



Distribution and spawning dynamics of capelin (*Mallotus villosus*) in Glacier Bay, Alaska: a cold water refugium

MAYUMI L. ARIMITSU,^{1,*} JOHN F. PIATT,²
MICHAEL A. LITZOW,^{2,3} ALISA A.
ABOOKIRE,^{2,3} MARC D. ROMANO^{2,4} AND
MARTIN D. ROBARDS^{2,5}

¹U.S. Geological Survey, Alaska Science Center, 3100 National Park Rd, Juneau, AK 99801, USA

²U.S. Geological Survey, Alaska Science Center, 1011 E. Tudor Rd., Anchorage, AK 99503, USA

³Present address: Michael A. Litzow and Alisa A. Abookire, National Marine Fisheries Service, 301 Research Ct., Kodiak, AK 99615, USA

⁴Present address: Marc D. Romano, U.S. Fish and Wildlife Service, 911 NE 11th Ave, Portland, OR 97232, USA

⁵Present address: Martin D. Robards, University of Alaska Fairbanks, P.O. Box 757500, Fairbanks, AK 99775, USA

ABSTRACT

Pacific capelin (*Mallotus villosus*) populations declined dramatically in the Northeastern Pacific following ocean warming after the regime shift of 1977, but little is known about the cause of the decline or the functional relationships between capelin and their environment. We assessed the distribution and abundance of spawning, non-spawning adult and larval capelin in Glacier Bay, an estuarine fjord system in southeastern Alaska. We used principal components analysis to analyze midwater trawl and beach seine data collected between 1999 and 2004 with respect to oceanographic data and other measures of physical habitat including proximity to tidewater glaciers and potential spawning habitat. Both spawning and non-spawning adult Pacific capelin were more likely to occur in areas closest to tidewater glaciers, and those areas were distinguished by lower temperature, higher turbidity, higher dissolved oxygen and lower chlorophyll *a* levels when compared with other areas of the bay. The distribution of larval Pacific capelin was not sensitive to glacial influence. Pre-spawning females collected farther from tidewater glaciers were at a lower maturity state than those sampled closer to tidewater glaciers,

and the geographic variation in the onset of spawning is likely the result of differences in the marine habitat among sub-areas of Glacier Bay. Proximity to cold water in Glacier Bay may have provided a refuge for capelin during the recent warm years in the Gulf of Alaska.

Key words: Glacier Bay, *Mallotus villosus*, marine climate, maturity, oceanography, spawning habitat

INTRODUCTION

Capelin were once an abundant and widespread species in the Gulf of Alaska and Bering Sea, but populations declined following the late 1970s regime shift (Anderson and Piatt, 1999; Hunt *et al.*, 2002; Mueter and Norcross, 2002). Once a major forage species for seabirds and marine mammals, they virtually disappeared from the diets of most marine predators after the regime shift (Piatt and Anderson, 1996; Sinclair and Zeppelin, 2002). While changing marine climate and predation are implicated in the decline of capelin, we know little about the influence of such factors on capelin in Alaska. In contrast to the Northern Atlantic, there is no commercial fishery directed on capelin in the Northeast Pacific and very few directed studies on their ecology in the region.

Capelin are a relatively high-energy content pelagic forage fish (Montevecchi and Piatt, 1984), and spawning aggregations may provide predictable prey resources to marine predators during a time when energetic demands are high (Womble *et al.*, 2005). Declines of marine predators such as Steller's sea lions (*Eumetopias jubatus*), harbor seals (*Phoca vitulina*), red-legged kittiwakes (*Rissa brevirostris*) and thick billed murre (*Uria lomvia*) have been linked to the decline of capelin and other preferred prey species in the Gulf of Alaska and Bering Sea after the late 1970s (Piatt and Anderson, 1996; Merrick, 1997; Trites and Donnelly, 2003).

During the late spring and summer, capelin concentrate nearshore in bays and fjords to spawn. In Alaska, capelin spawn in the intertidal on sandy beaches when water temperatures are between 5 and 9°C (Pahlke, 1985). Overwintering and migration

*Correspondence. e-mail: marimitsu@usgs.gov

Received 4 May 2007

Revised version accepted 28 September 2007

habits of capelin in the Gulf of Alaska are poorly known. The presence of immature and larval capelin during the fall and winter months in the nearshore areas of Prince William Sound and Kodiak Island, Alaska (Doyle *et al.*, 2002) suggests that capelin use these areas for rearing (Brown, 2002).

Glacier Bay, a fjord in southeastern Alaska, was designated as a national monument in 1925 and has been the focus of intensive research relevant to resource management in recent years (e.g., Piatt and Gende, 2007). During the summer months, the fjord is a core area for populations of several marine predators that are known to feed on capelin. For example, Glacier Bay supports perhaps a quarter of the world population of breeding Kittlitz's Murrelets (*Brachyramphus brevirostris*), a candidate species for listing under the Endangered Species Act (Agness, 2006) due to significant declines in the bay and elsewhere (Romano *et al.*, 2007). In contrast, Steller's sea lion numbers have increased at Glacier Bay haulouts by as much as 38% per annum, and 79% of marked animals from the endangered western stock have dispersed to the area (Gelatt *et al.*, 2007). Capelin has been identified as an important prey item for both the Kittlitz's murrelet, as documented by fish holding behavior (Agness, 2006), and the Steller's sea lion, as documented by remains in scat (Gelatt *et al.*, 2007).

Although capelin is an important forage species that responds rapidly to changes in marine climate (Rose, 2005), there is a scarcity of published information regarding the mechanisms that influence the distribution of capelin in Alaska. We sampled capelin using small-meshed midwater trawls and beach seines, and we characterized habitat using a conductivity–temperature–depth (CTD) water profiler and beach sediment type (Sharman *et al.*, 2005). In this paper, we examine the distribution of spawning, non-spawning adult and larval capelin relative to maturity, body condition and measures of habitat in Glacier Bay, Alaska.

