quad(s): ~~Juneau~~ B-6, C-6

Anadromous Waters Catalog Number of Waterway: 111-32-10320

Name of Waterway: Taku River ☑ USGS Name ☐ Local Name

☑ Addition ☐ Deletion ☐ Correction ☐ Backup Information

For Office Use

Nomination #	11-517	Fisheries Scientist	Date 6/13/11
Revision Year:	2012	Habitat Operations Manager	Date 6/13/11
Revision to: Atlas		AWC Project Biologist	Date 4/22/11
Both	X	Cartographer	Date 10/24/11
Revision Code:	B-1, B-2		

OBSERVATION INFORMATION

Species	Date(s) Observed	Spawning	Rearing	Present	Anadromous
eulachon	05/24/2008	✓	✓	✓	✓

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:

Elizabeth Flory conducted research to determine the eulachon distribution on the Taku River in 2008. In her report, she documents the presence of eulachon larvae throughout the lower reaches of the Taku River. She used larvae to determine eulachon distribution instead of adults because smaller spawning events can be detected.
Coordinates (Lat,Long): Upper(58.51968,-133.81992) Lower(58.45801,-133.9572)

Add eulachon spawning and rearing to stream

Name of Observer (please print): Caroline Jezierski

Signature: 146.63.61.200 (Web Nomination) Date: 04/19/2011

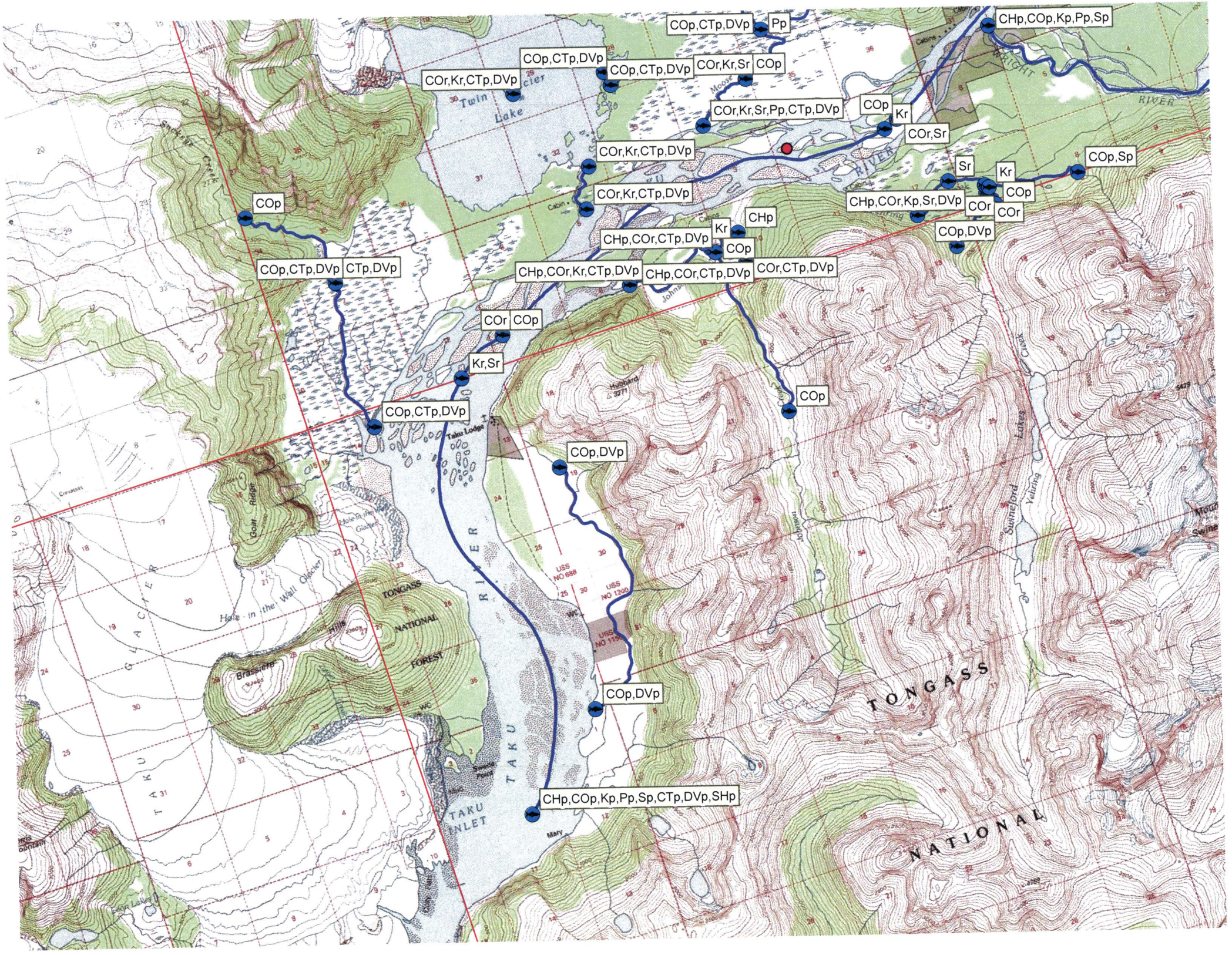
Agency:

Address: P.O. Box 110024 P.O. Box 110024
Juneau, AK 99811

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: _____ Revision 02/08

Name of Area Biologist (please print):


COp,CTp,DVp
Pp
CHp,COp,Kp,Pp,Sp
COp,CTp,DVp
COp,CTp,DVp
COr,Kr,Sr
COp
COr,Kr,CTp,DVp
COr,Kr,Sr,Pp,CTp,DVp
COp
Kr
COr,Sr
COr,Kr,CTp,DVp
COp,Sp
Sr
Kr
COp
COr,Kr,CTp,DVp
CHp,COr,Kp,Sr,DVp
COr
COr
COp
CHp
Kr
CHp,COr,CTp,DVp
COp
COp,DVp
COp,CTp,DVp
CTp,DVp
CHp,COr,Kr,CTp,DVp
CHp,COr,CTp,DVp
COr,CTp,DVp
COr
COp
Kr,Sr
COp
COp,CTp,DVp
COp,DVp
COp,DVp
CHp,COp,Kp,Pp,Sp,CTp,DVp,SHp
Twin Glacier
Lake
Moose
RIVER
Taku Lodge
TAKU RIVER
TAKU INLET
TONGASS NATIONAL FOREST
TONGASS NATIONAL
Hole in the Wall Glacier
Brassiere Hills
Golt Ridge
Johnson
Sutmelford Lakes
Yalbing
Hubbard
Mary

Eulachon Distribution in the Taku River, Juneau, Alaska, 2008.

A report prepared by:

Elizabeth Flory PhD
Aquatic Science Inc.
4546 River Road
Juneau AK 99801
USA

For:

Tulsequah Chief Mine Project
Redfern Resources Inc.
Vancouver

September 2008

Introduction

The Tulsequah Chief mine is located in British Columbia, Canada on the Tulsequah River, which is a tributary to the Taku River approximately 10km from the US/Canada border. Currently the only means of transportation into the mine are by air and water. Traditional access to the mine site was provided by conventional barging operations which are only possible in summer months depending on river flow. Concern about impacts to fishery resources has lead to a need for more information on eulachon (*Thaleichthys pacificus*) spawning in the Taku River.

Eulachon (*Thaleichthys pacificus*) are a short lived anadromous smelt found from Northern California to the southern Bering Sea (Hart 1973, Mecklenburg et al. 2002). During the spawning event, eulachon play an important ecological role as a seasonally available high lipid prey item affecting the movement of predators including: bird aggregations, marine mammals and fish (Womble 2005). Spawning typically occurs in the spring in river systems associated with a freshet (Hay and McCarter 2000).

In Southeast Alaska inside waters, there are at least twenty-eight rivers with known eulachon spawning, including the Taku River (Womble 2005, Wilson 2006). Eulachon spawning in the Taku River typically occurs in early April (E. Jones and L. Parisian, pers.comm.). In April 2006 before ice break up, harbor seals (*Phoca vitulina*) were hauled out on river ice, while eulachon schools were observed up river, indicating the fish moved underneath the ice access spawning grounds (E. Jones, pers.comm.).

Eggs are spawned demersally and adhere to coarse sand or small gravel substrate via a sticky stalk, which forms from the outer membrane of the egg (Smith and Saalfield 1955, Parente and Snyder 1970). The number of eggs produced increases with length and age, and can range from 8,500 to 67,500 eggs with an average of 26,000 (Spangler, 2002). Hatching duration varies throughout the range of eulachon spawning, lasting from 188 accumulated thermal units (ATU) in the Columbia River in the southern part of their range (Smith and Saalfeld 1955) to 242 ATU in the Kemano River (Triton 1990), 258 ATU in the Kitimat River (Pedersen et al. 1995), ~340 ATU in the Bella Coola River (Moody 2004) and 303 ATU in the Twentymile River in Alaska (Spangler, 2002). Hatching

appears to be related to temperature and accumulated thermal units (ATU), as the highest densities of drift occur when water temperatures are stable and change less than 2.8°C (Smith and Saalfeld 1955, Hart 1973, Spangler 2002). Hatching typically begins between three and five weeks after spawning, but tends to occur four to six weeks after spawning in SE Alaska (Andrew Eller, University of Alaska Fairbanks, pers. comm.).

Once hatched the 4-5 mm larvae rely on river currents to carry them to the estuary. The presence of larval eulachon in estuaries and marine waters adjacent to rivers is a strong indication that a river is used by eulachon for spawning (McCarter & Hay 2003). The highest densities of larval eulachon are found near the bottom of the water column (Spangler 2002) with peak larval drift occurring at night (Spangler 2002). Larval movement into the estuary after hatching is rapid. Larval eulachon distribution in estuaries indicates a residence, lasting anywhere from weeks to possibly months (McCarter and Hay 1999).

In many rivers, the spawning reach is more or less limited to the part of the river that is influenced by tides (Lewis et al. 2002) owing to them being relatively weak swimmers. In other systems, eulachon ascend well beyond the tidal influence eg. eulachon are reported to go as far as 80 km up the Susitna River (Barrett et al. 1984; Vincent-Lang and Queral 1984). The Taku River receives tidal influence just past the Taku Lodge, 35km up river from the mouth of Taku Inlet (Randy Host, USGS pers comm.). This study focused on a reach between river kilometer 31 and 57 to determine the upper limit of eulachon spawning in 2008 (Figure 1). Ichthyoplankton surveys in this study were designed to detect the furthest upstream spawning distribution of eulachon larvae in the Taku River.

Study Objectives

- Collect baseline information on the emergence timing and distribution of larval eulachon (*Thaleichthys pacificus*) on the Taku River.
- Locate and map the upper limit of adult spawner migration ie. the furthest distance upstream that is reached by spawning eulachon.

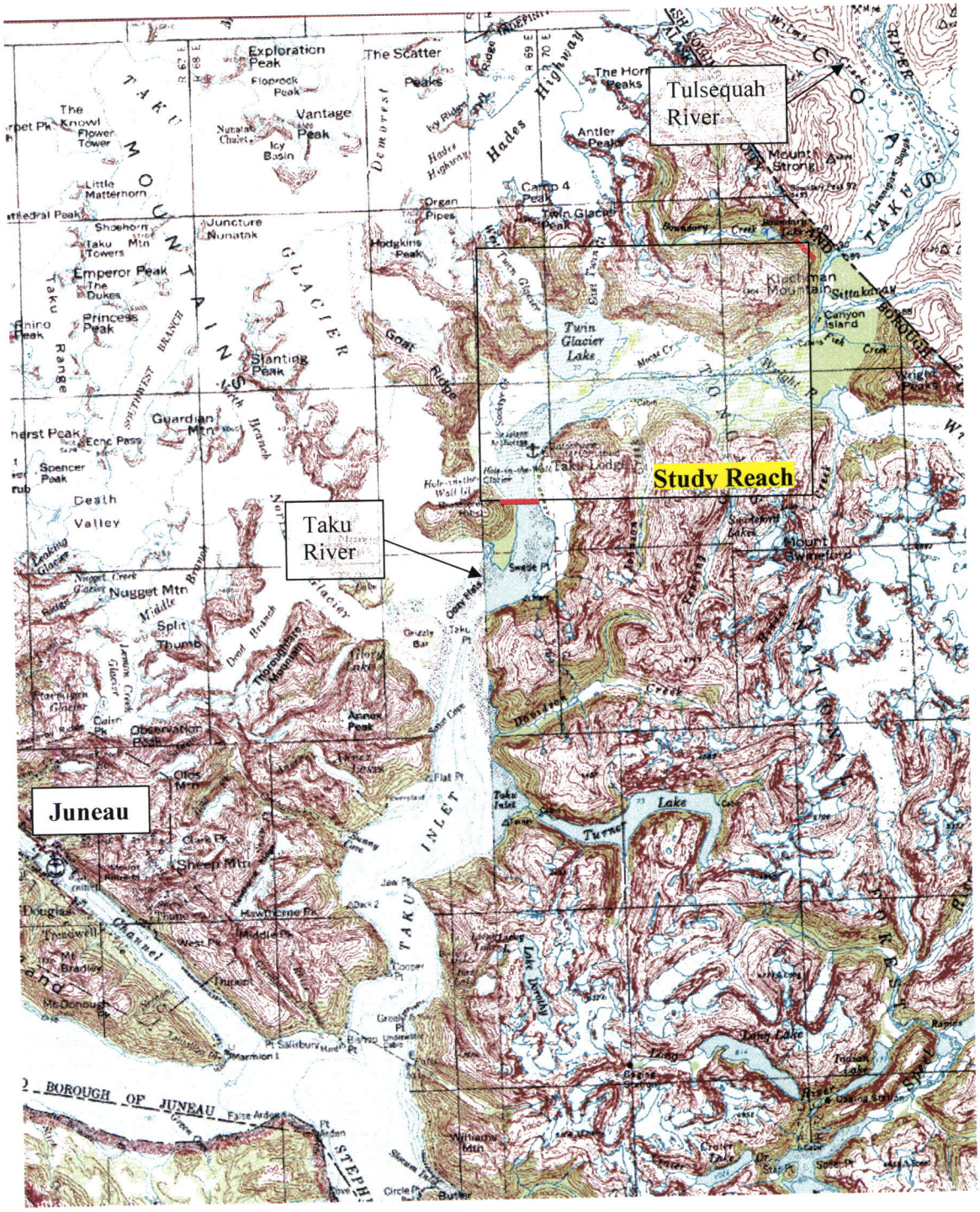


Figure 1: Location Map with study reach.

Methods

Adult eulachon were not targeted for this study owing to their potential ability to swim upstream underneath river ice undetected. The study focused on locating larvae moving downstream back to the ocean using the methods of McCarter and Hay 2003. Larvae are believed to hatch four to six weeks after spawning (Andrew Eller pers.comm.), so the distribution and timing of spawning can be determined from larval density in the water column.

Ichthyoplankton were collected from a boat at various sites along the Taku River. Two 350μm plankton nets with 20cm (8 inch) diameter openings were attached to a bongo frame and lowered from the winch of a 22ft skiff or 18ft jet boat according to location (Figures 2-3). A temperature data logger was placed in the river on the first sampling occasion to record water temperature every 15 minutes throughout the course of the study. The first sampling station was chosen 4 km below the Taku Lodge where congregations of seals and birds had been observed in April suggesting the presence of eulachon (Don Thomas pers. comm.). Stations were spaced 300m to 4 km apart with the aim of determining the upstream limit of distribution. Distances between stations were measured using Garmin "Mapsource" software.

At each station, surface water temperature, water depth and GPS co-ordinates were recorded. A General Oceanics flow meter attached to the bongo frame measured water flowing through the net allowing sample volume to be calculated. The boat was anchored or held stationary under power at the sampling site while the nets were lowered over the side and held just off the river bottom for three to eight minutes. Sampling time was recorded as the full time the nets were submersed in the water.

