**Scott W. Johnson**[1], **John F. Thedinga**, **A. Darcie Neff**, **Patricia M. Harris**, **Mandy R. Lindeberg**, **Jacek M. Maselko**, and **Stanley D. Rice**, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratories, 17109 Pt. Lena Loop Road, Juneau, Alaska 99801

# Fish Assemblages in Nearshore Habitats of Prince William Sound, Alaska


## Abstract

We sampled fish at eight locations in western Prince William Sound (PWS), Alaska, in April, July, and September 2006, and July 2007, to identify species assemblages and habitat use. At each location, fish were sampled with a 37-m long variable mesh beach seine in three nearshore habitats: bedrock outcrops, eelgrass meadows, and cobble beaches with kelp. A total of 49,060 fish representing 45 species were captured in 95 beach seine hauls. Catch-per-unit-effort (CPUE, all species) did not differ by season but did differ by habitat type–CPUE was greater in eelgrass and kelp than in bedrock. Seasonal pulses in catch were evident for some species; pink salmon were captured only in spring and summer, Pacific herring only in summer and fall, and capelin only in fall. Species richness was greater in summer (34) than in spring (23) or fall (28), and greater in eelgrass (34) than in bedrock (22) or kelp (33). Species that were good discriminators among seasonal collections were pink salmon, saffron cod, crescent gunnel, and Pacific herring, whereas species that were good discriminators among habitat collections were crescent gunnel, tubesnout, bay pipefish, saffron cod, and Arctic shanny. Of the most abundant species captured, most were juveniles based on estimated size at maturity. The summer fish assemblage in western PWS has changed over the last 20 years, especially with the appearance in large numbers of saffron cod. Sites in this study can be monitored periodically to track future changes in fish assemblages and habitat that may result from local and regional human disturbance.


## Introduction

Alaska has about 55,000 km of shoreline (Heard and Andersen 1999) and a wide diversity of nearshore habitats available to fish including eelgrass (*Zostera marina*) meadows, kelps, and exposed bedrock outcrops. These habitats are ecologically important for many fish species, providing shelter from predators and abundant food resources (Pollard 1984, Beck et al. 2003, Spalding et al. 2003). Prince William Sound (PWS), a large embayment with numerous islands, provides extensive nearshore habitats that are protected from more exposed conditions on the outer coast (Laur and Haldorson 1996). Although it is well established that over 100 fish species use the nearshore environment in Alaska (NOAA Fisheries 2009a), often in large numbers, what is unknown is their use of specific habitats and how that changes seasonally and with life stage.

Most coastal fish surveys in PWS have been in deeper water of embayments (Norcross and Frandsen 1996, Stokesbury et al. 1999, Ostrand et al. 2004) and not in shallow, nearshore habitats (<5 m deep and <20 m offshore). In the few nearshore surveys in PWS using SCUBA or beach seine, juvenile pink salmon (*Oncorhynchus gorbuscha*), Pacific cod (*Gadus macrocephalus*), Pacific tomcod (*Microgadus proximus*), and walleye pollock (*Theragra chalcogramma*) were observed or captured in large numbers (Laur and Haldorson 1996, Wertheimer and Celewycz 1996, Dean et al. 2000). Other species that use shallow, nearshore habitats in PWS for spawning or rearing include capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*), and Pacific sand lance (*Ammodytes hexapterus*) (Robards et al. 1999, Norcross et al. 2001, Brown 2002, Cooney 2007). Of all the fish species in PWS, Pacific herring is the most studied, largely in response to research needs identified by the *Exxon Valdez* oil spill (Brown et al. 1996, Johnson et al. 1997).