MATERIALS AND METHODS

Study area

Glacier Bay is a Y-shaped estuarine fjord that is undergoing rapid de-glaciation (Fig. 1). The bay is approximately 100 km long and several tidewater glaciers are located near the head of the bay. The bathymetry of the fjord is marked by constrictions and shallow sills, which contribute to localized oceanographic conditions. Deep and glacially influenced stratified waters characterize the upper bay, whereas turbulent upwelling and complete mixing of the water column is observed over the shallow sill

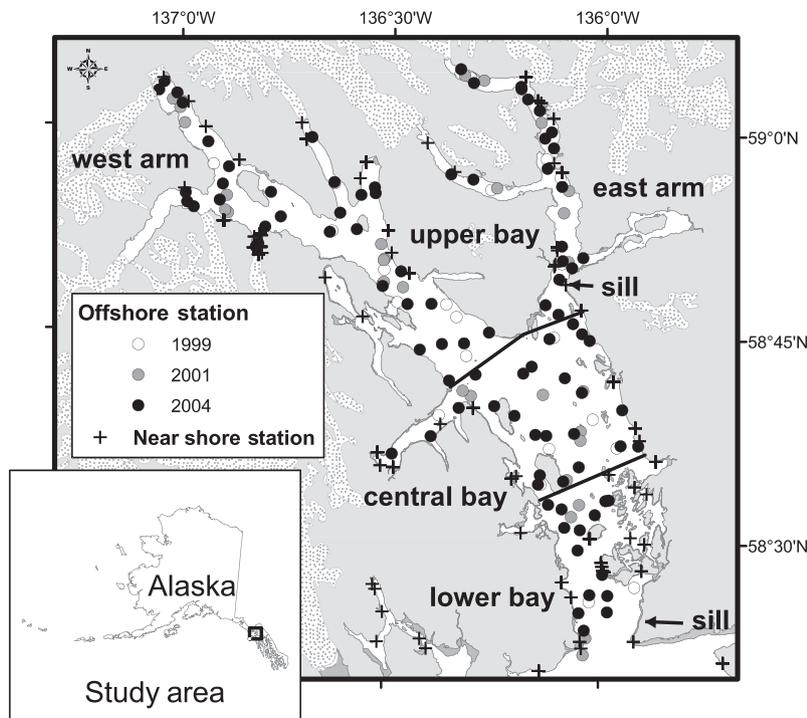


Figure 1. Map of study area and fishing effort by method. Stippled areas represent glaciers. Offshore trawl stations are indicated with circles and nearshore seine stations are indicated with plus signs. Sub-areas used in the analysis were determined by topographic and bathymetric features and are separated by black lines. Major sills are indicated with arrows. Note, the east arm and west arm combined represent the upper bay.

that marks the lower bay. The deep inner basin, which characterizes the central bay experiences intermediate stratification that is less influenced by tidal action than the lower bay during the summer months (Etherington *et al.*, 2007).

Data collection

We sampled offshore (>50 m from shore) and near-shore (<50 m from shore) fish communities during 1999–2004 to characterize the distribution and abundance of prey available to marine predators (Table 1, Fig. 1). We sampled 146 offshore stations with a modified herring trawl (see Abookire *et al.*, 2002; Abookire and Piatt, 2005 for details of methods). The midwater trawl had a mouth opening of 50 m², diminishing mesh size from 5 cm at the mouth to 1 cm at the codend and 1 mm in the collection cup. A trawl monitor system was used to manage the depth of the headrope. Average distance towed was 2.5 km, average tow speed was 4.6 km h⁻¹ and average tow duration was 35 min. We also sampled fish communities at 71 nearshore stations with 271 beach seine sets following methods described by Cailliet *et al.* (1986). The 37 m long seine had 28 mm stretched mesh at the wings and a 5 mm nylon mesh bag at the center. All fishing was conducted during daylight hours in the summer months (June–August). The catch was sorted by species, and fork length (FL, mm) measurements were taken from up to 50 randomly selected individuals of each species collected at a station. Catch per unit effort (CPUE) was standardized as number of fish km towed⁻¹ for midwater trawls, and number of fish set⁻¹ for beach seines. In 2004, all ovid capelin were frozen in seawater for further examination.

In 2004, we sampled the pelagic habitat at 86 midwater trawl stations using a CTD equipped with a fluorometer, oxygen sensor, photosynthetically active radiation (PAR) sensor and a beam transmissometer. For all stations, the CTD was lowered to 5 m above

the seafloor or 100 m. Discrete water samples were collected from 2, 8 and 40 m and vacuum filtered for total chlorophyll *a* (chl *a*) analyses using Whatman glass fiber filters. Samples were extracted in 90% acetone and chl *a* concentration was measured using a laboratory fluorometer. *In situ* chl *a* values were calibrated using the linear relationship between field fluorometer and laboratory measurements ($y = 0.3137x + 0.7747$, $R^2 = 0.81$). We calculated a turbidity index using the ratio of beam attenuation (which represents the loss of light as a result of absorption and scattering from suspended particles, phytoplankton, bacteria and dissolved organic material) to fluorescence.

In 2004, body condition and maturity were assessed for a random subsample of spawning females from the east and west arms ($N = 29$ and 30 , respectively), and all samples from the lower bay ($N = 14$). Fork length, body weight, and left and right ovary weight were recorded for each female. Stomach contents, if present, were weighed and identified to the lowest possible taxon. Oocytes from the center of the left ovary were examined and photographed. The greatest diameter along a horizontal plane was measured for 50 oocytes for maturity estimates as described by West (1990) and maturity class was assessed according to Forberg (1983).

Data analysis

Statistical analyses were performed by using JMP statistical software (SAS, 2003). When the assumptions of normality and homoscedasticity were violated for parametric tests, non-parametric tests were used as indicated. To describe the distribution of spawning, non-spawning adult and larval capelin, we consider stations conducted in four sub-areas within Glacier Bay including the east arm ($N = 19$), west arm ($N = 31$), central bay ($N = 25$) and lower bay ($N = 11$) (Fig. 1). For the purposes of this paper, we refer to the east arm and west arm as glacial areas and the central and lower bay as distal areas.

The location and extent of potential spawning habitat was assessed using intertidal sediment data and ground photos, obtained from Glacier Bay's Coast Mapping Inventory Program (Sharman *et al.*, 2005), following the methods of Moulton (2000). Beach sediment size suitable for successful spawning ranges from 0.5 to 25 mm grain diameter (Pitt, 1958; Nakashima and Wheeler, 2002). Suitable spawning beaches were homogenous beaches with primary, secondary and interstitial sediment types between 0.06 and 64 mm (i.e., fine sand to pebble designation). Segments containing >10% cobble, boulder, bedrock or

Table 1. Sampling dates and fishing effort (number of sets) by method in Glacier Bay during 1999–2004.