The contents of both left and right cod-end buckets from each plankton net were combined and flushed into a plastic sorting tray. After examination for larvae, the sample was transferred to a 1 liter bottle containing 70% ethanol for later examination with a microscope.

Sampling was conducted at low tide to avoid larval being displaced upstream by tidal action. Daily mean discharge rates of the Taku River were obtained from the USGS gage station at Canyon Island. Sampling was repeated weekly for four weeks. After the

first week, additional stations were added until the furthest upstream point that larval eulachon were found was established. More frequent samples were collected at the furthest downstream station to examine changes in eulachon density and determine peak spawning time.

Larval eulachon were positively identified by having an average ventral melanophore (pigment) count of 12 and gut length greater than three-fourths the body length (Hearne 1983, Young, 1984). Figure 4 shows the difference between coast-range sculpin larvae (top two larvae in photo) and eulachon larvae (bottom larvae). Andrew Eller (University of Alaska Fairbanks) identified eulachon larvae and Andrew Whiteley (University of Alaska Fairbanks) provided assistance in the identification of larval cottids (sculpins).

Larval eulachon density (D) measurements (number/m^3) were determined for each sampling station by calculating the quotient of the laboratory count (N) and the corresponding volume (V) of seawater (m^3) filtered through the plankton net:

$$D = N / V \quad (1)$$

The volume of water filtered through the net is determined using a General Oceanics® equation:

$$V = (A.F.K) / 999{,}999 \quad (2)$$

where:

V = volume of water filtered through the plankton net

A = area of net opening (m2)

F = number of revolutions recorded by a General Oceanics® model 2030R flow meter

K = rotor constant

and high speed rotor constant = 26,873 (7.0 cm rotor),

20 cm bongo net opening = 0.0283 m^2 or 0.0566 m^2 for both nets.

Figure 2: The plankton nets attached to the bongo frame.

Figure 3: 18ft jet boat and 22 ft skiff used to collect ichthyoplankton.

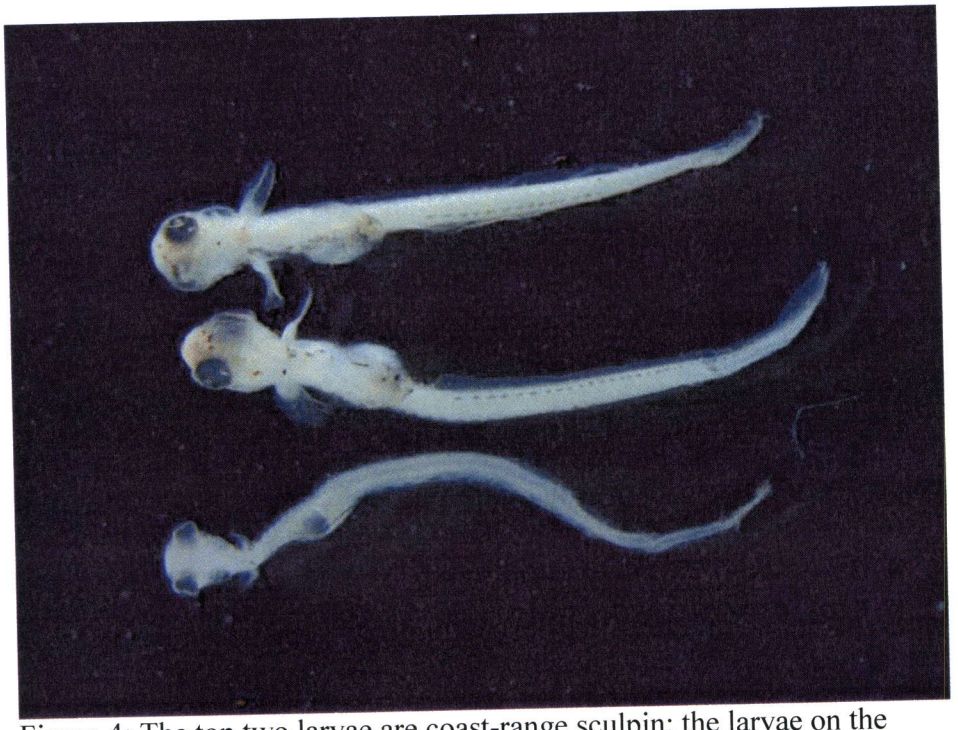


Figure 4: The top two larvae are coast-range sculpin; the larvae on the bottom is a eulachon. Larvae are approximately 5mm.

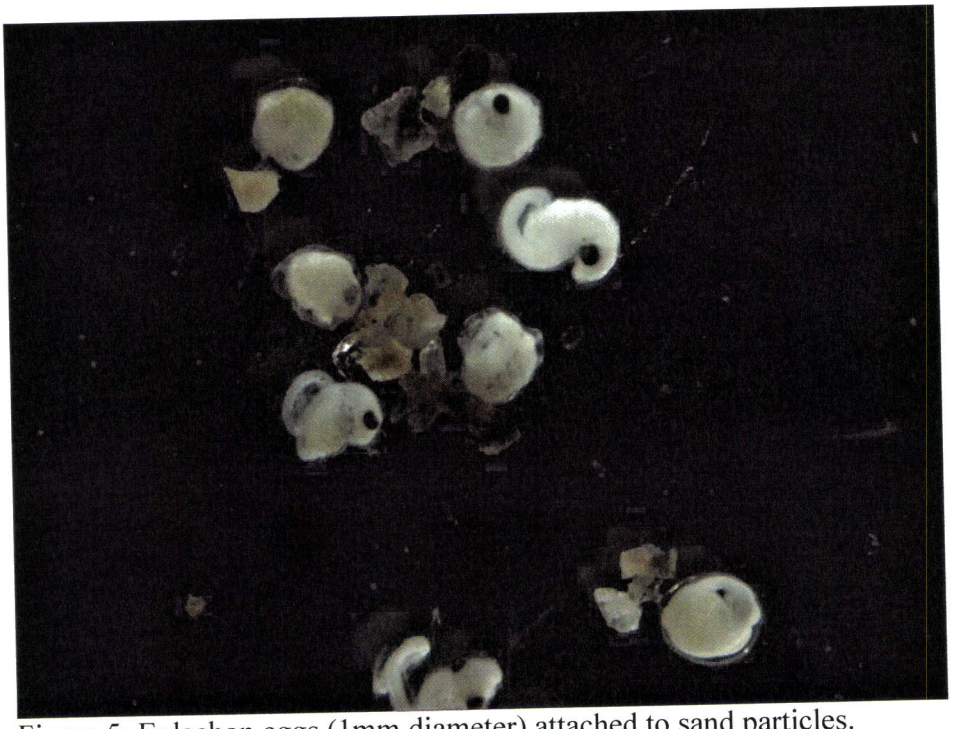


Figure 5: Eulachon eggs (1mm diameter) attached to sand particles.

Results

Four sampling trips were conducted between May 24 and June 12, 2008 to collect ichthyoplankton from 22 stations spaced along 26km of the Taku River. Two surveys were conducted during day trips to the site while an additional two surveys were conducted over a two day period to increase sampling frequency. Not all stations were surveyed on each occasion. River flow was low during the first survey restricting sampling sites to a narrow channel. Additional samples were collected at Station 1 on May 25, 27 and June 2, 10, 18 and 24. A total of 58 samples were collected and examined for larvae. Sampling depth varied from 0.8m at Station 4 to 6.6m at Station 12.

Larval eulachon were caught throughout the sampling period, but were not found at all stations. The furthest upstream location that larval eulachon (n=3) were encountered during the sampling period was Station 9, 1.4km from Yehring Creek and 12.6km upstream from the start of the survey reach (river kilometer 43.6). Table 1 gives the distances between stations as well as the density of larvae on each sampling occasion. Figure 7 shows changes in density of eulachon larvae, eggs and sculpin larvae during the course of the study. Density of eulachon larvae generally decreased upstream from station 1 to 9, although densities were slightly higher at Stations 4 and 5 than lower stations during May. Densities were much higher at Stations 1-5 (0-5km upstream from the start of the survey reach) compared to upstream stations (Stations 6 to 14). Densities declined steeply between Stations 5 and 9 (between river kilometer 36 and 43.6).

Densities of eulachon eggs decreased over the survey period with the highest density occurring during the first survey at the end of May. Sculpin larvae were found at all stations and densities increased over the survey period.

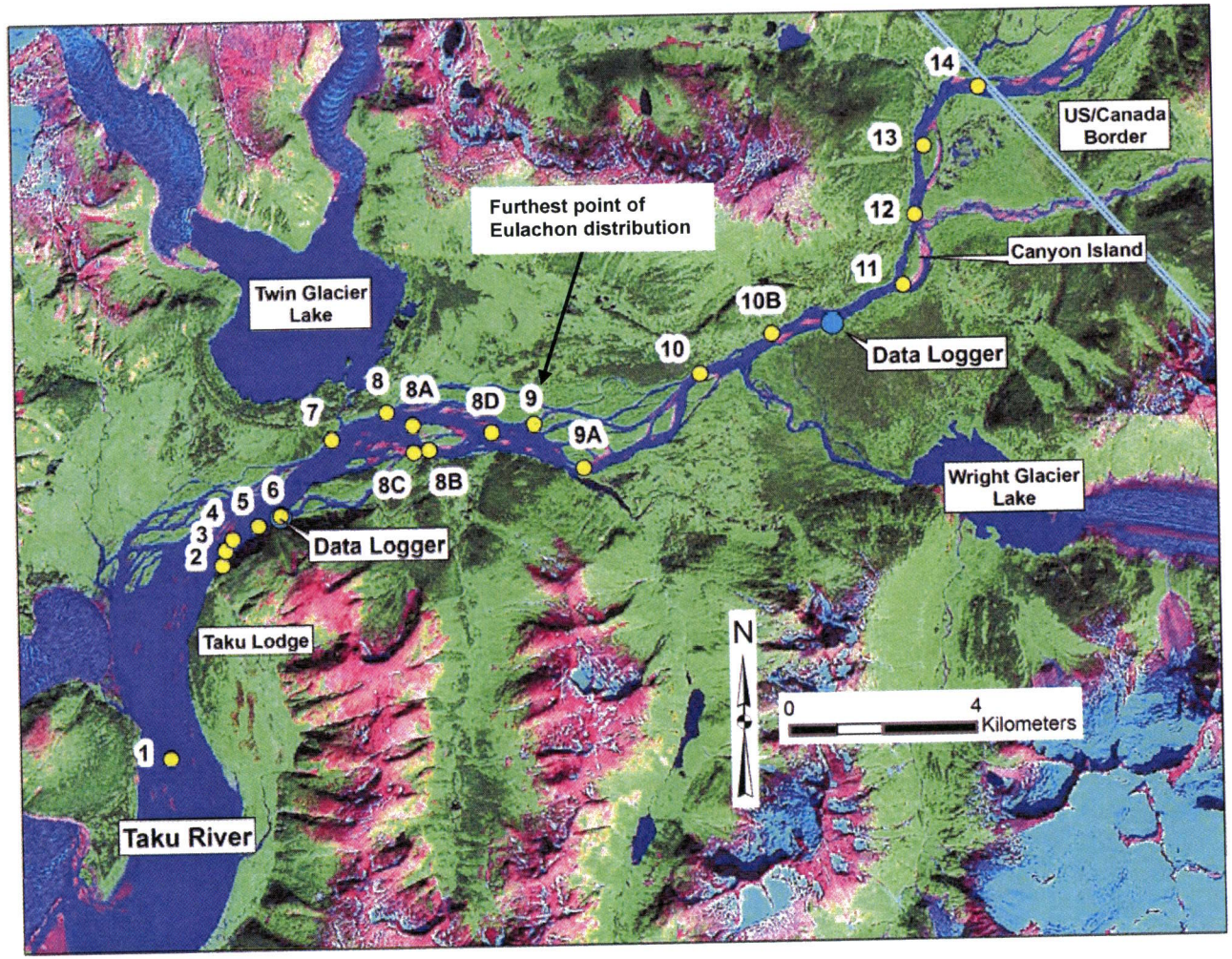


Figure 6. Sampling stations on the Taku River. Eulachon larvae were found at decreasing density from Stations 1 through 9

Table 1. Sample locations and density of Eulachon larvae of the Taku River 2008.

Station	GPS N	GPS W	Description	Distance Upstream (km)	Distance between stations (km)	Number of eulachon per cubic meter water			
						24-May	May29-30	June 5-6	12-Jun
1	58.45801	133.95720		0.0	0.0	5.74	7.12	11.79	12.32
2	58.49472	133.93604	Taku Lodge	4.3	4.3	0.34	0.48	14.24	4.77
3	58.49741	133.93471		4.6	0.3	0.76	ns	ns	ns
4	58.49958	133.93187		4.9	0.3	8.40	ns	ns	ns
5	58.50195	133.92233		5.2	0.3	0.53	8.03	6.55	ns
6	58.50373	133.91399	Johnson Creek	5.7	0.5	0.31	0.31	0.79	4.16
7	58.51801	133.89427	Twin Glacier	7.7	2.0	0.33	0.78	0.52	ns
8	58.52282	133.87393		9.0	1.3	0.18	0.12	1.44	0.64
8a	58.52022	133.86438	Moose Creek	9.6	0.6	ns	ns	3.56	ns
8b	58.51544	133.85880		10.2	0.6	ns	ns	0.29	0.17
8c	58.51505	133.86438		10.8	0.6	ns	ns	3.16	ns
8d	58.51837	133.83560		11.6	0.8	ns	ns	0.94	0.04
8e	58.52005	133.82776		12.1	0.5	ns	ns	ns	0
9	58.51968	133.81992		12.6	0.5	0	0.09	0	0
9a	58.51104	133.80225	Yehring Creek	14.0	1.4	ns	ns	0	0
9b	58.51311	133.79283		14.4	0.4	ns	ns	ns	0
10	58.52822	133.75835	Wright River	17.0	2.6	0	0	0	0
10B	58.53545	133.73166		18.8	1.8	ns	0	0	0
11	58.54379	133.68294	Canyon Island	21.8	3.0	0	0	ns	ns
12	58.55730	133.67773	Sittakanay River	23.3	1.5	ns	0	ns	ns
13	58.57030	133.67349		24.8	1.5	ns	0	ns	ns
14	58.58131	133.65259	Boundary Creek	26.5	1.7	ns	0	ns	ns

ns = not sampled

Additional sampling dates for Station 1 include: 5/25, 5/27, 6/2, 6/10, 6/18, 6/24