The primary objective of this study was to compare fish assemblages by season and habitat type in shallow, nearshore waters of PWS. We focused our efforts in western PWS where 1543 km of shoreline were mapped with the *ShoreZone* protocol in 2004 (NOAA Fisheries 2009b). *ShoreZone* uses aerial video imagery to classify and map intertidal and shallow sub-tidal geomorphology and biota across wide geographic ranges. These data enabled us to identify the dominant nearshore habitats available to fish. Our study is

[1]Author to whom correspondence should be addressed.
E-mail: scott.johnson@noaa.gov

unique because we concentrated our efforts in shallow, nearshore habitats (<5 m deep and <20 m offshore) that are often ignored in fisheries surveys. Because the nearshore is vulnerable to local and global human disturbances, including global climate change (Lubchenco et al. 1993, Johnson et al. 2003), a better understanding of how the nearshore supports living marine resources is needed to help managers protect essential habitats.

## Study Area

Prince William Sound is a prominent embayment in the Gulf of Alaska encompassing about 5400 km$^2$ (Weingartner 2007). Numerous islands within the Sound create a mosaic of habitat types including sheltered and rocky shores, fiords, tidewater glaciers, sand and gravel beaches, eelgrass meadows, exposed bedrock outcrops, and cobble beaches with kelp. Our study was in the western portion of PWS extending from waters near Whittier to Latouche Island (Figure 1). This area was chosen because it was mapped with *ShoreZone* in 2004, enabling us to identify the shoreline extent of different habitat types (e.g., 192 km of bedrock, 732 km of eelgrass, 837 km of kelp). We chose to sample bedrock outcrops, eelgrass, and kelp.

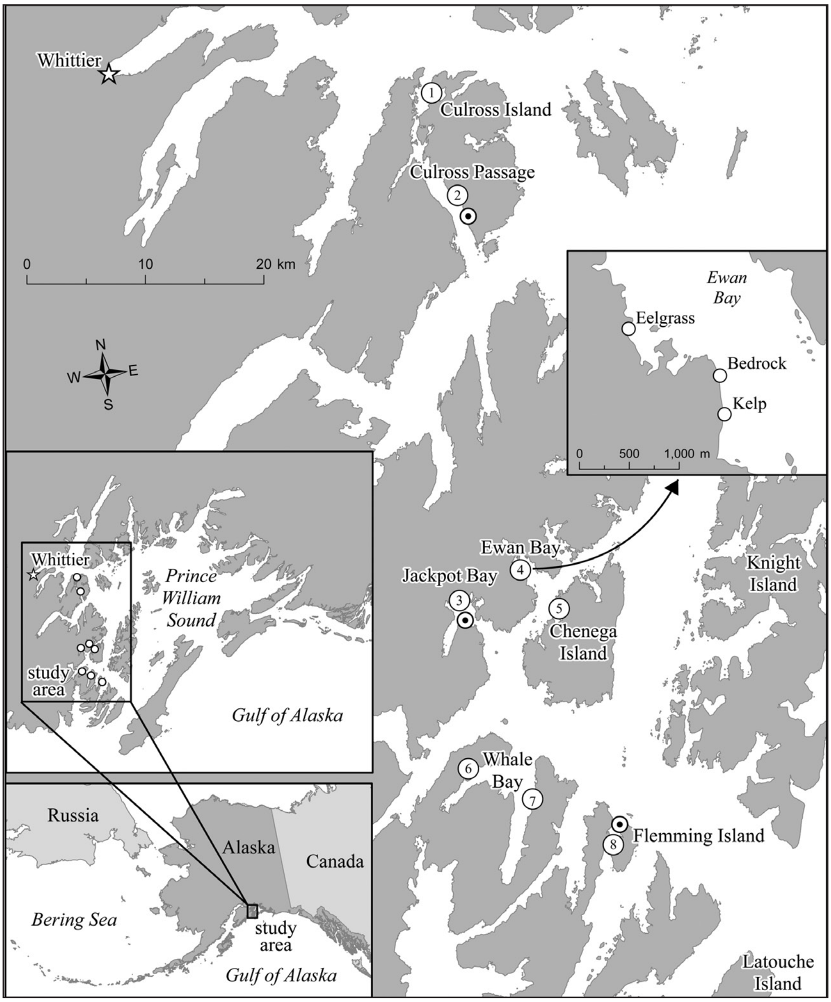


Figure 1. Eight study locations in western Prince William Sound, Alaska. At each location, fish were sampled in three habitat types (bedrock, eelgrass (*Zostera marina*), kelp (Laminariales); see inset of Ewan Bay for an example). Fish were sampled with a beach seine in 2006 and 2007. Locations of thermographs for measuring water temperature are indicated by circles with black centers.