Sampling dates	Year	Midwater trawl	Beach seine
6/10–6/23	1999	25	87
5/31–8/21	2000	–	164
6/29–8/7	2001	30	–
7/23–8/6	2003	–	20
6/22–7/14	2004	91	–
Total		146	271

the obvious presence of organisms such as mussels (*Mytilus* spp.) or algae that would interfere with substrate availability were removed from the analysis. Although the high end of the pebble designation is considerably larger than the documented beach sediment size for spawning capelin, visual inspection of ground photos aided in the exclusion of beach segments with larger pebbles as the primary substrate. Although we did not attempt to verify spawning at potentially suitable beaches, smaller pebbles were the primary substrate at three beaches in Glacier Bay where spawning capelin were collected in beach seines (Arimitsu *et al.*, 2007).

For maturity data, percent roe content (ovary weight/body weight) was highly correlated with mean oocyte diameter ($r = 0.82$, $N = 73$); and therefore we used mean oocyte diameter as a proxy for maturity and tested for area differences in maturity development with an ANOVA. Tukey–Kramer HSD ($\alpha = 0.05$) multiple comparison tests were used to detect pair-wise differences. We ranked maturity stage in order from lowest (IIb) equal to one and highest (VI) equal to seven, and used a Kruskal–Wallis one-way ANOVA to test for sub-area differences in maturity.

Principal components analysis (PCA) was used to reduce the variation contained within several correlated habitat parameters to a few uncorrelated axes (Manly, 1991). For this analysis, we averaged oceanographic variables over a 0–35 m depth range because most capelin were collected between these depths. Physical variables included in the PCA were temperature, turbidity index, dissolved oxygen, chl *a* concentration, salinity, PAR, distance to nearest tidewater glacier, distance to shore, distance to nearest potential spawning habitat, and thermocline and halocline depth and intensity (data were averaged in 5 m depth bins due to rapidly changing temperature and salinity conditions near the surface). All environmental variables were log transformed and standardized by subtracting the mean and dividing by the standard deviation (Zar, 1999). Backwards stepwise regression was used to find the best fit model for the response of $\log(\text{CPUE} + 1)$ to principal components (P to remain ≤ 0.10). We back-calculated the coefficients of the original standardized physical variables by multiplying the matrix of eigenvectors with the regression coefficients of principal components from the best fit model (Legendre and Legendre, 1998). We report the coefficients of the standardized variables because the magnitude of response of spawning, non-spawning adult and larval capelin abundance (log-transformed CPUE) is directly comparable.

RESULTS

Distribution

Mature capelin were collected in 38% of midwater trawl stations in 2004, the only year we sampled spawning fish in sufficient numbers to analyze. We also observed capelin in spawning condition at one midwater trawl station in 2001, two nearshore sites in 2000 and one nearshore site in 2003 (Fig. 2a). In 2004, prespawning capelin CPUE differed among sub-areas (ANOVA: $F_{[3, 82]} = 23.70$, $P < 0.0001$). CPUE in the east arm was greater than CPUE in other regions of the bay (Tukey–Kramer HSD, $P < 0.05$). Mature capelin occurred more frequently at stations within glacial areas ($N = 55$) compared with distal areas ($N = 36$; $\chi^2_{[1]} = 17.04$, $P < 0.0001$). All spawning capelin were collected at relatively shallow depths in the water column (<30 m). The occurrence of mature capelin was not related to bottom depth ($\chi^2_{[1]} = 1.22$, $P = 0.27$).

Adult (FL >60 mm) capelin were collected at 57% of midwater trawl stations sampled between 1999 and 2004 (Fig. 2b). Adult CPUE differed among sub-areas (ANOVA: $F_{[3, 142]} = 19.08$, $P < 0.0001$) and CPUE in the east arm was greater (Tukey–Kramer HSD, $P < 0.05$) than CPUE in other sub-areas. Overall, adult capelin were more likely to occur in glacial areas compared with distal areas ($\chi^2_{[1]} = 20.93$, $P < 0.0001$). The majority (83%) of adult capelin were collected at depths of less than 30 m, and there was a weak negative relationship between the occurrence of adults and bottom depth ($\chi^2_{[1]} = 4.40$, $P < 0.05$).

Larval capelin (FL <60 mm) were collected in 70% of midwater trawl stations (Fig. 2c). The relative abundance of capelin larvae differed among sub-areas (ANOVA: $F_{[3, 142]} = 5.97$, $P < 0.001$). CPUE in the east arm was higher than CPUE in the west arm and lower bay, but not different from the central bay (Tukey–Kramer HSD, $P < 0.05$). We found no difference in the probability of occurrence of larvae in glacial and distal sub-areas ($\chi^2_{[1]} = 0.28$, $P = 0.60$). The majority (99%) of larval capelin were collected at depths of less than 30 m. There was a weak relationship between occurrence of larvae and bottom depth ($\chi^2_{[1]} = 4.44$, $P < 0.05$).

Maturity

Prespawning females from the lower bay were less mature than those in glacial sub-areas (Table 2). Mean oocyte diameter differed among sub-areas (ANOVA: $F_{[2, 71]} = 21.15$, $P < 0.0001$). Maturity differed between glacial sub-areas and the lower bay

Figure 2. Distribution and relative abundance of (a) spawning capelin, (b) adult capelin (fork length >60 mm), and (c) larval capelin (fork length <60 mm), during all years combined. Beach seine (BS) catch per unit effort (CPUE) is standardized as fish tow⁻¹ and midwater trawl (MWT) CPUE is standardized as fish km towed⁻¹.

Table 2. Characteristics of mature female capelin collected in different sub-areas of Glacier Bay.