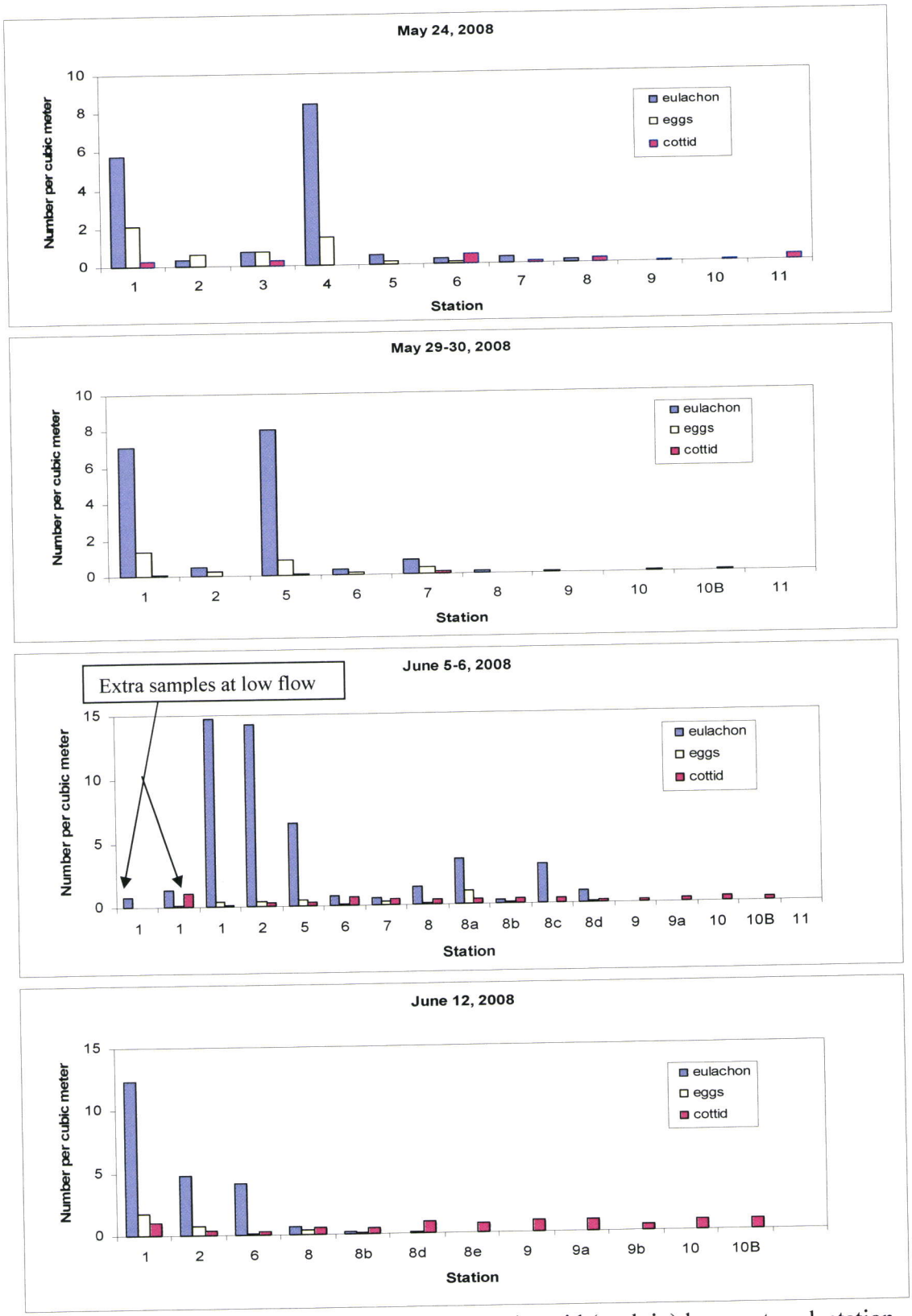


Figure 7: Density of eulachon larvae and eggs and cottid (sculpin) larvae at each station.

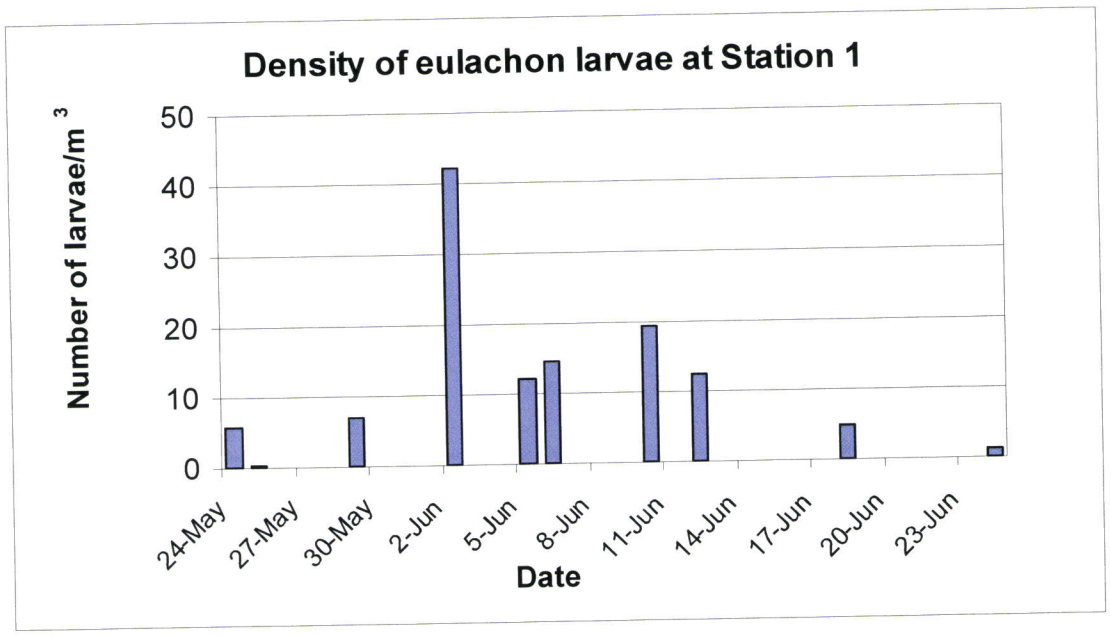


Figure 8: Change in density of eulachon larvae at Station 1 over the study period.

Figure 8 shows the change in density of larval eulachon at Station 1. The estimated peak emergence was determined by the highest count and density of larval eulachon at Station 1 and occurred on June 2 (n = 591, estimated 42 larvae/m^3). The volume of this sample had to be estimated due to a flow meter malfunction. Peak emergence occurred around the time of peak river discharge for the sampling period (Figure 9) and after water temperatures had exceeded 47°F. Changes in water temperature recorded every 15 minutes are shown in Figure 10. Water temperature increased during the last week of May, then remained steady until June 7 when temperatures dipped again.

Across all sites, a total of 2,625 larval eulachon, 356 eulachon eggs, 332 coast-range sculpin larvae (*Cottus aleuticus*), 12 coast-range sculpin eggs and 106 unidentifiable larvae were collected (Table 2).

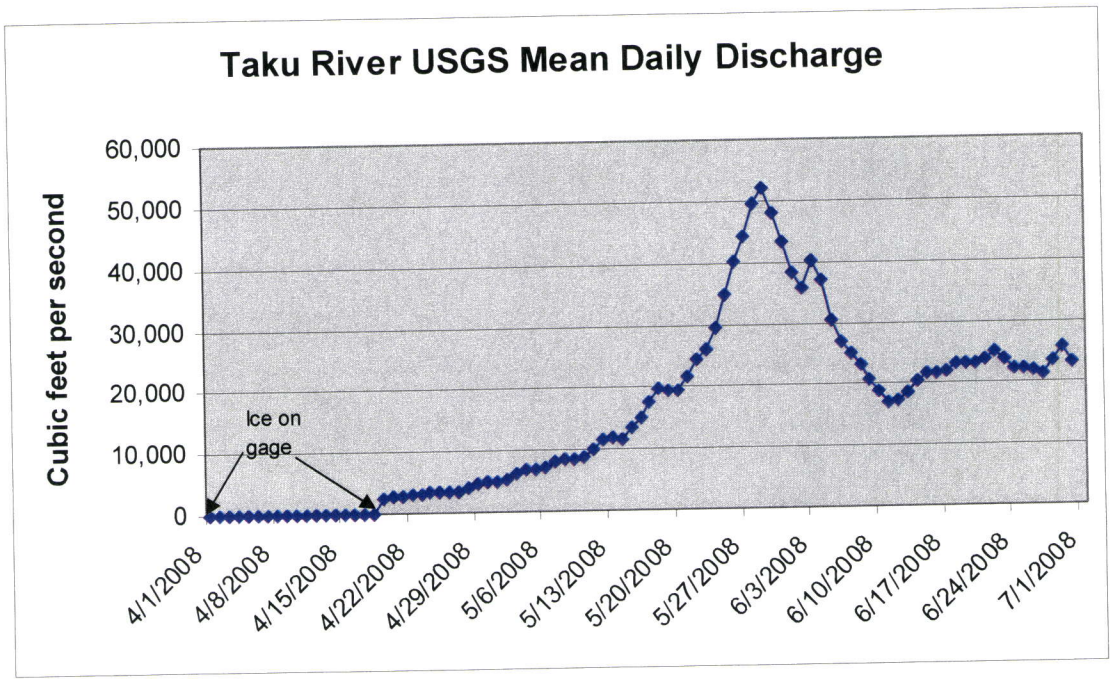


Figure 9: Daily mean discharge (cfs) at the USGS stream gaging station, Canyon Island. Provisional data from USGS.

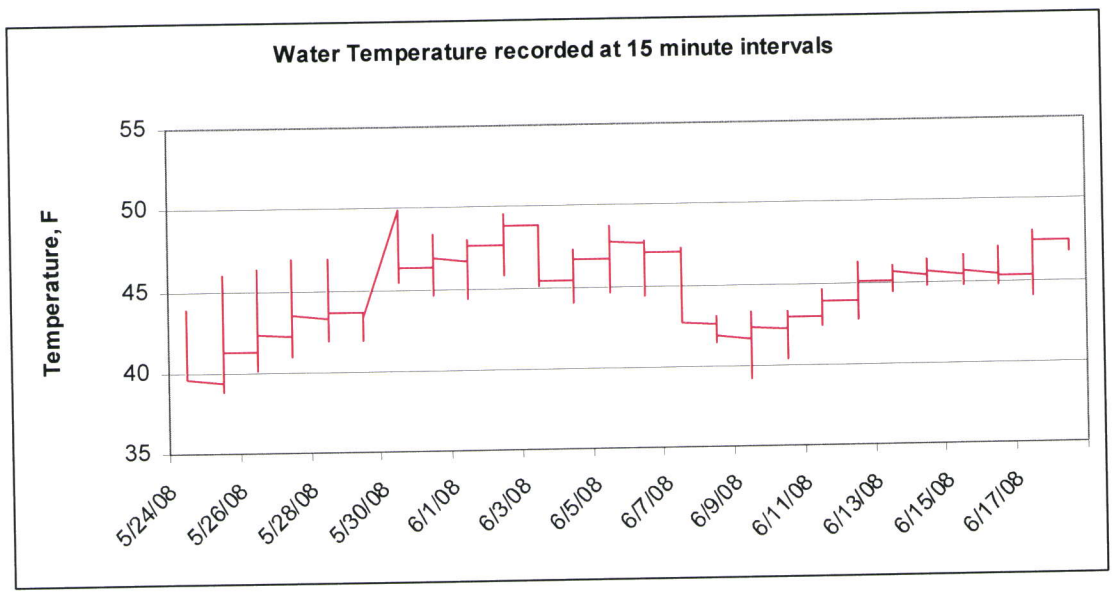


Figure 10: Records from a temperature logger positioned at Station 6 from May 24-29 and thereafter positioned between Station 10B and 11.

Table 2. Counts of eulachon (*T. pacificus*), coast-range sculpin (*C. aleuticus*) and unidentifiable larvae from the Taku River 2008.

Station	Date	Depth	Eulachon larvae	Eulachon eggs	Cottid	Cottid egg	Unidentified
1	5/24/08	1.5	97	36	5	0	0
	5/25/08	0.9	45	39	3	3	1
	5/27/08	0.76	19	11	0	0	0
	5/29/08	1.7	100	19	1	0	13
	6/2/08		591	19	5	0	4
	6/5/08	1.5	62	4	0	0	0
	6/5/08	1.5	109	12	1	0	0
	6/6/08	1.2	141	4	1	0	2
	6/10/08		266	24	3	0	0
	6/12/08	1.1	120	17	10	0	0
	6/18/08		48	23	7	0	0
	6/24/08		20	19	8	0	1
2	5/24/08	2.9	4	7	0	0	1
	5/29/08	3.1	11	6	0	0	8
	6/5/08	3	281	8	5	0	7
	6/12/08	2.4	56	9	4	0	0
3	5/24/08	2.1	10	10	4	0	1
4	5/24/08	0.8	52	9	0	0	0
5	5/24/08	4.5	9	3	0	1	1
	5/30/08	3.8	191	20	1	0	4
	6/6/08	4.3	117	9	5	0	2
6	5/24/08	1.9	3	1	5	0	0
	5/29/08	2.3	3	1	0	0	0
	6/5/08	1.7	6	1	5	0	0
	6/12/08	3.9	32	1	2	0	0
7	5/24/08	4.8	3	0	1	0	6
	5/30/08	5	25	12	4	0	3
	6/6/08	4.1	13	6	12	0	4
8	5/24/08	3.8	5	0	6	1	1
	5/29/08	4.2	3	0	0	0	1
	6/5/08	5	26	2	6	0	1
	6/12/08	3.3	10	6	9	0	1
8a	6/6/08	2.9	30	9	3	0	11
8b	6/5/08	3.5	3	1	4	0	0
	6/12/08	4.2	3	2	8	0	0
8c	6/6/08	1.8	83	0	11	0	12
8d	6/5/08	2.5	24	2	4	0	9
	6/12/08	2.8	1	3	26	0	1
8e	6/12/08	3.5	0	0	14	0	0
9	5/24/08	2.1	0	1	2	4	5
	5/30/08	3	3	0	1	0	0
	6/6/08	2.4	0	0	4	0	2
	6/12/08	2.3	0	0	25	0	0
9a	6/5/08	3	0	0	9	0	2
9a	6/12/08	2.5	0	0	25	0	0
9b	6/12/08	2.5	0	0	16	0	0
10	5/24/08	4.2	0	0	3	2	0
10	5/29/08	5.7	0	0	1	1	2
10	6/6/08	2.4	0	0	10	0	0
10	6/12/08	4	0	0	19	0	0
10B	5/29/08	2.1	0	0	1	0	0
10B	6/5/08	3.5	0	0	6	0	0
10B	6/12/08	3	0	0	18	0	0
11	5/24/08	1.6	0	0	5	0	0
11	5/30/08	2.1	0	0	0	0	0
12	5/30/08	6.6	0	0	3	0	0
13	5/30/08	2.5	0	0	1	0	0
14	5/29/08	2.6	0	0	0	0	0
			2625	**356**	**332**	**12**	**106**

Discussion

Ichthyoplankton surveys were selected for this study over other methods due to their ability to detect small spawning runs that might be missed by conventional fishing techniques (gill nets or seine nets) on adults. Substantial numbers of eulachon larvae can be caught in rivers and estuaries where no (or negligible) adult spawning is observed. Furthermore, the duration of the presence of larvae in adjacent estuaries seems to occur over a number of weeks, whereas the duration of spawning may be complete within days (McCarter and Hay 2003).

The plankton net tows in the current study were confined to daylight hours for safety and logistical reasons even though there is evidence that many larvae hatch at night. The major consideration in any survey design is insuring adequate spatial and temporal sampling coverage, fully utilizing available time and resources. Over 26km of the river was sampled on four occasions to determine the upstream limit of eulachon distribution. Decreasing density of eulachon larvae in upstream samples suggest the limit was close to Station 9, which lies 1.4km downstream from the mouth of the Yehring River or at river kilometer 43.6. Only 3 larvae were found at Station 9 on one out of four sampling events. These larvae were found during the estimated peak of larval outdrift. Water temperature appeared slightly warmer, yet stable, which may have encouraged emergence. Although spawning may have occurred further upstream, density of larvae was too low to be detected at sites further upstream, suggesting only small patches of spawning could be present. The greatest densities of larvae were recorded at Stations 1 through 6, which lie between 4km downstream of the Taku Lodge and 1.4km upstream near the mouth of Johnson Creek.

Exact river spawning locations, however, are difficult to determine by plankton net surveys alone. According to McCarter and Hay (2003), the cumulative down river effect of several separate spawning events within the same time period can often obscure distribution patterns even with extensive spatial and temporal sampling coverage. The densities of eulachon larvae might be expected to be higher at down river stations than up river stations, however, up river sites can sometimes produce higher density estimates immediately after hatching and are often characterized by the capture of large numbers of embryonic eggs as well as very small, curled larvae (McCarter and Hay 2003).