These habitat types do not represent all habitats available to fish (NOAA Fisheries 2009b), but are common in PWS and can be effectively sampled with a beach seine.

## Methods

Using *ShoreZone* habitat classifications, we identified all shoreline segments in western PWS that had at least 500 m of continuous eelgrass (n = 92) and selected eight segments with a random numbers generator in Microsoft Excel. Upon arrival at each eelgrass segment, we selected a suitable site for beach seining (e.g., approachable by skiff and free of obstructions); we then traveled by skiff from the eelgrass site to more exposed areas, often at the entrance of bays, and selected a bedrock site and a kelp site. The closest sites to eelgrass that were suitable for beach seining were selected. Thus, we sampled three habitat types with a beach seine at each location (Figure 1) for a total of eight bedrock, eight eelgrass, and eight kelp sites. Eight locations spread throughout western PWS were the maximum number of areas that we could sample in a 10-day vessel charter. We sampled in April, July, and September 2006, and July and August 2007; one seine haul per site per visit. For 2007, only July data is included in this paper; the August sampling period was part of a diel study and will be reported separately. For the purpose of this paper, April is spring, July is summer, and September is fall.

Bedrock outcrops are steep (>20% gradient) and usually located in exposed areas near the entrance of bays; vegetation is largely limited to the bedrock wall face and is dominated by patchy to lush kelps (Laminariales such as *Alaria marginata* and *Saccharina latissima* formerly *Laminaria saccharina*). Eelgrass meadows are typically located inside protected coves or bays with flat to moderate gradient (5-10%) and substrates consisting mostly of fine-grained sediments. In western PWS, eelgrass is minimally exposed even at the lowest tides (–0.26 m to –0.77 m). Kelp beds occupy semi-protected areas with moderate gradient (10-20%) and substrates of predominantly small and large cobbles. Kelps are dominated by patchy to lush Laminariales, and most kelp beds are subtidal. Of the three habitat types, cover provided by vegetation was greatest in eelgrass and least in bedrock.

### Fish Capture

Fish were captured in waters less than 5 m deep and less than 20 m from shore with a 37-m long variable mesh beach seine that tapered from 5 m deep at the center to 1 m deep at the ends. Outer panels were each 10 m of 32-mm stretch mesh, intermediate panels were each 4 m of 6-mm square mesh, and the bunt was 9 m of 3.2-mm square mesh. We set the seine as a round haul by holding one end on the beach, backing around in a skiff with the other end to the beach about 18 m from the start, and pulling the seine onto shore. The seine had a leadline and a floatline so that the bottom contacted the substrate and the top floated on the surface. All seine sites were sampled during daylight hours and within 2 hr of low tide (range: +1.0 m to –1.5 m below MLLW).

After retrieval of the net, the entire catch was sorted, identified to species, counted, and a sub-sample (up to 50 fish) of each species was measured either to the nearest millimeter fork length (FL) or, in species without a distinct fork in caudal fin, to total length (TL). The number of fish in large catches was estimated gravimetrically. To achieve this, a random sub-sample of approximately 500 fish was removed from the total catch and the remaining fish were collectively weighed to the nearest 0.1 kg. Fish in the sub-sample were counted and weighed to the nearest gram. A mean weight of fish determined from the sub-sample was used to estimate the number of fish in the total catch. The proportion of each species in the sub-sample was also used to determine the species composition of the total catch. Fish were anesthetized in a mixture of 1 part carbonated water to 2 parts seawater for identification and measurement. Smaller individuals (<40 mm length) that could not be identified to species in the field were identified to family (e.g., Cottidae).