Sub-area	N	Mean Julian date	Mean (±SD)	Mean	% of fish feeding
			oocyte diameter (mm)	roe content (%)	
East Arm	29	180	1.001 ± 0.084	26.9 ± 0.07	13
West Arm	30	181	0.928 ± 0.157	22.4 ± 0.08	23
Lower Bay	14	196	0.732 ± 0.171	12.9 ± 0.07	50

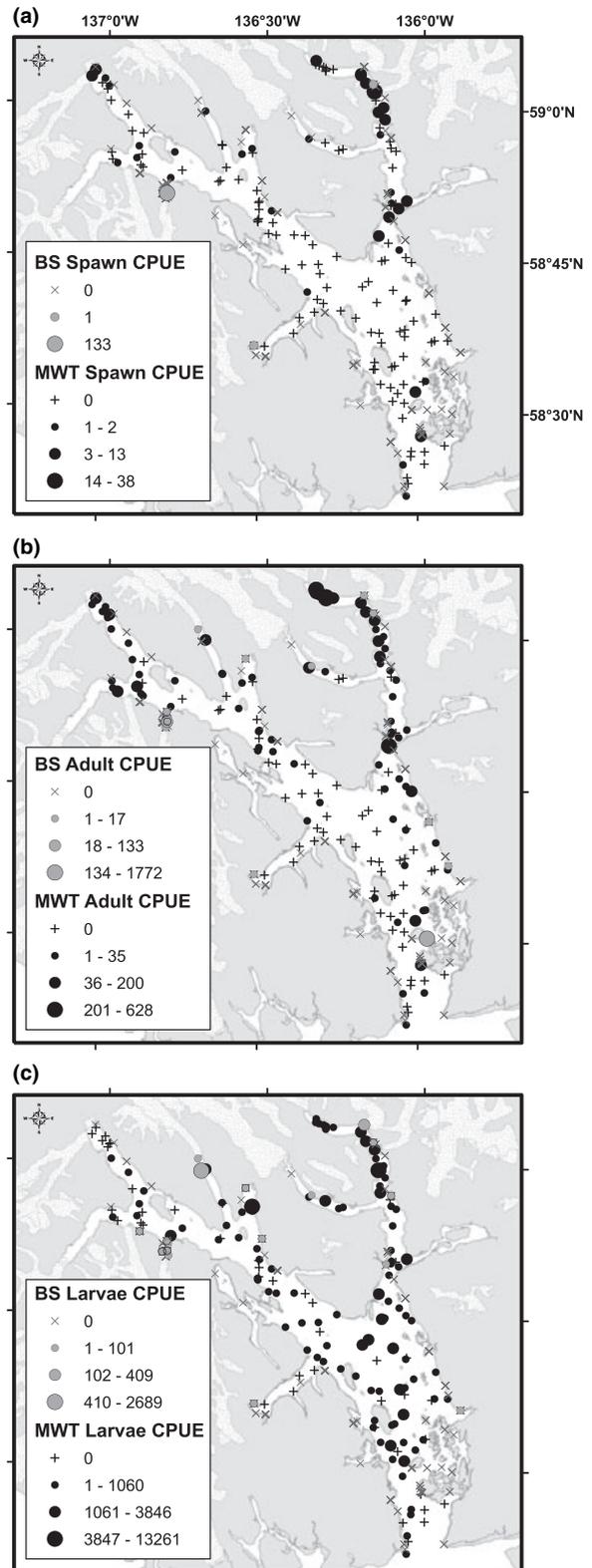
(Tukey–Kramer HSD, $P < 0.05$), but not between the east and west arms (Tukey–Kramer HSD, $P > 0.05$). Maturity stage differed among sub-areas (Kruskal–Wallis: $H_{[2]} = 26.50$, $P < 0.0001$). The lowest maturity classes IIb–IIIb (early maturing to maturing) were represented primarily by lower bay samples whereas the highest maturity class VI (spent) were collected only in the east arm. Lower bay samples were collected 15–16 days later than samples in the west and east arms, indicating that lower bay fish were at a lower maturity stage at a later date.

Fifty percent of the capelin we examined from the lower bay were actively feeding in contrast to 23 and 13% in west and east arm samples, respectively. The majority (67%) of feeding, spawning females we sampled were in maturity class III (maturing), 5% were in maturity class IV (fast maturing), and the remaining 27% were in maturity class V (mature). Capelin from the lower bay were feeding on copepods and other crustaceans and capelin from the west arm were feeding on euphausiids and other crustaceans. In contrast, capelin from the east arm were feeding primarily on smelt larvae.

Body condition

Mean fork length (±SD) for ripe females was 98.6 ± 9.6 mm ($N = 188$) and for spawning males was 111.7 ± 10.6 mm ($N = 89$). Two notably small ripe females (71, 72 mm) were collected in the east arm. Both were still undergoing metamorphosis into their adult form, a process that usually occurs between the first and second year of growth (Bailey *et al.*, 1977).

Length frequency plots for larval fish suggest that spawning occurred earlier in 1999 than in 2004. In



1999, all sampling was conducted in early to late June and the highest proportion of the catch comprised fish in the 30–40 mm range. Sampling in 2004 was conducted about 2 weeks later than in 1999 (Table 1) and the highest proportion of the catch comprised fish in the 20–30 mm range (Fig. 3). Adult capelin were smaller in length during 1999 compared with adults in 2001 and 2004, when lengths appeared to have a bi-modal distribution (Fig. 3).

Habitat

A total of 218 beach segments appeared to include potential spawning habitat based on sediment type (Fig. 4). The west arm contained 70 segments, east arm contained 51 segments, central bay contained 27

segments, the lower bay contained 42 segments and the remainder were located outside of Glacier Bay proper. Large stretches of potentially suitable beaches for capelin spawning were identified outside the main entrance of Glacier Bay, and smaller beach segments were identified throughout the bay itself (Fig. 4).

We detected several differences among sub-areas in oceanographic characteristics (Fig. 5). Glacial areas were significantly cooler ($F_{[3,82]} = 24.75, P < 0.0001$), had higher dissolved oxygen concentrations (ANOVA: $F_{[3,82]} = 22.92, P < 0.0001$), and had lower chl *a* concentrations (ANOVA: $F_{[3,82]} = 22.01, P < 0.0001$) than distal areas. Turbidity also varied among sub-areas (Welch's ANOVA: $F_{[3,35]} = 5.20, P = 0.005$). Salinity differed among sub-areas (ANOVA:

Figure 3. Length frequency by year for capelin sampled at offshore stations and expressed as a proportion of the catch for larval capelin (fork length <60 mm) and adult capelin (fork length >60 mm).