Counts of eulachon larvae in other studies have generally ranged from 0 to 3,000 larvae per 6 minute tow. Ninety-nine percent of Fraser River samples collected between 1995 and 2002 produced counts between 0 and 500 larvae per 6 minute tow (McCarter and Hay 2003). The highest count of larvae in the current study was 591 during a 5 minute tow. Counts above station 5 were less than 100 on each sampling occasion. This would suggest the limit of upstream distribution was being approached at Station 9.

The furthest ever upstream distribution of eulachon in the Taku system is thought to be at Bull Slough, near the Tulsequah River in Canada, recorded during surveys conducted by Alaska Dept of Fish and Game (Kisner, 1979, Pers. comm. Parisian). Migration this far upriver was noted only during exceptionally large runs, which occurred approximately four times since 1979. Typically, spawning is focused in the lower river around the Taku River Lodge. In recent salmonid smolt trapping (minnow traps) studies, ADFG personnel have not captured eulachon adults above Canyon Island.

Eulachon embryonic egg and larval outdrift in the Taku River in 2008 appeared to begin during the middle of May, peaked during the first week of June and declined by mid-June. A small number of eggs were still being captured on June 12 suggesting a protracted spawning period at the lower sites or they may simply have failed to hatch. Given that eulachon larvae typically emerge four to six weeks after spawning in the region, spawning likely took place around mid to late April, which matches closely with the timing of marine mammal observations.

The data shows no apparent correlation between station depth and larval density. Depth is dependent of river flow and varied over time at each station. Larval density appeared more dependent on station location upstream rather than water depth, but many more sites would need to be sampled at different depths across the river at each station to reveal any correlation with spawning and depth of water. In the Fraser River, British Columbia, the deeper, swifter side margins were found to produce higher larval eulachon densities than either mid-river or shallower, slower moving sides of the river despite higher sediment loads (Hay and McCarter 2003). In BC, there is a connection between spawning eulachon and certain rivers that have strong, spring freshets that drain major glaciers or snowpacks (Hay and McCarter 2000).

Future studies would be beneficial in gathering information on the variability of eulachon spawning distribution and timing between years. Sampling coverage could be reduced as the patterns of several years of data are established and key representative sampling sites are identified. Future studies could repeat sampling at stations 1, 2, 5, 8, 8b, 8d, 9 and 9a as well as new sites between 9 and 9a to further pinpoint the upper limit of distribution, and sites upstream to determine any spawning further upstream in future. Ichthyoplankton surveys could also be designed to produce abundance estimates of spawning eulachon biomass in the Taku system. Information could also be gathered on the use of tributaries versus the main Taku River channel for eulachon spawning.

References

Barrett, B.M., Thompson, F.M., and Wick, S.N. 1984. Adult anadromous fish investigations: May-October 1983. Susitna Hydro Aquatic Studies, report No.1. APA document No.1450. Anchorage: Alaska Dept. Fish & Game.

Hart, J. L. (1973). Eulachon. Pacific fishes of Canada. *Fisheries Research Board of Canada, Bulletin* 180: 148-150.

Hay, D.E and P.B.McCarter (2000). Status of the eulachon *Thaleichthys pacificus* in Canada. Fisheries and Ocean Science Branch, Nanamio, B.C. Research Document 2000/145

Hearne, M. (1983). Identification of larval and juvenile smelts (Osmeridae) from California and Oregon using selected morphometric characters. M.S. Thesis. San Francisco State University, San Francisco, CA. 142p.

Lewis, A.F.J., McGurk, M.D. and Galesloot, M.G. 2002. Alcan's Kemano River eulachon (*Thaleichthys pacificus*) monitoring program 1988-1998. Consultant's report prepared by Ecofish Research Ltd. For Alcan Primary Metal Ltd., Kitimat, B.C. 136p.

McCarter, P. B., and D. E. Hay (1999). Distribution of spawning eulachon stocks in the central coast of British Columbia as indicated by larval surveys. PSARC P99-8, 48 p.

McCarter, P. B. and Hay, D. E.. 2003. Eulachon embryonic egg and larval outdrift sampling manual for ocean and river surveys. Can. Tech Rep. Fish. Aquat. Sci. 2451: 33p.

Mecklenburg, C. W., T. A. Mecklenburg, and L. K. Thorsteinson (2002). Fishes of Alaska. *American Fisheries Society.*

Moody, M.F. (2004). 2003. Nuxalk Nation incubation studies of the eulachon (*Thaleichthys pacificus*). Nuxalk Nation Fisheries Department, Bella Coola, British Columbia.

Parente, W.D. and Snyder, G.R. 1970. A pictoral record of the hatching and early development of the eulachon. Northwest Science 44(1).

Pedersen, R.K., U.N. Orr and D.E. Hay. 1995. Distribution and preliminary stock assessment (1993) of the eulachon, *Thaleichthys pacificus*, in the Lower Kitimat, British Columbia. *Can. MS Rep. Fish. Aquat. Sc*. 2340: 1-23.

Smith, W.E. and R.W Saalfeild (1955). Studies on Columbia River smelt, *Thaleichthys pacificus*, (Richardson). *Fisheries Research Papers* 1(3):2-23, Washington Department of Fisheries, Olympia, Washington.

Spangler, E. A. K. (2002). The ecology of eulachon (*Thaleichthys pacificus*) on the Twentymile River, Alaska. M.S. thesis, University of Alaska Fairbanks, p. 124

Triton Environmental Consultants. 1990. Life history of eulachon, *Thaleichthys pacificus*, of the Kemano and Wahoo Rivers, B.C. results of 1989 investigations. Draft report prepared for Aluminum Company of Canada LTD. Triton Ref: 2039/ WP 3677, 51 p.

Vincent-Lang, D.S. and Queral, I. 1984. Eulachon spawning in the lower Susitna River. Chapter 5. In: Aquatic habitat and instream flow investigations, May-October 1983. Edited by C.C. Estes, and D.S. Vincent-Lang. Susitna Hydro Aquatic Studies, Report No.3, Vol. 5. APA document No.1934. Anchorage: Alaska Dept. of Fish & Game. P.1-32 and appendices.

Willson, M.F., Armstrong, R.H. Hermans, M.C. and Koski, K. 2006. Eulachon: A review of biology and annotated bibliography. Alaska Fisheries Science Center (AFSC) Processed Report 2006-12, National Marine Fisheries Service, Juneau, Alaska. 229pp.

Womble, J.N., Willson, M.F. Sigler, M.F. Kelly. B.P. and G.R.Van Blaricom. (2005) Distribution of Stellar sea lions *Eumetopias jubatus* in relation to spring –spawning fish in SE Alaska, Marine Ecology Progress Series, Vol.294:271-282

		Eulachon		Cottid		Sample	Flow Meter						Density		
Station	Date	Larvae	Eggs	Larvae	Eggs	Time	start	end	Difference	Distance(m)	volume(20)	volume(.2)	Eulachon	eggs	cottid
1	5/24/08	97	36	5	0	6	13700	23717	10017	269.2	84524.8	16.9	5.74	2.13	0.30
2	5/24/08	4	7	0	0	4	24034	30953	6919	185.9	58383.4	11.7	0.34	0.60	0.00
3	5/24/08	10	10	4	0	4	31431	39211	7780	209.1	65648.7	13.1	0.76	0.76	0.30
4	5/24/08	52	9	0	0	4	39356	43022	3666	98.5	30934.2	6.2	8.40	1.45	0.00
5	5/24/08	9	3	0	1	4	43461	53531	10070	270.6	84972.0	17.0	0.53	0.18	0.00
6	5/24/08	3	1	5	0	6	53691	59399	5708	153.4	48164.8	9.6	0.31	0.10	0.52
7	5/24/08	3	0	1	0	6	59582	64953	5371	144.3	45321.2	9.1	0.33	0.00	0.11
8	5/24/08	5	0	6	1	5.4	65433	81493	16060	431.6	135516.4	27.1	0.18	0.00	0.22
9	5/24/08	0	1	2	4	6	82042	103751	21709	583.4	183183.4	36.6	0.00	0.03	0.05
10	5/24/08	0	0	3	2	5.2	104358	127855	23497	631.4	198270.8	39.7	0.00	0.00	0.08
11	5/24/08	0	0	5	0	10	133290	143189	9899	266.0	83529.1	16.7	0.00	0.00	0.30
1	05/29/08	100	19	1	0	5	175191	183512	8321	223.6	70213.7	14.0	7.12	1.35	0.07
2	05/29/08	11	6	0	0	5	184033	197630	13597	365.4	114733.3	22.9	0.48	0.26	0.00
5	05/30/08	191	20	1	0	5.3	346395	360485	14090	378.6	118893.3	23.8	8.03	0.84	0.04
6	05/29/08	3	1	0	0	5	197807	203563	5756	154.7	48569.9	9.7	0.31	0.10	0.00
7	05/30/08	25	12	4	0	5	327334	346331	18997	510.5	160299.2	32.1	0.78	0.37	0.12
8	05/29/08	3	0	0	0	5	204258	219714	15456	415.3	130419.7	26.1	0.12	0.00	0.00
9	05/30/08	3	0	1	0	5	298702	318351	19649	528.0	165800.8	33.2	0.09	0.00	0.03
10	05/29/08	0	0	1	1	4.3	218650	236115	17465	469.3	147371.9	29.5	0.00	0.00	0.03
10B	05/29/08	0	0	1	0	8	236115	248693	12578	338.0	106134.8	21.2	0.00	0.00	0.05
11	05/30/08	0	0	0	0	5	294816	298702	3886	104.4	32790.6	6.6	0.00	0.00	0.00
12	05/30/08	0	0	3	0	6.3	278185	294634	16449	442.0	138798.8	27.8	0.00	0.00	0.11
13	05/30/08	0	0	1	0	5	264743	278184	13441	361.2	113416.9	22.7	0.00	0.00	0.04
14	05/29/08	0	0	0	0	6	248813	261820	13007	349.5	109754.8	22.0	0.00	0.00	0.00

Appendix 1: Number of eulachon and cottid larvae and eggs with flow meter data and calculation of density (numbers/m^3).

Station	Date	Eulachon		Cottid		Sample	Flow Meter						Density		
		Larvae	Eggs	Larvae	Eggs	Time	start	end	Difference	Distance(m)	volume(20)	volume(.2)	Eulachon	eggs	cottid
1	06/05/08	62	4	0	0	3	369372	372601	3229	86.8	27246.7	5.4	11.38	0.73	0.00
1	06/05/08	109	12	1	0	5	372601	377891	5290	142.2	44637.7	8.9	12.21	1.34	0.11
1	06/06/08	141	4	1	0	3	542211	547901	5690	152.9	48013.0	9.6	14.68	0.42	0.10
2	06/05/08	281	8	5	0	5	381498	393191	11693	314.2	98667.1	19.7	14.24	0.41	0.25
5	06/06/08	117	9	5	0	5	531498	542076	10578	284.3	89258.5	17.9	6.55	0.50	0.28
6	06/05/08	6	1	5	0	5	393784	398262	4478	120.3	37785.9	7.6	0.79	0.13	0.66
7	06/06/08	13	6	12	0	5	516601	531292	14691	394.8	123964.6	24.8	0.52	0.24	0.48
8	06/05/08	26	2	6	0	5	398552	409240	10688	287.2	90186.7	18.0	1.44	0.11	0.33
8a	06/06/08	30	9	3	0	5	510197	515188	4991	134.1	42114.7	8.4	3.56	1.07	0.36
8b	06/05/08	3	1	4	0	5	409314	415474	6160	165.5	51978.9	10.4	0.29	0.10	0.38
8c	06/06/08	83	0	11	0	5	494095	509664	15569	418.4	131373.3	26.3	3.16	0.00	0.42
8d	06/05/08	24	2	4	0	5	415848	431054	15206	408.6	128310.2	25.7	0.94	0.08	0.16
9	06/06/08	0	0	4	0	5	477510	493212	15702	422.0	132495.5	26.5	0.00	0.00	0.15
9a	06/05/08	0	0	9	0	5	432663	452991	20328	546.3	171530.3	34.3	0.00	0.00	0.26
10	06/06/08	0	0	10	0	5	477510	493212	15702	422.0	132495.5	26.5	0.00	0.00	0.38
10B	06/05/08	0	0	6	0	5	453301	464547	11246	302.2	94895.2	19.0	0.00	0.00	0.32
1	06/12/08	120	17	10	0	4	556517	562290	5773	155.1	48713.3	9.7	12.32	1.74	1.03
2	06/12/08	56	9	4	0	4	562301	569263	6962	187.1	58746.3	11.7	4.77	0.77	0.34
6	06/12/08	32	1	2	0	4	569832	574395	4563	122.6	38503.2	7.7	4.16	0.13	0.26
8	06/12/08	10	6	9	0	5	574801	583990	9189	246.9	77538.0	15.5	0.64	0.39	0.58
8b	06/12/08	3	2	8	0	5	584483	594659	10176	273.5	85866.4	17.2	0.17	0.12	0.47
8d	06/12/08	1	3	26	0	5	595201	611550	16349	439.3	137955.0	27.6	0.04	0.11	0.94
8e	06/12/08	0	0	14	0	5	612367	623835	11468	308.2	96768.5	19.4	0.00	0.00	0.72
9	06/12/08	0	0	25	0	6	625432	640810	15378	413.3	129761.6	26.0	0.00	0.00	0.96
9a	06/12/08	0	0	25	0	6.17	641993	658773	16780	450.9	141591.8	28.3	0.00	0.00	0.88
9b	06/12/08	0	0	16	0	6	660114	680742	20628	554.3	174061.8	34.8	0.00	0.00	0.46
10	06/12/08	0	0	19	0	6.15	681413	695615	14202	381.7	119838.3	24.0	0.00	0.00	0.79
10B	06/12/08	0	0	18	0	5.4	696314	709561	13247	356.0	111779.9	22.4	0.00	0.00	0.81
1	5/25/08	45	39	3	3	8	43302	155662	112360	3019.5	948108.3	189.6	0.24	0.21	0.02
1	5/27/08	19	11	0	0	8	44849	165592	120743	3244.7	1018845.2	203.8	0.09	0.05	0.00
1	06/02/08	591	19	5	0	5	259681	258009	1672	44.9	14108.6	2.8	209.45	6.73	1.77
1	06/10/08	266	24	3	0	4	547923	556008	8085	217.3	68222.3	13.6	19.50	1.76	0.22
1	06/18/08	48	23	7	0										
1	06/24/08	20	19	8	0	8	716853	727001	10148	272.7	85630.1	17.1	1.17	1.11	0.47

Appendix 1 continued.

Vol. 294: 271–282, 2005 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published June 9

Distribution of Steller sea lions *Eumetopias jubatus* in relation to spring-spawning fish in SE Alaska

Jamie N. Womble[1,4,*], Mary F. Willson[1], Michael F. Sigler[2], Brendan P. Kelly[1], Glenn R. VanBlaricom[3]

[1]School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 11120 Glacier Highway, Juneau, Alaska 99801, USA
[2]National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratory, 11305 Glacier Highway, Juneau, Alaska 99801, USA
[3]School of Aquatic and Fishery Sciences, Washington Cooperative Fish and Wildlife Research Unit, University of Washington, Mailstop 355020, Seattle, Washington 98195, USA
[4]*Present address:* National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratory, 11305 Glacier Highway, Juneau, Alaska 99801, USA

ABSTRACT: Energetic demands are high for Steller sea lions *Eumetopias jubatus* during spring, when females are pregnant and lactating and males are preparing for extended fasts on breeding territories. Therefore, we predicted that the distribution of sea lions in SE Alaska in spring would be influenced by the distribution of spring spawning aggregations of high-energy prey species (Pacific herring *Clupea pallasii* and eulachon *Thaleichthys pacificus*). The spatial distribution of sea lions during spring reflected the distribution of spawning eulachon in northern Southeast Alaska, particularly in Lynn Canal and along the Yakutat forelands. Haulouts with peak numbers of sea lions in spring were located significantly closer to eulachon spawning sites than haulouts that peaked at other times of year. Some haulouts were occupied only during the eulachon spawning period. The maximum number of sea lions at haulouts in spring was inversely correlated with the distance to the closest eulachon aggregation and was positively associated with the number of eulachon within 20 km. Aerial surveys conducted every 7 to 10 d during March through May in 2002 and 2003 revealed large numbers of sea lions in the water at herring spawning sites in 2002 and 2003; however, there were no significant relationships between the number of herring spawning sites and number of sea lions (except at distances >60 km). The number of sea lions was greater at herring spawning sites in 2003, corresponding to higher herring biomass. Seasonally aggregated, high-energy prey species influence the seasonal distribution of sea lions and may be critical to their reproductive success.