### Temperature and Salinity

Tidbit (Onset Computer Corporation, Pocasset, MA) thermographs were placed at three study locations (Figure 1) at about -3.0 m depth to continuously record water temperature every 2 hr. Thermographs were attached to the mid-section of a 1-m polypropylene line; a 10 kg anchor was on one end of the line and a small float on the other end. Thermographs were deployed in late April 2006 and retrieved in September 2006. New thermographs were deployed again in the same locations in September 2006 and retrieved in August 2007. Surface salinity (practical salinity scale, PSS) at 20-cm depth was measured once at each seine site during each sampling period with a hand-held refractometer.

### Data Analysis

Catch data are expressed in absolute numbers (i.e., total catch) and catch-per-unit-effort (CPUE) based on number of fish per seine haul. Percent frequency of occurrence (FO) was also determined for some of the most abundant species – FO represents the number of seine hauls in which a species was captured divided by the total number of seine hauls multiplied by 100. Species richness refers to the total number of fish species captured. Individuals identified only to family (e.g., juvenile Cottidae) were counted in the total catch, but were only considered as a separate species for species richness calculations if no other species from the same family were captured.

Differences in CPUE (all species) and species richness among seasons and habitat types in spring, summer, and fall 2006 were examined by two-way ANOVA. Because CPUE data did not meet the assumption of normality even with transformation, ANOVA was used on ranked CPUE observations (SigmaStat 1997). An ANOVA of ranks is conditionally distribution free and has good efficiency; the true level of significance is usually close to the approximate level of significance used in the test, regardless of the underlying population distribution (Conover 1980). If a significant difference was found in CPUE or species richness among seasons or habitat types, Holm-Sidak pairwise multiple comparisons were used to isolate groups that differed from each other (SigmaStat 1997). Differences in CPUE and species richness between summer 2006 and summer 2007 were examined by the Wilcoxon signed rank test. To examine for differences in species composition among seasons and habitat types (all sampling periods), we conducted a two-way (season-habitat) analysis of similarity (ANOSIM) using a Bray-Curtis similarity index; similarity matrices are presented as a dendrogram and non-metric multi-dimensional scaling (nMDS) ordination plot (Clarke and Warwick 2001). A fourth-root transformation of the catch data was used to reduce the influence of very abundant species. To determine which species contributed most to either the similarity or dissimilarity within and among seasons and habitat types, a similarity percentage analysis (SIMPER) was used (Clarke and Warwick 2001). Spearman rank correlation was used to examine the relationship between CPUE and species richness with water temperature and salinity across all seasons and habitats in 2006.

## Results

### Fish Fauna

A total of 49,060 fish representing 45 species were captured in 95 seine hauls (all sampling periods, Table 1). Eight species accounted for 98% of the total catch: Pacific herring, saffron cod (*Eleginus gracilis*), pink salmon, capelin, bay pipefish (*Syngnathus leptorhynchus*), crescent gunnel (*Pholis laeta*), tubesnout (*Aulorhynchus flavidus*), and walleye pollock (Table 1). Some of these species were captured infrequently but in large numbers (e.g., capelin—total catch = 6670 fish, FO = 10%), whereas others were captured frequently but in small numbers (e.g., crescent gunnel–total catch = 551 fish, FO = 76%; Figure 2). Unexpectedly large numbers of saffron cod were captured (15,910 fish, FO = 52%); they have not been reported before in PWS. Many species (49%) were captured in only small or incidental numbers (<10 fish total catch); eight species were represented by a total catch of one fish (Table 1). In addition to Pacific herring, pink salmon, and walleye pollock, other commercially important species captured were chum salmon (*O. keta*), lingcod (*Ophiodon elongatus*), Pacific cod, coho salmon (*O. kisutch*), sockeye salmon (*O. nerka*), and rockfish (*Sebastes* spp.) (Table 1).