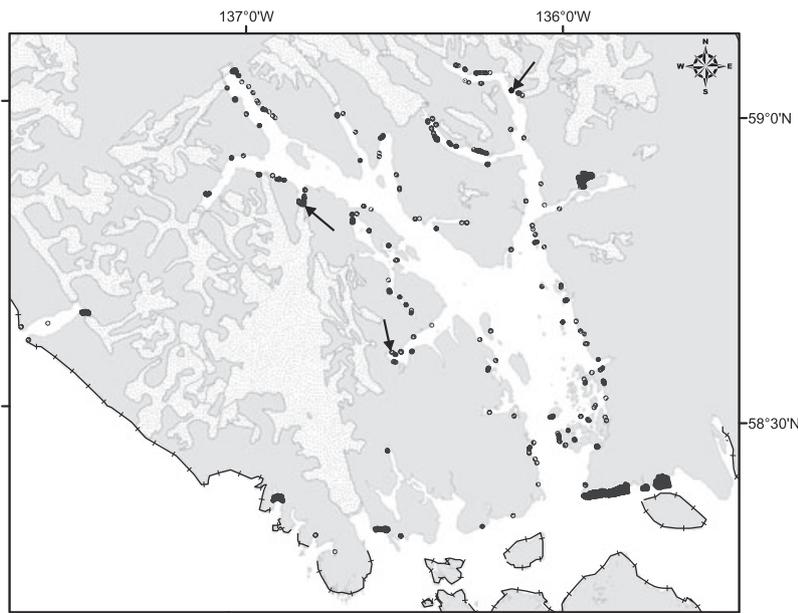
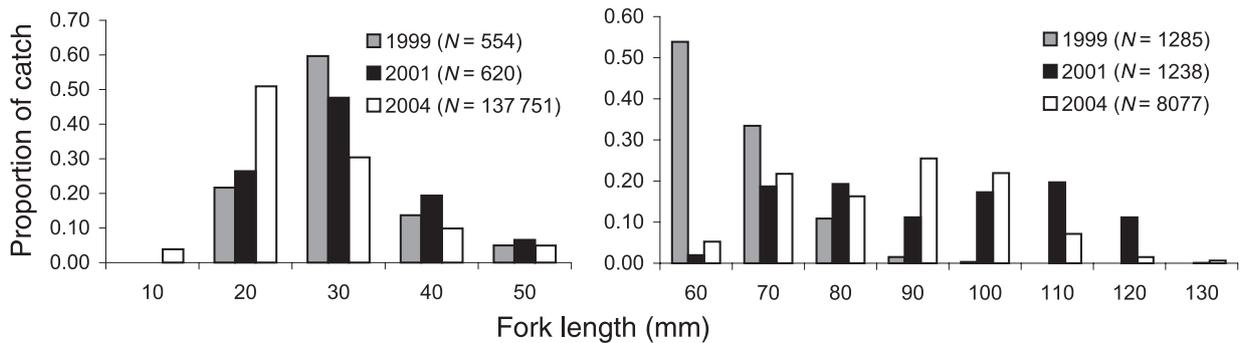


Figure 4. Potential capelin spawning habitat (black-shaded areas along the shoreline) in Glacier Bay. The entire shoreline was surveyed by Sharman *et al.* (2005) unless indicated by black cross-hatched lines. Arrows indicate beaches where spawning capelin were collected in beach seines during this study.

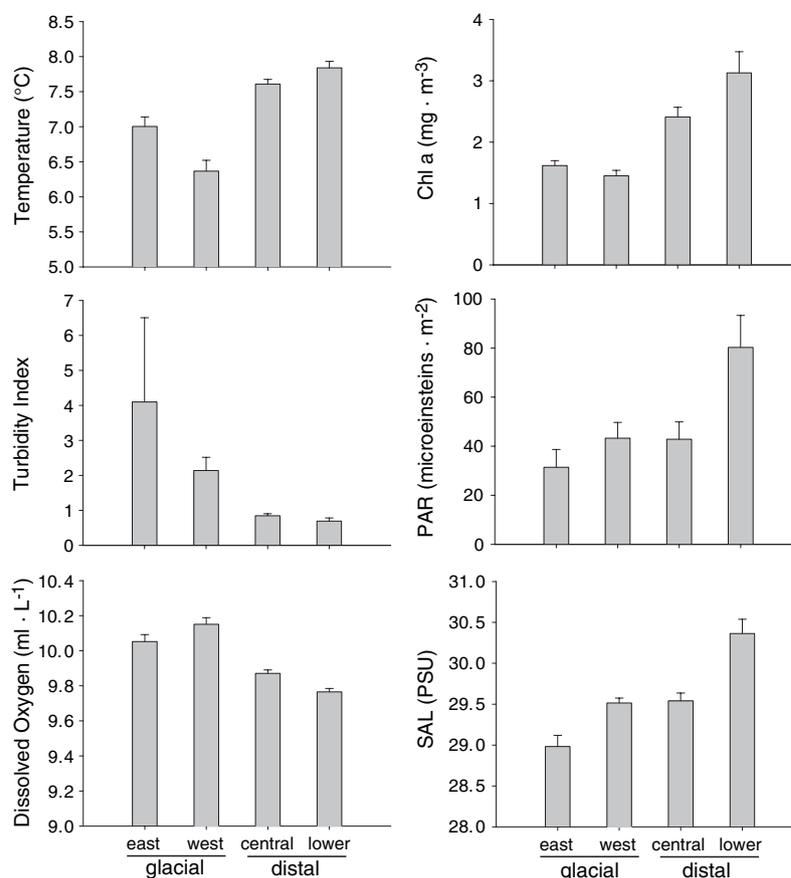


Figure 5. Mean (\pm SD) temperature, chlorophyll *a* concentration, turbidity index, photosynthetically active radiation (PAR), dissolved oxygen and salinity (SAL) for sub-areas in Glacier Bay during summer 2004.

$F_{[3,82]} = 19.63$, $P < 0.0001$), with the lowest values in the east arm and the highest values in the lower bay. However, average salinity in the central bay did not differ from the west arm (Tukey–Kramer HSD, $P > 0.05$). The lower bay had higher PAR values than other sub-areas (ANOVA: $F_{[3,82]} = 4.52$, $P < 0.01$). The first four principal components (PC) explained 75% of the variation contained in the physical parameters. Temperature, turbidity index, dissolved oxygen, chl *a* concentration, distance to glacier and halocline intensity were correlated with PC 1 ($r \geq |0.76|$), while halocline depth was correlated with PC 2 ($r = -0.71$) and thermocline depth was correlated with PC 4 ($r = 0.75$). PC 3 was most correlated with distance to shore ($r = -0.52$) (Table 3).