KEY WORDS: Steller sea lion · *Eumetopias jubatus* · Pacific herring · *Clupea pallasii* · Eulachon · *Thaleichthys pacificus* · SE Alaska · Forage fishes · Spawning aggregations

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

The distribution and abundance of a species is influenced by many abiotic and biotic factors of the environment, including the distribution and abundance of prey. Seasonal changes in prey resources are common, but those at predictable times and locations may be especially important to predators. Seasonally aggregated prey resources can influence timing of breeding cycles, reproductive rates, body size, group size, and distribution of predators (Payne et al. 1986, Hansen 1987, Mehlum et al. 1996, Ben-David 1997, Hilderbrand et al. 1999, Skov et al. 2000, Swartzman & Hunt 2000, Heyman et al. 2001, Blundell et al. 2002, MacLeod et al. 2004). For most mammalian species, good body condition is critical during the energetically-demanding phases of breeding and lactation (Robbins 1983, Gittleman & Thompson 1988), and the availability of aggregated high-energy prey may be important in achieving good body condition and ultimately in reproductive success.

*Email: jamie.womble@noaa.gov

© Inter-Research 2005 · www.int-res.com

Costs of lactation for females and energetic costs associated with territorial maintenance for males are critical facets of the reproductive biology of pinnipeds. Lactation is the most costly aspect of mammalian reproduction (Gittleman & Thompson 1988), and differences in the length of the lactation period and offspring dependency among pinniped species are probably related to the amount of energy that each species is able to store prior to parturition (Costa 1993). For Steller sea lion *Eumetopias jubatus* females, foraging trips continue throughout a protracted lactation period that may range from less than 1 to 3 yr (Pitcher & Calkins 1981). Energy requirements of dependent pups increase during late lactation, thus increasing the energetic demand upon the female (Oftedal et al. 1987). Steller sea lions depend upon the marine environment for foraging, and they use terrestrial sites for birthing, caring for young, resting, and avoidance of aquatic predators (Bartholomew 1970, Bonner 1984). Thus, they are central-place foragers (Orians & Pearson 1977) while their pups are land-bound.

Productivity in the marine environment varies seasonally (Laws et al. 1988), and seasonally predictable aggregations of prey may provide an important concentration of food for predators. Pacific salmon *Oncorhynchus* spp. are energy-rich anadromous fishes that spawn in rivers along the North Pacific rim (Groot & Margolis 1991), attracting numerous avian and mammalian predators (Willson & Halupka 1995, Willson et al. 1998, Gende et al. 2001). Also important are other energy-rich fishes, such as Pacific herring *Clupea pallasii*, capelin *Mallotus villosus*, Pacific sand lance *Ammodytes hexapterus*, northern lampfish *Stenobrachius leucopsarus*, and eulachon *Thaleichthys pacificus*. All these fish species occur seasonally in the diet of Steller sea lions in Alaska (Pitcher 1981, Merrick et al. 1997, Sinclair & Zeppelin 2002, Winship & Trites 2003), but little is known about their life history, spawning patterns, and distribution in Alaska, with the exception of herring (Rounsefell 1930, Rounsefell & Dalgreen 1935, Carlson 1980). These seasonally abundant, energy-rich forage fish are critical to the biology of many predators (Springer 1992, Byrd et al. 1997, Skov et al. 2000, Bishop & Green 2001, Litzow et al. 2002, Marston et al. 2002, Rodway et al. 2003). Of the several species of forage fishes, extensive information is available only for Pacific herring and eulachon spawning sites in SE Alaska, and this study focuses on these species.

Although several previous observations have noted pinnipeds aggregating at concentrations of forage fishes in the north Pacific (Bigg 1988, Gende et al. 2001, Marston et al. 2002), no studies have specifically addressed the possible ecological importance of ephemeral concentrations of energy-rich prey fishes as it relates to Steller sea lion life-history. Spring spawning aggregations of forage fishes may be important to Steller sea lion ecology for several reasons. First, energetic demands are high for sea lions during spring when females are pregnant and lactating and males are preparing for extended fasts on their breeding territories (Winship et al. 2002, Winship & Trites 2003). Second, spring spawning aggregations generally occur at relatively predictable sites and times. Third, herring and eulachon are densely aggregated in spring and are high in lipid content and energy density (Perez 1994, Anthony et al. 2000, Iverson et al. 2002). Therefore, spawning aggregations of eulachon and herring may be of substantial seasonal significance to the nutrition and energy budgets of sea lions when energy demands are at a peak. Under the hypothesis that aggregations of spring-spawning forage fishes are important to the reproductive ecology of Steller sea lions in SE Alaska (SEAK), we predicted that the spatial distribution of sea lions in spring would reflect the distribution of such eulachon and herring aggregations.

The objectives of this study were to provide insight into the seasonal foraging ecology of sea lions by (1) determining the seasonal distribution of sea lions at haulouts in spring, (2) documenting the numbers of sea lions at spring spawning aggregations of herring and eulachon in SE Alaska, and (3) relating the distribution of sea lions to herring and eulachon aggregations. Specifically, we tested the following predictions: (1) Haulouts with peak numbers of sea lions in spring are closer to herring and eulachon aggregations than haulouts with peak numbers at other times of year; (2) the number of sea lions at haulouts in spring is inversely correlated with the distance to the closest herring and eulachon spawning aggregation; (3) the number of sea lions at haulouts in spring is correlated with the number of herring and eulachon spawning aggregations within a limited radius based on foraging-trip distances of sea lions; (4) the number of sea lions observed at spawning aggregations is correlated with the estimated biomass of spawning fishes.

MATERIALS AND METHODS

Seasonal distribution of Steller sea lions: monthly aerial surveys. Steller sea lions at 25 terrestrial haulouts in northern Southeast Alaska (NSEAK) (Fig. 1) were counted from an airplane monthly from March 2001 through December 2002 to assess their seasonal distribution and use of haulout sites. Surveys were conducted from a floatplane (Cessna 206) with an experienced survey pilot between 10:00 and 16:00 h (Withrow 1982) and within 3 hr of low tide, weather permitting. The observer-photographer sat in the front right-hand seat and photographed sea lions on shore

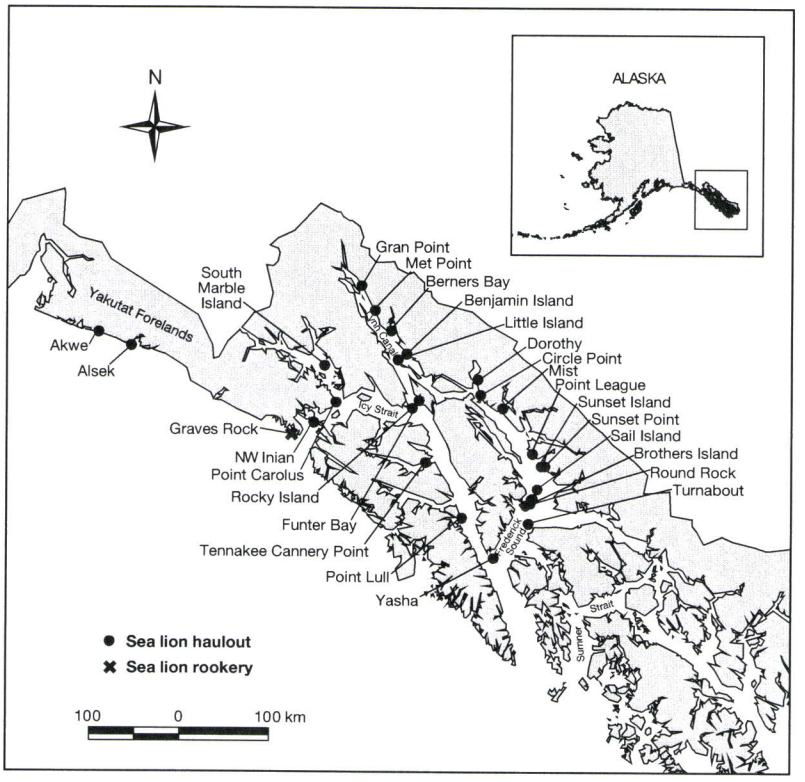


Fig. 1. *Eumetopias jubatus*. Haulout sites surveyed monthly in SE Alaska and 2 sites on Yakutat forelands surveyed only in spring

through an open window from an altitude of 250 to 300 m at a speed of 183 to 210 km h^{-1}. Along the Yakutat forelands, 2 haulout sites were surveyed, between February and May only, by the US Forest Service (Bill Lucey, Yakutat Ranger District, Yakutat, Alaska, pers. comm.)

Photographic slides of haulouts were taken using a 35 mm auto-focus camera (Nikon 8008S) equipped with a 70 to 210 mm zoom lens and an auto-focus digital camera (Nikon D1X) equipped with a 70 to 300 mm zoom lens. Overlapping photographs were taken if more than 1 photograph was needed to count sea lions at each haulout.

The clearest slide image was projected onto white paper, and each sea lion was marked and counted twice by an experienced counter using a hand-held tally counter. Digital photographic images were stored on digital media cards and later downloaded to a computer. The clearest digital image of each group was imported into geographic information system (GIS) software and each image was counted twice.

Number of Steller sea lions in water at eulachon and herring aggregations. During the spawning season of herring and eulachon (March to May) in 2002 and 2003, we counted sea lions visible on the surface of the water at spring spawning aggregations of Pacific herring and eulachon (Fig. 2). Aerial surveys were conducted as for monthly surveys, but at an altitude of 316 m.

During 2002, Pacific herring and eulachon spawning sites in NSEAK were surveyed 3 to 5 times during the spawning season at approximately 7 to 10 d intervals; however, sites south of Sumner Strait in southern SE Alaska (SSEAK) were surveyed only once. During 2003, all sites in NSEAK and SSEAK were surveyed 3 to 5 times. We attempted to enumerate all sea lions at herring and eulachon spawning sites; transects were flown parallel to the shoreline approximately 200 m offshore. When sea lions were detected at the surface of the water, we circled them and took photographs. If sea lions were diving (a dive usually lasts from 60 to 90 s), we circled until all sea lions were at the surface. For eulachon spawning sites, we surveyed the entire shoreline of the estuary/bay associated with the river where eulachon spawn. For herring, the entire shoreline associated with herring spawn was surveyed. We assumed fishes were present if we observed (1) commercial and/or subsistence fishing activity, (2) fish schools, (3) spawn/milt on the surface of the water (for herring only), or (4) presence of avian predator aggregations.

Geographical ecology: geographical information system (GIS) database. To synthesize the geographical ecology of Steller sea lions, herring and eulachon, all known current sea lion haulouts in the study area were compiled from observations and a database from the National Marine Fisheries Service. Location and timing of herring and eulachon aggregations were obtained from Alaska Department of Fish & Game and unpublished sources. These data were incorporated into a database and imported into a GIS software package. A map was created with coverages of Steller sea lion haulouts (Fig. 1), herring spawning locations, and eulachon spawning locations (Fig. 2).

The GIS database was used to determine the distance between Steller sea lion haulout sites and Pacific herring and eulachon spring spawning sites. In particular, we determined (1) swimming distance from sea lion haulouts to the closest eulachon and herring aggregation; (2) number of herring and eulachon spawning aggregations within a swimming distance of

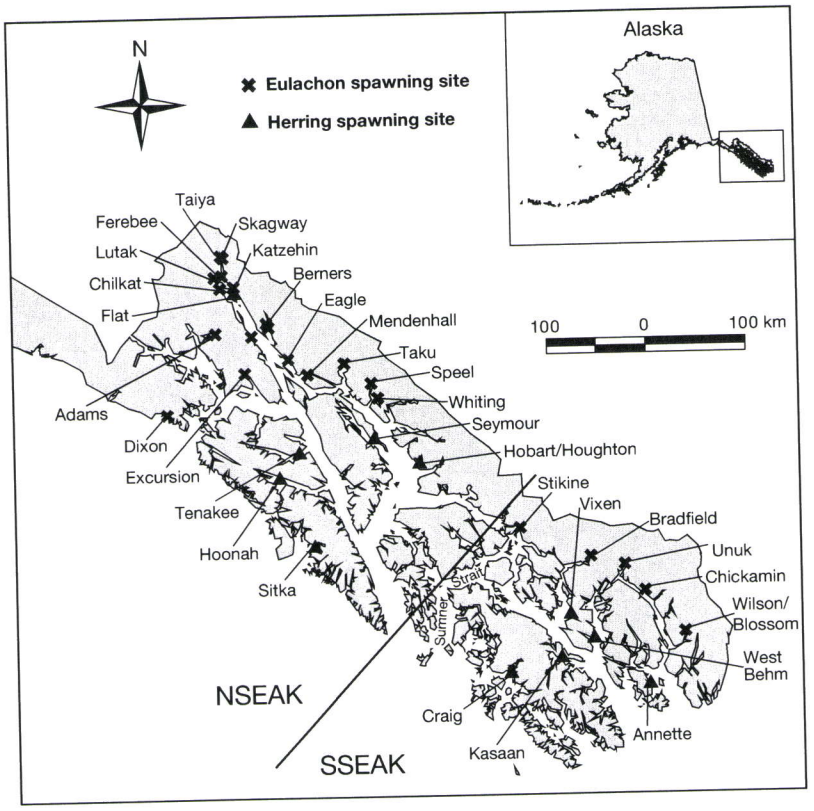


Fig. 2. *Clupea pallasii* and *Thaleichthys pacificus*. Spawning sites surveyed during spring 2002 and 2003

20, 40, 60, 80, and 100 km. These distances were based on the range of distances that sea lions may travel on a foraging trip from a haulout (Merrick & Loughlin 1997, Loughlin et al. 2003, Raum-Suryan et al. 2004).

Seasonal haulout classification. The seasonal use of haulouts was determined by examining the monthly counts of Steller sea lions. We classified haulouts according to seasonal patterns of occupation. Some haulouts peaked in more than 1 season. A peak in number of sea lions was defined as a count that was at least 80% of the maximum count of sea lions at a haulout for that year. We also tried values of 70 and 90% of the maximum count of sea lions, and found little difference in the outcome. Seasons were defined as winter (December to February), spring (March to May), summer (June to August), and fall (September to November). The haulouts were classified as Spring Peak Haulouts (peak numbers of sea lions during spring), Spring Ephemeral Haulout (only occupied by sea lions during spring), other haulouts (peak numbers of sea lions in summer, fall or winter).

Fish biomass estimation. Herring biomass was determined from spawn deposition surveys in areas in which commercial herring fisheries were monitored during the spring-spawning season of 2002 and 2003 (K. Hebert, unpubl. data, Alaska Department of Fish and Game). The spawn deposition methods combined SCUBA diver estimates of herring egg deposition, estimates of total area receiving spawn, and average fecundity to derive an estimate of herring spawning biomass (Pritchett & Hebert 2003).

Biomass data were not available for eulachon spawning sites in SE Alaska, with the exception of Berners Bay (Sigler et al. 2004).