Best-fit models included PC 1 and PC 2 as significant explanatory variables for adult capelin CPUE ($F_{[2,83]} = 19.98$, $R^2 = 0.32$, $P < 0.0001$) and spawning capelin CPUE distributions ($F_{[2,83]} = 9.08$, $R^2 = 0.18$, $P < 0.01$). PC 2 and PC 3 were included in the best-fit model for larval CPUE distribution ($F_{[2,83]} = 4.80$, $R^2 = 0.10$, $P < 0.05$), although PC 2 was marginally significant (Table 4).

Regression coefficients for the original standardized variables suggest that distance to potential spawning habitat, water temperature, halocline depth and turbidity were more important to spawning and adult CPUE than other habitat characteristics (Table 5). Spawning and adult CPUE was higher at lower temperatures, while larval CPUE was higher in warmer temperatures. Adult CPUE had a positive response to halocline depth and turbidity index. Larvae had a positive relationship to distance from glacier while spawning and adult fish had a negative response. Larval CPUE was most influenced by thermocline intensity and salinity.

DISCUSSION

Across their circumpolar range, shifts in capelin distribution and abundance are related to the magnitude and persistence of ocean temperature change (Rose, 2005). Capelin redistribute to areas where their preferred water temperature occurs in response to changing environmental conditions (Frank *et al.*, 1996). Capelin abruptly disappeared from trawl

Table 3. Correlation between physical parameters and principal component (PC) axes 1 through 4.

Parameter (units)	PC 1 (41%)	PC 2 (14%)	PC 3 (11%)	PC 4 (9%)
Temperature (°C)	0.85	0.20	0.40	-0.07
Turbidity index	-0.78	-0.24	-0.03	-0.19
Dissolved oxygen (mg L ⁻¹)	-0.90	-0.12	-0.26	0.18
Chlorophyll <i>a</i> concentration (mg m ⁻³)	0.78	-0.03	0.29	-0.10
Salinity (PSU)	0.63	-0.24	-0.51	-0.31
Photosynthetically active radiation (microEinsteins m ⁻³)	0.43	0.25	-0.36	0.08
Distance to glacier (km)	0.80	0.08	0.28	-0.14
Distance to shore (km)	0.40	0.38	-0.52	0.29
Distance to potential spawning habitat (km)	0.53	0.44	-0.16	0.50
Thermocline depth (m)	0.17	-0.43	0.11	0.75
Thermocline intensity (°C)	-0.46	0.59	0.42	0.08
Halocline depth (m)	0.27	-0.71	0.27	0.30
Halocline intensity (PSU)	-0.76	0.41	0.23	0.17

Percentages in parentheses represent the amount of variability explained by each PC axis.

Table 4. Parameter estimates for multiple regression of dependent variables (log catch per unit effort of spawning, adult or larval capelin) to principal components (PC).

Dependent variable	R ² (model)	PC1	PC2	PC3	PC4
Spawn	0.18**	-0.0536**	-0.0675*		
Adult	0.32***	-0.1590***	-0.2108**		
Larvae	0.10*		0.1692 ^{NS}	0.2522*	

Asterisks indicate significance at $P < 0.0001$ (***), $P < 0.01$ (**) and $P < 0.05$ (*). NS indicates $0.05 < P < 0.10$ and blank cells indicate independent variables that were not included in the best fit model.

surveys and seabird diets throughout the Gulf of Alaska as water temperatures warmed markedly after the regime shift of 1977 (Piatt and Anderson, 1996; Anderson and Piatt, 1999). However, evidence suggests that in some locations, such as inshore areas of Kodiak, Lower Cook Inlet and Glacier Bay, where

Table 5. Parameter estimates for the response of spawning, adult and larval catch per unit effort to standardized physical variables.

Physical variable	Spawn	Adult	Larvae
Temperature	-0.0302	-0.0912	0.1123
Turbidity index	0.0301	0.0912	-0.0357
Dissolved oxygen	0.0270	0.0812	-0.0706
Chlorophyll <i>a</i> concentration	-0.0166	-0.0491	0.0578
Salinity	-0.0023	-0.0048	-0.1394
Photosynthetically active radiation	-0.0226	-0.0690	-0.0450
Distance to glacier	-0.0227	-0.0679	0.0693
Distance to shore	-0.0284	-0.0873	-0.0630
Distance to potential spawning habitat	-0.0345	-0.1058	0.0203
Thermocline depth	0.0179	0.0565	-0.0305
Thermocline intensity	-0.0189	-0.0609	0.1646
Halocline depth	0.0297	0.0938	-0.0317
Halocline intensity	-0.0032	-0.0127	0.1017

Coefficients are calculated by multiplying the matrix of eigenvalues for each physical variable by the parameter estimates for significant principal components in Table 4.

waters remained cold due to coastal upwelling or glacial influence, capelin remained locally abundant (Pahlke, 1985; Kreiger and Wing, 1986, Speckman *et al.* 2005). Similarly, catches of capelin in National Marine Fisheries Service Gulf of Alaska bottom trawl surveys were mostly restricted to colder inshore bays after the regime shift, and eventually expanded in distribution as temperatures cooled again in the 1990s (Mueter and Norcross, 2002). We believe that inshore areas, such as glacial fjords or other areas where the bathymetry promotes upwelling, may act as cold water refugia for capelin during periods of ocean warming.

Spawning of capelin in Alaska occurs over an extended period, probably in response to regional differences in oceanography and timing of the spring bloom. Length frequency of larval capelin in trawl catches gives evidence for the early onset of spawning in Glacier Bay (Fig. 3). Doyle *et al.* (2002) found that spawning occurs between late May and October in Alaska. However, earlier spawning events in southeastern Alaska have been documented from Lutak Inlet and Portage Cove near Haines in April 1993 and 2001, respectively (Chilkat Valley News Archive website, 20 April 2005: <http://www.chilkatvalleynews.com/archive/2001-14-5.html>).

In Glacier Bay, spawning capelin tended to aggregate in glacial waters that were characterized by close proximity to potentially suitable spawning

beaches, cool temperatures, lower salinity and high turbidity. In Glacier Bay, spawning capelin were collected in waters ranging from 4.8 to 8.1°C, well within the usual range from 2 to 10°C (Rose, 2005). Pelagic fish tend to spawn in areas where survival for emergent larvae will be high (Cushing, 1990). Upwelling as a result of glacial runoff at tidewater glaciers has been offered as a mechanism for the observed high productivity in glacial areas (Greisman, 1979). Additionally, higher concentrations of nutrients such as nitrates are found in glacial systems which may also enhance productivity (Apollonio, 1973). Thus, glacial areas like Glacier Bay may offer optimum conditions for survival of early larval capelin. Localized bathymetric differences among regions in Glacier Bay may also explain patterns of non-spawning and spawning capelin distribution. Numerous shallow sills and constrictions backed by deep basins cause local mixing and upwelling and higher tidal velocities (Etherington *et al.*, 2007), especially in the lower bay and the entrance to the east arm (Fig. 1). We observed high abundances of adults over both of these shallow regions (Fig. 2b). Tidal enhancement of deep-water renewal over the sill at the entrance to the east arm (Matthews and Quinlan, 1975), and glacial stream input from a tributary to the northeast of the sill likely contribute to the productivity over this area.

Physical differences between the glaciated upper arms of Glacier Bay may explain the higher abundance of mature and adult fish observed in the east arm compared with the west arm. Lower salinity and higher turbidity in the east arm may be due to the east arm's constricted passage where glacial stream runoff has less marine surface area in which to diffuse. A high tolerance to salinity fluctuations is expected for intertidal spawning fish (Stergiou, 1989) and highly turbid waters may be advantageous for planktivorous fish because it allows them to avoid predators while maintaining the ability to capture zooplankton (De Robertis *et al.*, 2003). Higher abundance and earlier maturation of capelin in the east arm compared to other regions of the bay were coincident with the initiation of the spring bloom near the head of the east arm. In early spring of 2001 and 2004, elevated levels of chl *a* were detected near the head of the east arm, while chl *a* levels in other areas of the bay were still relatively low (USGS unpublished data).

Spawning capelin aggregate in cold water refugia within Alaskan inshore bays and fjords. These areas have provided hotspots for feeding whales, seabirds and other marine predators. If ocean climate in the Gulf of Alaska returns to a cold regime, we predict

that cold water refugia will seed the expansion of capelin back into the Gulf of Alaska.

ACKNOWLEDGEMENTS

This project was funded by U.S. Geological Survey (Natural Resources Preservation Program), Glacier Bay National Park (Resource Management) and the National Park Service (Inventory and Monitoring Program). We thank Captains D. Foley (R/V *Steller*) and M. Hottmann (R/V *Pandalus*) and their crews for assistance during the cruises. Thanks to A. Agness, J. Anson, T. Bowden, B. Congdon, M. Dohner, J. Douglas, J. Driscoll, K. Emmerson, K. Juk, A. Miller, N. Naslund, L. Nussman, L. Parker, L.J. Piatt, S. Scott and K. Weersing who helped in the field. Logistical support was provided at the park by M. Moss, S. Boudreau, M. Kralovec, L. Sharman, P. Hooze and L. Etherington. Laboratory space and use of equipment were provided by L. Eisner (National Marine Fisheries Service, Auke Bay Labs) and N. Hillgruber (University of Alaska, Fairbanks). We also thank S. Speckman, N. Tojo and M. Adkison for statistical advice. S. Speckman, S. Gende and two anonymous reviewers provided insight into earlier drafts of this paper.

REFERENCES

- Abookire, A.A. and Piatt, J.F. (2005) Oceanographic conditions structure forage fishes into lipid-rich and lipid-poor communities in lower Cook Inlet, Alaska, USA. *Mar. Ecol. Prog. Ser.* **287**:229–240.
- Abookire, A.A., Piatt, J.F. and Speckman, S.G. (2002) A nearsurface, daytime occurrence of two mesopelagic fish species (*Stenobrachius leucopsarus* and *Leuroglossus schmidti*) in a glacial fjord. *Fish. Bull.* **100**:376–380.
- Agness, A.M. (2006) *Effects and Impacts of Vessel Activity on the Kittlitz's Murrelet (Brachyramphus brevirostris)* in Glacier Bay, Alaska. MS thesis, University of Washington, pp. 131.
- Anderson, P.J. and Piatt, J.F. (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol. Prog. Ser.* **189**:117–123.
- Apollonio, S. (1973) Glaciers and nutrients in Arctic Seas. *Science* **180**:491–493.
- Arimitsu, M.L., Piatt, J.F., Romano, M.D. and Douglas, D.C. (2007) Distribution of forage fishes in relation to the oceanography of Glacier Bay. In: *Proceedings of the Fourth Glacier Bay Science Symposium, October 26–28, 2004*. J.F. Piatt & S.M. Gende (eds) Reston, VA: U.S. Geological Survey Scientific Investigations Report 2007-5047, pp. 102–106.
- Bailey, R.F.J., Able, K.W. and Leggett, W.C. (1977) Evidence for the presence of a metamorphic check in capelin (*Mallotus villosus*) otoliths and implications for age determination. *J. Fish. Res. Board Can.* **34**:2008–2014.
- Brown, E.D. (2002) Life history, distribution, and size structure of Pacific capelin in Prince William Sound and the northern Gulf of Alaska. *ICES J. Mar. Sci.* **59**:983–996.