Statistical analyses. For parametric analyses, data were square root-transformed when they did not meet equal variance and normality assumptions of analysis of variance (ANOVA) (Zar 1999). A Spearman rank-order correlation coefficient (Siegel & Castellan 1988) was used to determine the association between (1) the maximum number of sea lions and the minimum distance to eulachon and herring aggregations and (2) the number of forage fish aggregations within designated distances of sea lion haulouts.

To determine if the sea lion count data were spatially auto-correlated, we examined whether nearby haulouts were more closely related than distant haulouts (e.g. Sullivan 1991). Data on maximum sea lion counts were examined for both 2002 and 2003. For all pair-wise combinations of haulout locations, the squared difference of maximum sea lion count and the inter-pair distance were computed. The squared difference was averaged by a 10 nautical mile (n mile) length interval (the variogram) and plotted versus inter-pair distance. Distance between haulouts was not a significant predictor of the average squared difference between maximum sea lion counts. Therefore, we concluded that the sea lion count data were not spatially correlated at the scale of the 10 n mile length intervals (2002, linear regression, $p = 0.47$, $df = 9$; 2003, linear regression, $p = 0.90$, $df = 9$).

RESULTS

Seasonal distribution of Steller sea lions

The distribution of sea lions at haulouts varied seasonally. Some sea lion haulouts were only occupied seasonally, whereas other sites were occupied year-round but with peak numbers of sea lions during certain seasons (Table 1, Fig. 3).

Table 1. *Eumetopias jubatus*. Maximum (max.), mean, and standard deviation of counts of Steller sea lions at haulouts in NSEAK. nc: no count

Location	2001			2002		
	Max.	Mean	SD	Max.	Mean	SD
Alsek[a]	770 (Apr)	326.9	272.7	1347 (Apr)	779.0	502.0
Dorothy[a]	15 (May)	1.5	4.7	283 (Apr)	27.71	20.39
Berners Bay[a]	13 (Apr)	1.08	1.08	0	0	0
Gran Point	850 (May)	323.2	351.2	1087 (Apr)	390.42	404.9
Mist	371 (May)	71.33	118.3	319 (Apr)	75.78	100.1
Met Point	129 (May)	30.3	46.1	221 (Nov)	59.62	74.5
South Marble Island	746 (Apr)	422.77	199.9	791 (Oct)	468.83	201.4
Sunset Island	706 (Jul)	246.88	264.5	740 (May)	271.06	233.8
Graves Rocks	1114 (Aug)	551.88	359.9	1218 (Jul)	513.75	354.3
Benjamin Island	797 (Oct)	248.66	243.2	747 (Dec)	268.16	252.8
Round Rock	42 (Oct)	14.4	16.2	63 (Oct)	32.38	21.8
Point Lull	266 (Apr)	78.22	90.9	218 (Mar)	101.4	92.0
Sunset Point	nc	nc	nc	229 (Apr)	53.64	81.8
Southwest Brothers	1283 (Aug)	483.25	355.3	1752 (Aug)	544.07	424.1
Yasha Island	769 (Aug)	283	204.6	1664 (Jul)	324.21	445.6
Sail Island	644 (Aug)	279.25	249.0	1124 (Sep)	281.07	385.9
Tenakee Cannery Point	182 (Oct)	34.6	60.8	251 (Dec)	55.21	82.2
Circle Point	286 (Oct)	76.88	104.8	240 (Oct)	60.68	84.0
Turnabout Island	181 (Oct)	27.75	62.7	187 (Oct)	27.75	62.6
West Brothers	421 (Oct)	74	151.2	291 (Dec)	66	109.9
NW Inian Island	291 (Oct)	126.77	81.7	345 (Jul)	129.5	90.4
Rocky Island	255 (Oct)	93.5	96.1	385 (Oct)	121.46	110.6
Point Carolus	114 (Oct)	19.8	38.7	278 (Oct)	30.15	77.1
Point League	50 (Mar)	6.55	16.4	364 (Dec)	59.07	109.8
Little Island	376 (Sep)	116.3	178.2	685 (Sep)	62.6	182.6
Funter Bay	44 (Feb)	11.38	5.06	40 (Jan)	10	18.3

[a]haulout occupied only during spring

Spatial relationships between sea lion haulouts and forage fish aggregations

Prediction 1: haulout type versus distance to closest eulachon and herring aggregation. Spring peak haulouts were located significantly closer to eulachon spawning sites than haulouts that peaked at other times of year (ANOVA, 2001: $F_{1,22} = 5.92$, $p = 0.024$; 2002: $F_{1,23} = 8.13$, $p = 0.009$). Spring peak haulouts were located on average 28.0 ± 9.01 km from the closest eulachon spawning site (Fig. 4). Spring ephemeral haulouts at Berners Bay, Alsek, Akwe, and Dorothy were occupied only in spring near eulachon runs. Haulouts that peaked at other times of year were located on average 70.63 ± 6.95 km from the closest eulachon spawning site (Fig. 4). However, the distance to herring spawning sites was not significantly different between spring peak and other peak haulouts (ANOVA, 2001: $F_{1,22} = 1.25$; $p = 0.28$; 2002: $F_{1,22} = 0.73$, $p = 0.401$). Spring peak haulouts were located on average 37.4 ± 7.6 km from the closest herring spawning site whereas haulouts that peaked at other times of year were located 26.33 ± 3.64 km from the closest herring spawning site (Fig. 4).

Prediction 2: number of sea lions versus distance to closest forage fish aggregation. The maximum number of sea lions at haulouts in spring was inversely correlated with the distance to the closest forage fish aggregation (herring and eulachon combined) only in 2002 (2002: $r_s = -0.43$, $n = 25$, $p < 0.025$; 2003: $r_s = -0.18$, $n = 25$, $0.10 < p < 0.25$ (Fig. 5). Although, there was no significant association in 2003, there was a similar trend to that in 2002. The maximum number of sea lions at haulouts in spring was correlated between 2002 and 2003 ($r^2 = 0.60$, $F_{1,23} = 35.13$, $n = 25$, $p < 0.05$).

When analyzed separately the correlation of sea lions with distance to eulachon aggregations was marginally significant in 2002 but not in 2003 (2002: $r_s = -0.31$, $n = 25$, $0.05 < p < 0.10$; 2003: $r_s = -0.18$, $n = 25$, $0.10 < p < 0.25$). There was no significant correlation between the maximum number of sea lions at haulouts in spring and distance to herring aggregations (2002: $r_s = -0.06$, $n = 25$, $p > 0.25$; 2003 $r_s = 0.16$, $n = 25$, $0.10 < p < 0.25$).

Prediction 3: number of sea lions versus number of eulachon and herring aggregations. The maximum number of sea lions at haulouts in spring was positively associated with the number of eulachon and herring (combined) spawning sites within 20 km in 2002 and 2003 (2002: $r_s = 0.56$, $n = 24$, $p < 0.0025$; 2003: $r_s = 0.42$, $n = 24$, $p < 0.025$) (Table 2). However, this relationship reflects only an association with eulachon spawning sites, because there was little association with the number of herring spawning sites except at distances greater than 60 km (Table 2).

Steller sea lions in water at spring-spawning fish aggregations

The sea lions in the water during spring at the spawning aggregations of herring and eulachon were counted. The numerical response of sea lions to eulachon spawning sites was much greater in NSEAK than in SSEAK. Eulachon spawning sites in NSEAK at Berners Bay, Lutak Inlet, and Taku Inlet attracted over 200 sea lions during the spawning season in 2002. The number of sea lions peaked at Taku Inlet (235 sea

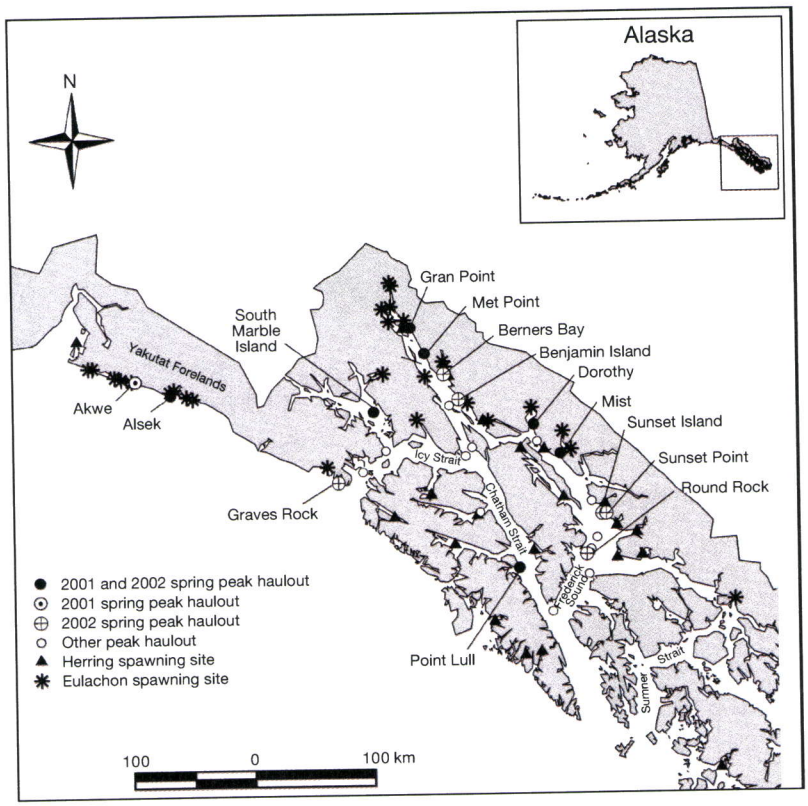


Fig. 3. *Eumetopias jubatus*. Haulouts where numbers of sea lions ashore peaked in 2001 and 2002 in relation to spawning locations of eulachon and herring in SE Alaska

lions) on April 10, at Berners Bay (949 sea lions) on April 18, and at Lutak Inlet (506 sea lions) on April 29, 2002. The maximum number of sea lions observed at Berners Bay, Lutak Inlet, and Taku Inlet was greater in 2002 than in 2003. During 2003, only Berners Bay and Taiya Inlet attracted over 200 sea lions. In SSEAK, the only sea lion aggregation detected at an eulachon spawning site was a group of 25 sea lions observed at Bradfield Canal (Fig. 6).

Sea lions attended herring spawning sites in NSEAK and SSEAK. At most herring spawning sites, the maximum number of sea lions observed was greater in 2003 than in 2002, corresponding to higher herring biomass at 4 of the spawning sites (Fig. 7). Herring spawning sites at Craig, Sitka, and Seymour attracted more than 200 sea lions in both years. Tenakee, Hoonah Sound, and Hobart herring spawning sites had 50 to 199 sea lions present (Fig. 7A).

Prediction 4: number of sea lions versus herring biomass. Although sea lions were recorded in the water at herring spawning sites in NSEAK and SSEAK, the correlation between the maximum number of sea lions (square-root) and the (log) biomass of herring was only marginally significant ($r^2 = 0.23$, $n = 14$, $p = 0.08$) (Fig. 8).

DISCUSSION

Sea lion distribution in relation to eulachon spawning sites

The spatial distribution of sea lions during spring clearly reflects the distribution of spawning eulachon in NSEAK, particularly in Lynn Canal and along the Yakutat forelands. Sea lions were concentrated near spawning runs and in areas with a high density of spawning runs. In some cases, haulouts (i.e. Alsek, Dorothy, Berners Bay and Akwe) were occupied only during the time of a nearby eulachon spawning run. Similarly in British Columbia at Sands Head near the mouth of the Fraser River, sea lions were observed only in spring between late March and late May from 1978 to 1982, which coincided with eulachon entering the Fraser River to spawn (Bigg 1988).

The concentration of sea lions in these areas reduced the travel distance to the spawning runs and thus decreased foraging costs for sea lions. Use of haulouts close to rich prey resources allows females with dependent pups to conserve travel energy and allocate more resources to pups (Boyd 1998). In addition, using haulout sites close to rich prey resources may allow dependent young to accompany their mothers to sea,

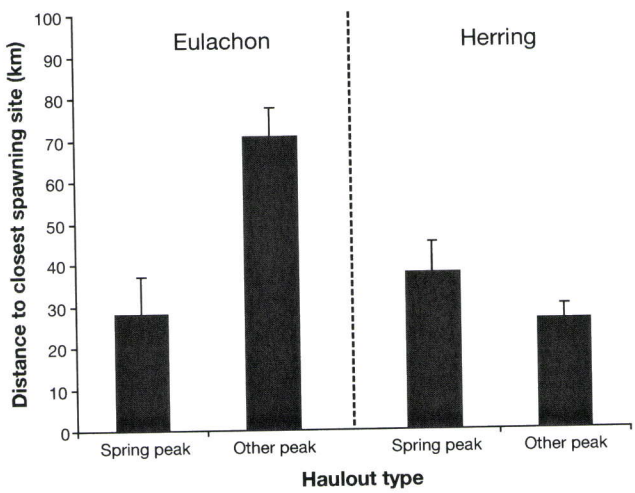


Fig. 4. *Eumetopias jubatus*. Mean distance to closest eulachon spawning and herring spawning site from spring peak and other haulouts

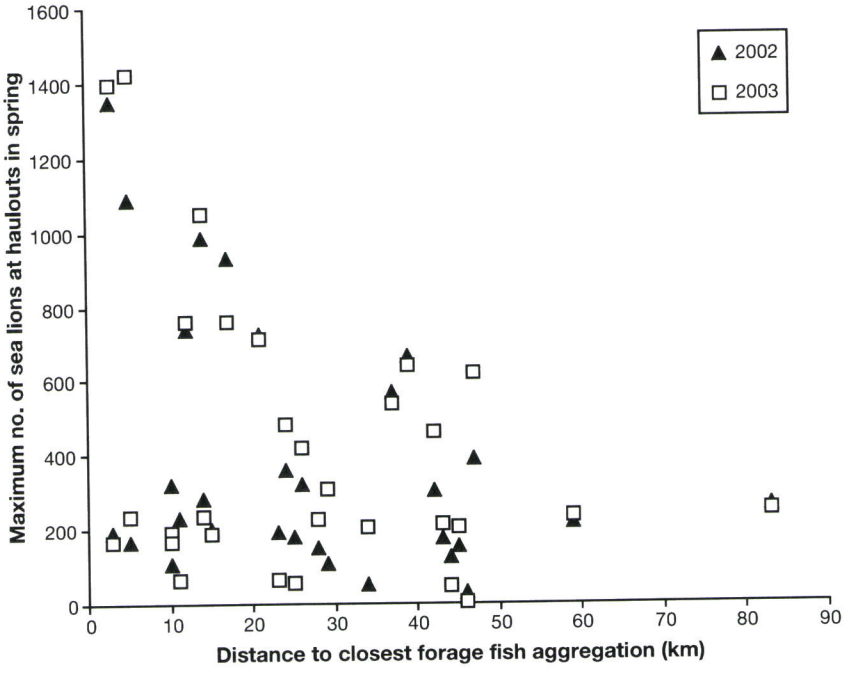


Fig. 5. *Eumetopias jubatus*. Scatterplot of maximum number of sea lions at haulouts in spring in relation to closest forage fish aggregation

as the average distance traveled by sea lion pups less than 9 mo olds was ≤15 km in SE Alaska (Raum-Suryan et al. 2004).

Use of haulouts closest to spawning runs also permits better tracking of the arrival and departure of the temporary and localized prey. The pulsed nature of eulachon runs makes the spawning period difficult to detect, and sea lions move to haulouts and raft in areas close to eulachon spawning sites.

However, as evident from Fig. 5, some haulouts were not located close to spawning runs, thus suggesting that some sea lions are not responding to the runs. They may be exploiting other unassessed prey resources. It is also possible that non-breeding individuals are less likely to capitalize on spawning runs than breeding individuals.