- Cailliet, G., Love, M. and Ebeling, A. (1986) *Fishes A Field and Laboratory Manual on Their Structure, Identification and Natural History*. Prospect Heights, Illinois: Waveland Press, Inc., pp. 194.
- Cushing, D.H. (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.* **26**:249–294.
- De Robertis, A., Ryer, C.H., Veloza, A. and Brodeur, R.D. (2003) Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Can. J. Fish. Aquat. Sci.* **60**:1517–1526.
- Doyle, M.J., Busby, M.S., Duffy-Anderson, J.T., Piquelle, S.J. and Matarese, A.C. (2002) Aspects of the early life history of capelin (*Mallotus villosus*) in the northwest Gulf of Alaska: a historical perspective based on larval collections October 1977 – March 1979. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC **132**:32.
- Etherington, L.L., Hooge, P.N., Hooge, E.R. and Hill, D.F. (2007). Oceanography of Glacier Bay, Alaska: implications for biological patterns and productivity in a glacial fjord estuary. *Estuaries Coasts* **30**:927–944.
- Forberg, K.G. (1983) Maturity classification and growth of capelin, *Mallotus villosus villosus* (M), oocytes. *J. Fish Biol.* **22**:485–496.
- Frank, K.T., Carscadden, J.E. and Simon, J.E. (1996) Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. *Can. J. Fish. Aquat. Sci.* **53**:1473–1486.
- Gelatt, T.S., Trites, A.W., Hastings, K., Jenison, L., Pitcher, K. and O’Corry-Crow, G. (2007) Population trends, diet, genetics and observations of Steller sea lions in Glacier Bay National Park. In: *Proceedings of the Fourth Glacier Bay Science Symposium, October 26028, 2004*. J.F. Piatt & S.M. Gende (eds) Reston, VA: U.S. Geological Survey Scientific Investigations Report 2007-5047, pp. 145–149.
- Greisman, P. (1979) On upwelling driven by the melt of ice shelves and tidewater glaciers. *Deep Sea Res.* **26A**:1051–1065.
- Hunt, G.L., Stabeno, P., Walters, G. et al. (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep Sea Res. Part II.* **49**:5821–5853.
- Kreiger, K.J. and Wing, B.L. (1986) *Hydroacoustic monitoring of prey to determine humpback whale movements*. Auke Bay, Alaska: Auke Bay Laboratory, National Marine Fisheries Service, NOAA, pp. 62.
- Legendre, P. and Legendre, L. (1998) *Numerical Ecology*. San Diego, CA: Elsevier Inc., pp. 853.
- Manly, B.F.J. (1991) *Multivariate Statistical Methods*. New York: Chapman & Hall, pp. 214.
- Matthews, J.B. and Quinlan, A.V. (1975) Seasonal characteristics of water masses in Muir Inlet, a fjord with tidewater glaciers. *J. Fish. Res. Board Can.* **32**:1693–1703.
- Merrick, R.L. (1997) Current and historical roles of apex predators in the Bering Sea ecosystem. *J. Northw. Atl. Fish. Sci.* **22**:343–355.
- Montevecchi, W.A. and Piatt, J.F. (1984) Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. *Comp. Biochem. Physiol.* **78A**:15–20.
- Moulton, L.L. (2000) *Distribution of Potential Surf Smelt and Pacific Sandlance Spawning Habitat in San Juan County*. Mount Vernon, WA: Report to Northwest Straits Commission, 19 pp. Available from <http://sjcmrc.org/programs/foragefish.htm> [accessed 19 March, 2007].
- Mueter, F.J. and Norcross, B.L. (2002) Spatial and temporal patterns in the demersal fish community in the shelf and upper slope regions of the Gulf of Alaska. *Fish. Bull.* **100**:559–581.
- Nakashima, B.S. and Wheeler, J.P. (2002) Capelin (*Mallotus villosus*) spawning behavior in Newfoundland waters – the interaction between beach and demersal spawning. *ICES J. Mar. Sci.* **59**:909–916.
- Pahlke, K.A. (1985) *Preliminary Studies of Capelin (Mallotus villosus) in Alaskan Waters*. Juneau, AK: Alaska Department of Fish and Game, Informational Leaflet 250, pp. 64.
- Piatt, J.F. and Anderson, P.J. (1996) Response of common murrelets to the Exxon Valdez oil spill and long-term changes in the Gulf of Alaska marine ecosystem. In: *Proceedings of the Exxon Valdez Oil Spill Symposium*. S.D. Rice, R.B. Spies, D.A. Wolf & B.A. Wright (eds) Bethesda: American Fisheries Symposium, pp. 720–737.
- Piatt, J.F. and Gende, S.M., eds. (2007) *Proceedings of the Fourth Glacier Bay Science Symposium*. Reston, VA: U.S. Geological Survey Scientific Investigations Report 2007-5047, pp. 246.
- Pitt, T.K. (1958) Distribution, spawning and racial studies of the capelin, *Mallotus villosus* (Muller), in the offshore Newfoundland area. *J. Fish Res. Board Can.* **15**:275–293.
- Romano, M.D., Piatt, J.F., Drew, G.S. and Bodkin, J.L. (2007) Temporal and spatial variability in distribution of Kittlitz’s Murrelet in Glacier Bay. In: *Proceedings of the Fourth Glacier Bay Science Symposium, October 26028, 2004*. J.F. Piatt & S.M. Gende (eds) Reston, VA: U.S. Geological Survey Scientific Investigations Report 2007-5047, pp. 117–119.
- Rose, G.A. (2005) Capelin (*Mallotus villosus*) distribution and climate: a sea “canary” for marine ecosystem change. *ICES J. Mar. Sci.* **62**:1524–1530.
- SAS (2003) *JMP 5.0.1.2. Statistical Discovery Software for Windows*. NC: S. Cary.
- Sharman, L.C., Eichenlaub, B., Vanselow, P. et al. (2005) *Alaska Coastal Resources Inventory and Mapping Program*. Gustavus: National Park Service, Glacier Bay National Park and Preserve.
- Sinclair, E.H. and Zeppelin, T.K. (2002) Seasonal diet trends among the western stock of Steller sea lions (*Eumetopias jubatus*). *J. Mammal.* **83**:973–990.
- Speckman, S.G., Piatt, J.F., Minte-Vera, C.V. and Parrish, J.K. (2005) Parallel structure among environmental gradients and three trophic levels in a subarctic estuary. *Prog. Oceanogr.* **66**:25–65.
- Stergiou, K.I. (1989) Capelin *Mallotus villosus* (Pisces: Osmeridae), glaciations, and speciation: a nomothetic approach to fisheries ecology and reproductive biology. *Mar. Ecol. Prog. Ser.* **56**:211–224.
- Trites, A.W. and Donnelly, C.P. (2003) The decline of Steller sea lions (*Eumetopias jubatus*) in Alaska: a review of the nutritional stress hypothesis. *Mamm. Rev.* **33**:3–28.
- West, G. (1990) Methods of assessing ovarian development in fishes: a review. *Aust. J. Mar. Freshwater Res.* **41**:199–222.
- Womble, J.N., Willson, M.F., Sigler, M.F., Kelly, B.P. and VanBlaricom, G.R.. (2005) Distribution of Steller sea lions *Eumetopias jubatus* in relation to spring-spawning fish in SE Alaska. *Mar. Ecol. Prog. Ser.* **294**:271–282.
- Zar, J.H. (1999) *Biostatistical Analysis*, 4th edn. Upper Saddle River: Prentice Hall, pp. 663.