In Lynn Canal on April 18, 2002, approximately 4% (949 sea lions) of the estimated sea lion population of SE Alaska was observed in Berners Bay at a eulachon spawning aggregation. On the same day there were an additional 1244 sea lions at the 3 haulout sites in Lynn Canal within 60 km of Berners Bay. It is probable that sea lions using these haulout sites during this time period are also visiting the eulachon spawning aggregation at Berners Bay and so may account for as much as 10% of the estimated sea lion population in SE Alaska (Sigler et al. 2004). On April 21, 2003, 5.5% of the estimated sea lion population of SE Alaska was found at Berners Bay and at haulouts within 60 km (Sigler et al. 2004). The total number of sea lions attending the runs may be considerably larger. It is likely that there is turnover in the number of sea lions visiting the eulachon spawning sites, as they may return to haulouts to provision their pups.

Although sea lions were numerous at eulachon spawning sites in NSEAK, few were detected at eulachon spawning sites in SSEAK. There are several possible explanations for this. Eulachon runs in SSEAK may not be as large as those in NSEAK; however, there are currently no data available for eulachon biomass in SE Alaska, with the exception of Berners Bay (Sigler et al. 2004). In addition, some bays in NSEAK have more than one river used by spawning eulachon, and thus potentially a greater concentration of eulachon for predators to exploit. In some areas such as Berners Bay, additional forage fish species including Pacific herring and capelin spawn in the bay during spring. Finally, in some areas in British Columbia near the southern border of SSEAK, the size of eulachon spawning runs has decreased and industrial trawl fish-

Table 2. *Eumetopias jubatus*. Spearman rank correlation coefficients between number of forage fish aggregations (eulachon and herring) at designated distances and the maximum number of sea lions at haulouts in spring of 2002 and 2003. All FFa: all forage fish aggregations, i.e. eulachon and herring combined

Distance (km)	Eulachon				Herring				All FFa			
	2002		2003		2002		2003		2002		2003	
	r	p	r	p	r	p	r	p	r	p	r	p
0–20	0.44	<0.025	0.26	<0.25	0.32	<0.10	0.26	<0.25	0.56	<0.0025	0.42	<0.025
0–40	0.31	<0.10	0.17	<0.25	0.01	>0.25	−0.11	>0.25	0.33	<0.10	0.14	<0.25
0–60	0.08	>0.25	−0.23	<0.25	−0.32	<0.10	−0.23	<0.25	0	>0.25	−0.01	>0.25
0–80	0.05	>0.25	0.01	>0.25	−0.36	>0.05	−0.46	<0.025	−0.09	>0.25	−0.15	<0.25
0–100	−0.06	>0.25	−0.09	>0.25	−0.38	>0.05	−0.39	<0.05	−0.18	<0.25	−0.24	<0.25

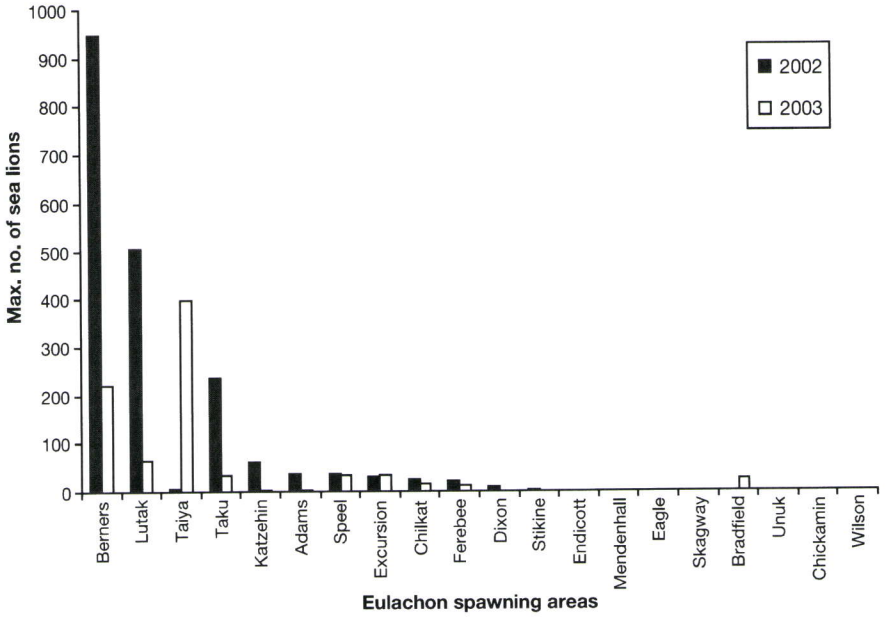


Fig. 6. *Eumetopias jubatus*. Maximum numbers in the water at eulachon spawning sites in SE Alaska in 2002 and 2003

eries have been developed (Hay et al. 1996) that have the potential to diminish the biomass of fish available to predators.

Sea lion distribution in relation to herring spawning sites

In contrast to the observed responses to eulachon runs, sea lions were not observed to congregate at haulouts near herring spawning aggregations. However, large numbers of sea lions were observed in the water at herring spawning sites in 2002 and 2003, although there were no significant relationships between the number of herring spawning sites and numbers of sea lions except at distances >60 km, which is probably not biologically meaningful. These concentrations of sea lions were associated (marginally significant) with estimates of herring biomass. Furthermore, annual differences in the number of sea lions observed corresponded to annual differences in herring biomass, particularly in some locations (Sitka Sound, Craig, Hoonah Sound and Hobart).

Herring appear to be an important prey resource for sea lions in spring, as evidenced by the number of sea lions counted in the water at herring spawning sites, but they are important in fall and winter in some areas (Thomas & Thorne 2001). Herring was the most frequent prey item in sea lion scat during winter at Benjamin Island in SE Alaska, from 2001 to 2003 (88.9% frequency of occurrence; n = 678 scat samples) (Womble & Sigler unpubl. data). The importance of herring in the diet of sea lions throughout the fall and winter in some areas may explain the lack of observed associations between sea lion numbers and herring spawning sites. If sea lions are exploiting herring throughout the winter, it may not be advantageous to change haulout locations during the spring spawning season, since herring form high-density aggregations during fall for up to 6 mo of the year (Thomas & Thorne 2001). Although the energy density and fat content of herring decreases in spring prior to the spawning season (Paul et al. 1998), herring are still higher in energy content than other species such as pollock (Iverson et al. 2002).

Other seasonal prey resources

Other seasonal prey species, such as Pacific salmon, provide high-energy resources at other times of year and may influence the distribution of sea lions. For example, the total number of sea lions in Frederick Sound increased during July, August, and September (J. Womble unpubl. data) and coincided with the return of pink salmon *Oncorhynchus gorbuscha* to the area. Frederick Sound is one of the main migratory corridors for pink salmon returning to SEAK spawning grounds in July and August (Heard 1991). Energy densities of salmon are higher after oceanic feeding than after entry into fresh water (Hendry & Berg 1999), thereby providing seasonally available high-energy prey to sea lions.

Detecting seasonal pulses in sea lion distribution and diet

Although seasonal changes in the distribution and abundance of sea lions have been documented (Bonnot 1951, Bartholomew & Boolootian 1960, Kenyon & Rice 1961, Mathisen & Lopp 1963, Smith 1972, Mate 1975, Harestad 1977, Sullivan 1980, Calkins & Pitcher 1982, Bigg 1988, Sease & York 2003), previous efforts have focused predominantly on the breeding season. Documenting the abundance of Steller sea lions in the breeding season is important; however, elucidating seasonal shifts in abundance and distribution is also im-

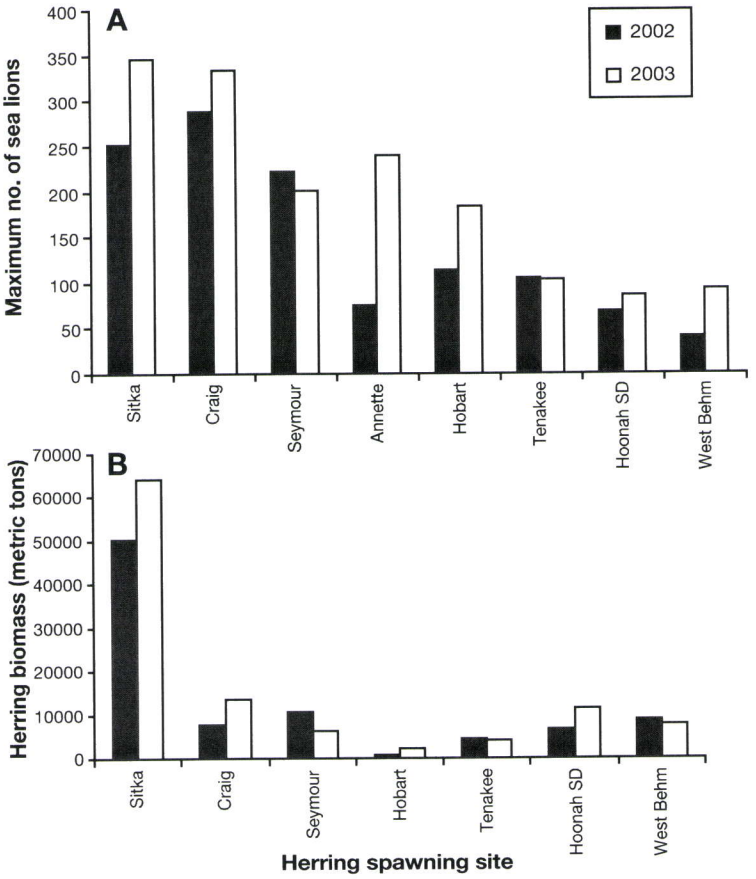


Fig. 7. *Eumetopias jubatus* and *Clupea pallasii*. (A) Maximum numbers of sea lions in the water and (B) estimated herring biomass at herring spawning sites in SE Alaska in 2002 and 2003. Herring biomass data provided by Alaska Department of Fish and Game, Division of Commercial Fisheries, Alaska

portant as it relates to life-history characteristics of sea lions and their prey species. The availability, concentration, and energy density of prey species changes seasonally, so some fish species may be more valuable to exploit than others at particular times of year (Jangaard 1974, Montevecchi & Piatt 1984, Mårtensson et al. 1996, Iverson et al. 2002). Furthermore, data on seasonal shifts in sea lion abundance are important in furthering our understanding and interpretation of annual trends in the abundance of sea lions (Bigg 1988).

Traditional methods of determining the presence of prey species in pinniped diets, such as scat analysis, may not be sufficient to detect pulsed prey resources. Eulachon probably comprise an important prey species for sea lions in spring but they are not a commonly detected prey species in sea lion scat during the breeding season (Merrick et al. 1997, Sinclair & Zeppelin 2002), and dietary studies during the breeding season would not reflect the seasonal importance of eulachon. At Benjamin Island, eulachon were found in only 8.6% of scat samples collected quarterly from 2001 to 2003; however, their frequency was greatest in April (19.0% frequency of occurrence; n = 152 scat samples) and corresponded to the spring-spawning season of eulachon (J. Womble & M. Sigler unpubl. data). Furthermore, when Steller sea lions aggregate at the eulachon and herring spawning sites in spring, they do not return to haulout sites regularly but often raft up, rest, and defecate in the water near the spawning site, so even weekly scat collection at haulouts during the spring may not reflect the importance of this seasonally pulsed prey in the diet. In addition, prey species with small otoliths, such as eulachon and capelin, may be underestimated in the diet when consumed together with large species such as pollock (Tolitt et al. 2003). Thus, scat collections should be used in combination with other methods such as fatty acid (Iverson et al. 1997) and stable isotope analysis (Kurle 2002) and should be conducted frequently enough to determine the presence of seasonally pulsed prey, such as eulachon.

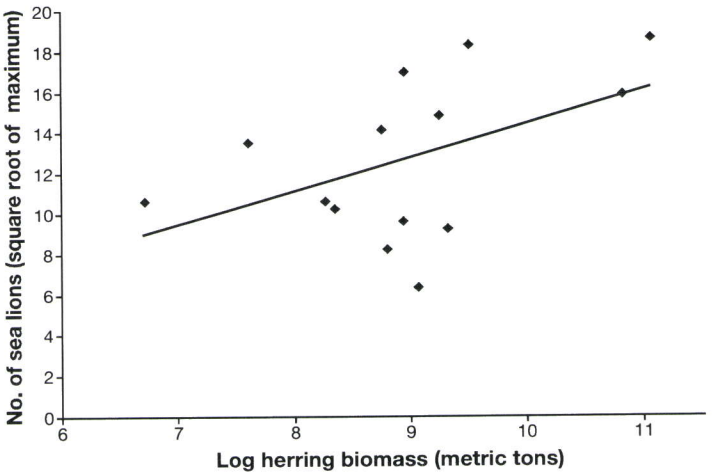


Fig. 8. *Clupea pallasii*. Scatterplot of (log) herring biomass in relation to (square-root) maximum number of sea lions *Eumetopias jubatus* at herring spawning sites in SE Alaska for 2002 and 2003

Implications of spring-spawning fish aggregations for Steller sea lions

To meet the energetic demands of the costly otariid reproductive strategy, using haulouts that are close to high-density, high-energy prey resources is advantageous during spring, an energetically demanding time for sea lions. Foraging at spring spawning fish aggregations should allow Steller sea lion males to arrive at rookeries in good body condition. Larger, more fit males are likely to successfully defend territories for longer periods of time (Boyd & Duck 1991) and mate with more females, thus increasing their reproductive success (Bartholomew 1970). Females nursing a dependent pup may need to consume twice the energy that a female without a pup would require (Winship et al. 2002) and may be pregnant and simultaneously nursing a pup during spring. Good body condition for females prior to the breeding season is critical for sea lions to give birth to healthy pups and to have the ability to nourish their young for an extended lactation period. Pitcher et al. (1998) found that the probability of a female sea lion being pregnant during late gestation was positively related to body condition, including mass and blubber index. Thus access to high-energy prey resources during late gestation may be critical for successful reproduction in female sea lions. Ultimately, seasonally aggregated, high-energy prey species, particularly eulachon, influence the seasonal distribution of sea lions in some areas of SEAK. To further our understanding of the importance of seasonally pulsed resources to sea lion life history, it will be necessary to examine body condition, foraging costs, and fitness directly.

Acknowledgements. We thank J. Norvell of Tal Air, a skilled pilot and keen observer, for many safe hours in the air. M. Masden also provided aerial survey expertise in Ketchikan. J. Scott-Ashe, K. Blejwas, M. Kunnasranta, K. White, B. Williams and numerous volunteers have persevered in all seasons during aerial surveys. W. Lucey (USFS) conducted aerial surveys along the Yakutat forelands. K. Hebert (ADF&G) provided herring data for SEAK. L. J. Haldorson, T. C. Shirley, and 3 anonymous reviewers provided helpful reviews of earlier drafts of the manuscript. Funding for this study was provided by the Rasmuson Fisheries Research Fellowship Center at the University of Alaska Fairbanks to J.N.W., University of Alaska, National Marine Fisheries Service-Steller Sea Lion Research Initiative Award # NA16FX1419, and the National Marine Fisheries Service-Auke Bay Laboratory. Monthly aerial surveys were carried out under Marine Mammal Protection Act permit no. 782-153202.

LITERATURE CITED

Anthony JA, Roby DD, Turco TR (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J Exp Mar Biol Ecol 248:53–78

Bartholomew GA (1970) A model for the evolution of pinniped polygyny. Evolution 24:546–559

Bartholomew GA, Boolootian RA (1960) Numbers and population structure of the pinnipeds on the California Channel Islands. J Mammal 41:366–375

Ben-David M (1997) Timing of reproduction in wild mink: the influence of spawning Pacific salmon. Can J Zool 75: 376–383

Bigg MA (1988) Status of the Steller sea lion, *Eumetopias jubatus*, in Canada. Can Field-Nat 102:315–336

Bishop MA, Green SP (2001) Predation on Pacific herring *Clupea pallasii* spawn by birds in Prince William Sound, Alaska. Fish Oceanogr 10 (Suppl 1):149–158

Blundell GM, Ben-David M, Bowyer RT (2002) Sociality in river otters: cooperative foraging strategies or reproductive strategies? Behav Ecol 13:134–141

Bonner WN (1984) Lactation strategies in pinniped: problems for a marine mammalian group. Symp Zool Soc 51: 253–272

Bonnot P (1951) The sea lions, seals, and sea otter of the California coast. Calif Fish Game 37:371–389

Boyd IL (1998) Time and energy constraints in pinniped lactation. Am Nat 152:717–728

Boyd IL, Duck CD (1991) Mass changes and metabolism in territorial male Antarctic fur seals *Arctocephalus gazella*. Physiol Zool 64:375–392

Byrd GV, Merrick RL, Piatt JF, Norcross BL (1997) Seabird, marine mammal, and oceanography coordinated investigations (SMMOCI) near Unimak Pass, Alaska. In: Forage fishes in marine ecosystems. Proceedings of an International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97-01, University of Alaska, Fairbanks, p 351–364

Calkins DG, Pitcher KW (1982) Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska. In: Environmental Assessment of the Alaska Continental shelf. Final reports of Principal Investigators. U.S. Department of the Commerce and U.S. Department of Interior, OCSEAP, Anchorage, AK, Volume 19, p 445–546

Carlson HR (1980) Seasonal distribution and environment of Pacific herring near Auke Bay, Lynn Canal, Southeastern Alaska. Trans Am Fish Soc 109:71–78

Costa DP (1993) The relationship between reproductive and foraging energetics and the evolution of Pinnipedia. Symp Zool Soc 66:293–314

Gende SM, Womble JN, Willson MF, Marston BH (2001) Cooperative foraging in Steller sea lions (*Eumetopias jubatus*). Can Field-Nat 115:355–356

Gittleman JL, Thompson SD (1988) Energy allocation in mammalian reproduction. Am Zool 28:863–875

Groot C, Margolis L (eds) (1991) Pacific salmon life histories. University of British Columbia Press, Vancouver

Hansen AJ (1987) Regulation of bald eagle reproductive rates in southeast Alaska. Ecology 6:1387–1392

Harestad AS (1977) Seasonal abundance of northern sea lions, *Eumetopias jubatus* (Schreber), at McInnes Island, British Columbia. Syesis 10:173–174

Hay DE, Boutillier J, Joyce M, Langford G (1996) The eulachon (*Thaleichthys pacificus*) as an indicator species in the North Pacific. In: Forage fishes in marine ecosystems. Proceedings of an International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97-01, University of Alaska, AK, p 509–530

Heard WR (1991) Life history of pink salmon *Oncorhynchus gorbuscha*. In: Groot C, Margolis L (eds) Pacific salmon

life histories. University of British Columbia Press, Vancouver, p 119–230
Hendry AP, Berg OK (1999) Secondary sexual characteristics, energy use, senescence, and the cost of reproduction in sockeye salmon. Can J Zool 77:1663–1675
Heyman WD, Graham RT, Kjeríve B, Johannes RE (2001) Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. Mar Ecol Prog Ser 215:275–282
Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C (1999) The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Can J Zool 77:132–138
Iverson SJ, Frost KJ, Lang SLC (2002) Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: factors contributing to among and within species variability. Mar Ecol Prog Ser 241:161–181
Jangaard PM (1974) The capelin *Mallotus villosus*: biology, distribution, exploitation, utilization and composition. Bull Fish Res Board Can 186:1–70
Kenyon KW, Rice DW (1961) Abundance and distribution of the Steller sea lion. J Mammal 42:223–234
Kurle CM (2002) Stable-isotope ratios of blood components from captive northern fur seals *Callorhinus ursinus* and their diet: applications for studying the foraging ecology of wild otariids. Can J Zool 80:902–909
Laws EA, Bienfang PK, Ziemann DA, Conquest LD (1988) Phytoplankton population dynamics and the fate of production during the spring bloom in Auke Bay, Alaska. Limnol Oceanogr 33:57–65
Litzow MA, Piatt JF, Prichard AK, Roby DD (2002) Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey. Oecologia 132:286–295
Loughlin TR, Sterling JT, Merrick RL, Sease JL, York AE (2003) Diving behavior of immature Steller seal ions (*Eumetopias jubatus*). Fish Bull US Natl Mar Fish Serv 101:566–582
MacLeod K, Fairbairns R, Gill A, Fairbairns B, Gordon J, Blair-Myers C, Parsons ECM (2004) Seasonal distribution of minke whales *Balaenoptera acutorostrata* in relation to physiography and prey off the Isle of Mull, Scotland. Mar Ecol Prog Ser 277:263–274
Marston BH, Willson MF, Gende SM (2002) Predator aggregations during eulachon *Thaleichthys pacificus* spawning runs. Mar Ecol Prog Ser 231:229–236
Mårtensson PE, Gotaas ARL, Nordøy ES, Blix AS (1996) Seasonal changes in energy density of prey of northeast Atlantic seals and whales. Mar Mammal Sci 12:635–640
Mate BR (1975) Annual migration of the Steller sea lion and California sea lion along the coast of Oregon. Rapp P-V Réun Cons Perm Int Explor Mer 169:455–461
Mathisen OA, Lopp RJ (1963) Photographic census of the Steller sea lion herds in Alaska, 1956–1958. US Fish Wildl Serv Spec Sci Rep Wildl 424
Mehlum F, Hunt GL, Klusek Z, Decker MB, Nordlund N (1996) The importance of prey aggregations to the distribution of Brünnich's guillemots in Storfjordern, Svalbard. Polar Biol 16:537–547
Merrick RL, Loughlin TR (1997) Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. Can J Zool 75:776–786
Merrick RL, Chumbley MK, Byrd GV (1997) Diet diversity of Steller sea lions *Eumetopias jubatus* and their population decline in Alaska: a potential relationship. Can J Fish Aquat Sci 54:1342–1348
Montevecchi WA, Piatt JF (1984) Composition and energy contents of mature inshore spawning capelin *Mallotus villosus*: implications for seabird predators. Comp Biochem Physiol A 78:15–20
Oftedal OT, Bonness DJ, Tedman RA (1987) The behavior, physiology, and anatomy of lactation in the Pinnipedia. In: Genoways HH (ed) Current mammalogy, Vol 1. Plenum Press, New York, p 175–245
Orians GH, Pearson NE (1977) On the theory of central place foraging. In: Horn DJ, Stairs GR, Mitchell RD (eds) Analysis of ecological systems. Ohio State University Press, Columbus, p 153–177
Paul AJ, Paul JM, Brown ED (1998) Fall and spring somatic energy content for Alaskan Pacific herring (*Clupea pallasi*) relative to age, size, and sex. J Exp Mar Biol Ecol 223: 133–142
Payne PM, Nicolas JR, O'Brien L, Powers KD (1986) The distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel, *Ammodytes americanus*. Fish Bull US Natl Mar Fish Serv 84:271–277
Perez MA (1994) Calorimetry measurements of energy value of some Alaskan fishes and squids. NOAA Techn Rep NMFS AFSC-32
Pitcher KW (1981) Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. US Nat Mar Fish Bull 79: 467–472
Pitcher KW, Calkins DG (1981) Reproductive biology of Steller sea lions in the Gulf of Alaska. J Mammal 62: 599–605
Pitcher KW, Calkins DG, Pendleton GW (1998) Reproductive performance of female Steller sea lions: an energetics-based reproductive approach. Can J Zool 76:2075–2083
Pritchett D, Hebert K (2003) Southeast Alaska/Yakutat Annual Herring Research Report, 2000/2002 Season. Regional Information Report 1J03–26. Alaska Department of Fish and Game, Division of Commercial Fisheries, Juneau, Alaska
Raum-Suryan, KL Rehburg, MJ, Pendleton, KW, and Gelatt, TS (2004) Development of dispersal, movement patterns, and haulout use by pup and juvenile Steller sea lions *Eumetopias jubatus* in Alaska. Mar Mammal Sci 20: 823–850
Robbins CT (1983) Wildlife feeding and nutrition. Academic Press, New York
Rodway MS, Regehr HM, Ashley J, Clarkson PV, Goudie RI, Hay DE, Smith CM, Wright KG (2003) Aggregative response of harlequin ducks to herring spawning in the Strait of Georgia, British Columbia. Can J Zool 81:504–514
Rounsefell GA (1930) Contribution to the biology of the Pacific herring, *Clupea pallasii*, and the condition of the fishery in Alaska. Bull US Bur Fish Vol XLV:227–320
Rounsefell GA, Dalgreen EH (1935) Races of herring, *Clupea pallasii*, in southeastern Alaska. Bull US Bur Fish Vol XLVIII:119–141
Sease JL, York AE (2003) Seasonal distribution of Steller's sea lions at rookeries and haul-out sites in Alaska. Mar Mammal Sci 19:745–763
Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioral sciences. 2nd edition. McGraw-Hill Book, New York
Sigler MF, Womble JN, Vollenweider JJ (2004) Availability to Steller sea lions *Eumetopias jubatus* of a seasonal prey resource: a pre-spawning aggregation of eulachon *Thaleichthys pacificus*. Can J of Fish Aquat Sci 61:1475–1484
Sinclair EH, Zeppelin TK (2002) Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). J Mammal 84:973–990
Skov HJ, Durinck J, Andell P (2000) Associations between wintering avian predators and schooling fish in the Skag-

gerrak–Kattegat suggest reliance on predictable aggregations of herring *Clupea harengus*. J Avian Biol 31: 135–143

Smith ID (1972) Sea lions wintering along the outer coast of Vancouver Island. J Fish Res Board Can 29:18764–1766

Springer AM (1992) A review: walleye pollock in the North Pacific. How much difference do they really make? Fish Oceanogr 1:80–96

Sullivan PJ (1991) Stock abundance estimation using depth-dependent trends and spatially correlated variation. Can J Fish Aquat Sci 48: 1691–1703

Sullivan RM (1980) Seasonal occurrence and haul-out use in pinnipeds along Humboldt County, California. J Mammal 61:754–760

Swartzman G, Hunt GL (2000) Spatial association between murres *Uria* spp., puffins (*Fratercula* spp.) and fish shoals near Pribilof Islands, Alaska. Mar Ecol Prog Ser 206: 297–309

Thomas GL, Thorne RE (2001) Night-time predation by Steller sea lions: new insight into the feeding habits of these mammals will help conservation attempts. Nature 411:1013

Tolitt DJ, Wong M, Winship AJ, Rosen DAS, Trites AW (2003) Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of Steller's sea lion *Eumetopias jubatus*. Mar Mammal Sci 19: 724–744

Willson MF, Halupka KC (1995) Anadromous fish as keystone species in vertebrate communities. Conserv Biol 9: 489–497

Willson MF, Gende SM, Marston BH (1998) Fishes and the forest: expanding perspectives on fish/wildlife interactions. BioScience 48:455–462

Winship AJ, Trites AW (2003) Prey consumption of Steller sea lions *Eumetopias jubatus* off Alaska: how much prey do they require? Fish Bull US Natl Mar Fish Serv 101:147–167

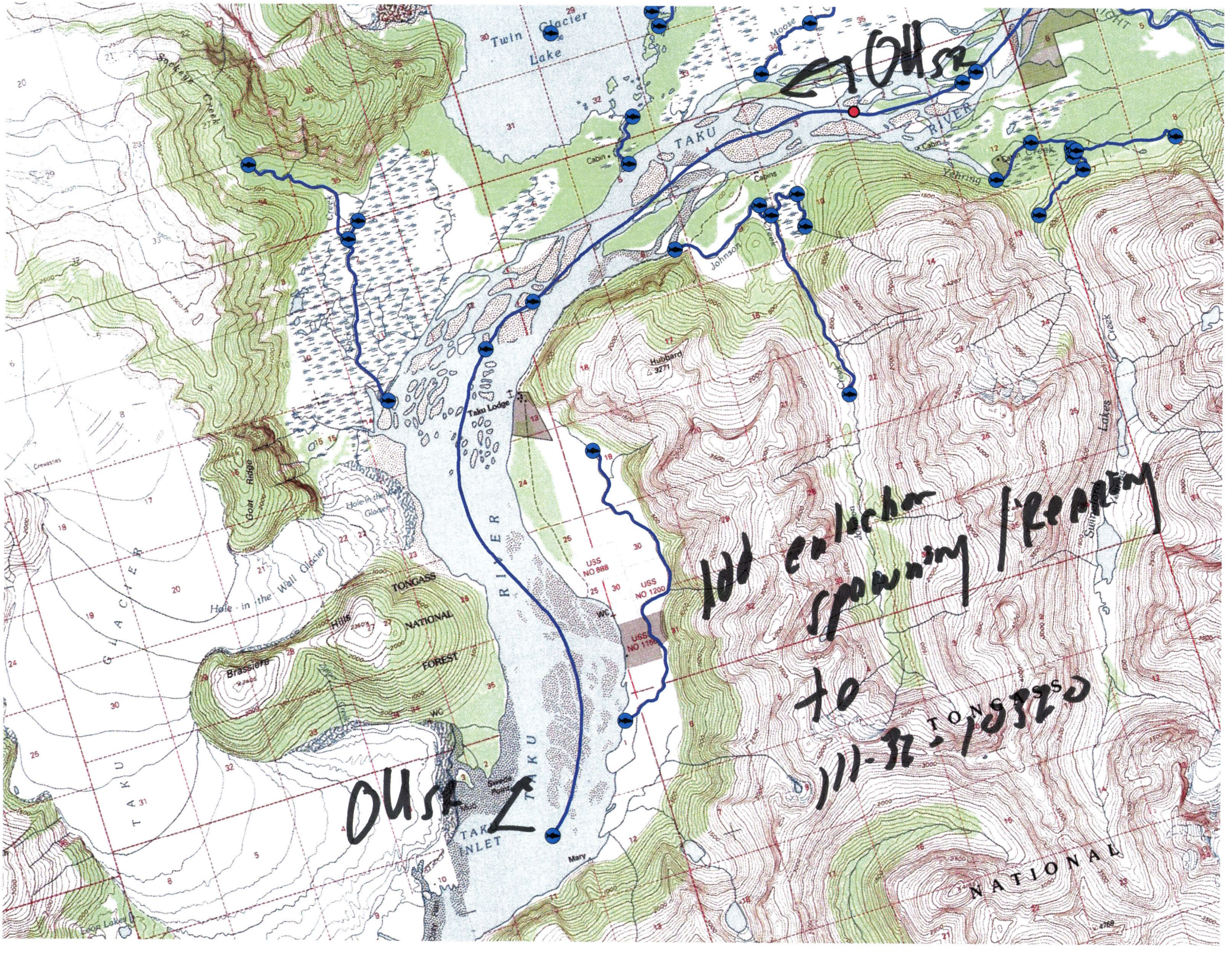
Winship AJ, Trites AW, Rosen DAS (2002) A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska. Mar Ecol Prog Ser 229:291–312

Withrow DE (1982) Using aerial surveys, ground truth methodology, and haul out behavior to census Steller sea lions, *Eumetopias jubatus*. MS thesis, University of Washington, Seattle, WA

Zar JH (1999) Biostatistical analysis. 4th edn. Prentice-Hall, Upper Saddle River, NJ

Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

Submitted: January 14, 2004; Accepted: December 21, 2004
Proofs received from author(s): May 9, 2005


Twin Glacier Lake
Moose
TAKU
RIVER
Cabin
Cabins
Yehring
Johnson
Creek
Taku Lodge
Hubbard
3271
Goat Ridge
Hole in the Wall Glacier
TONGASS
NATIONAL
FOREST
Brassiere
Hills
USS NO 888
USS NO 1200
USS NO 1160
WC
Swede Point
TAKU INLET
Mary
Sulfur
Lakes
Creek
NATIONAL
TONGASS
Ouse
Ouse
Not earlier spawning
to
11-12-10