Catch-per-unit-effort (all species) was not significantly different ($P = 0.246$) among seasons but differed significantly ($P < 0.001$) among habitat types in 2006 (Figure 3). Across all habitat types in 2006, total catch was 4653 fish in spring, 5274 fish in summer, and 10,176 fish in fall (Table 1). Catches were variable; median CPUE was 28 fish (n = 24 hauls) in spring, 41 fish (n = 24 hauls) in summer, and 57 fish (n = 23 hauls) in fall (Table 1). Catches varied greatly with season for some species; juvenile pink salmon were captured only in spring and summer, Pacific herring in summer and fall, and capelin only in fall. Across all seasons in 2006, total catch by habitat type was 1286 fish in bedrock, 7819 fish in eelgrass, and 10,998 fish

TABLE 1. Species list by total catch, sampling period, and habitat type in western Prince William Sound, Alaska in 2006 and 2007; fish were captured with a beach seine. CPUE = catch per beach seine haul.

| Common name | Scientific name | Total catch | Catch by month and year | | | | Catch by habitat type (2006) | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Apr 06 | Jul 06 | Sep 06 | Jul 07 | Bedrock | Eelgrass | Kelp |
| Pacific herring | *Clupea pallasii* | 16,266 | 0 | 1585 | 1436 | 13,245 | 943 | 1556 | 522 |
| Saffron cod | *Eleginus gracilis* | 15,910 | 18 | 2358 | 1210 | 12,324 | 20 | 3489 | 77 |
| Pink salmon | *Oncorhynchus gorbuscha* | 7006 | 4226 | 166 | 0 | 2614 | 220 | 949 | 3223 |
| Capelin | *Mallotus villosus* | 6670 | 0 | 0 | 6670 | 0 | 8 | 0 | 6662 |
| Bay pipefish | *Syngnathus leptorhynchus* | 602 | 131 | 235 | 160 | 76 | 8 | 450 | 68 |
| Crescent gunnel | *Pholis laeta* | 551 | 85 | 264 | 55 | 147 | 25 | 317 | 62 |
| Tubesnout | *Aulorhynchus flavidus* | 514 | 21 | 67 | 331 | 95 | 1 | 365 | 53 |
| Walleye pollock | *Theragra chalcogramma* | 422 | 0 | 120 | 80 | 222 | 9 | 151 | 40 |
| Arctic shanny | *Stichaeus punctatus* | 117 | 52 | 33 | 6 | 26 | 5 | 61 | 25 |
| Threespine stickleback | *Gasterosteus aculeatus* | 104 | 0 | 29 | 75 | 0 | 1 | 98 | 5 |
| Chum salmon | *Oncorhynchus keta* | 94 | 20 | 53 | 0 | 21 | 3 | 23 | 47 |
| Lingcod | *Ophiodon elongatus* | 93 | 5 | 64 | 12 | 12 | 2 | 64 | 15 |
| Pacific sand lance | *Ammodytes hexapterus* | 80 | 1 | 52 | 2 | 25 | 0 | 1 | 54 |
| Whitespotted greenling | *Hexagrammos stelleri* | 77 | 5 | 21 | 22 | 29 | 3 | 28 | 17 |
| Padded sculpin | *Artedius fenestralis* | 76 | 27 | 19 | 21 | 9 | 6 | 35 | 26 |
| Snake prickleback | *Lumpenus sagitta* | 71 | 3 | 41 | 20 | 7 | 1 | 63 | 0 |
| Pacific cod | *Gadus macrocephalus* | 68 | 0 | 23 | 20 | 25 | 4 | 38 | 1 |
| Juvenile greenling | Hexagrammidae | 61 | 3 | 50 | 0 | 8 | 2 | 47 | 4 |
| Masked greenling | *Hexagrammos octogrammus* | 56 | 6 | 18 | 20 | 12 | 3 | 18 | 23 |
| Juvenile sculpin | Cottidae | 51 | 23 | 7 | 4 | 17 | 5 | 4 | 25 |
| Tidepool sculpin | *Oligocottus maculosus* | 39 | 5 | 17 | 8 | 9 | 9 | 13 | 8 |
| Copper rockfish | *Sebastes caurinus* | 20 | 0 | 12 | 1 | 7 | 3 | 1 | 9 |
| Frog sculpin | *Myoxocephalus stelleri* | 15 | 5 | 3 | 3 | 4 | 0 | 8 | 3 |
| Manacled sculpin | *Synchirus gilli* | 11 | 0 | 4 | 3 | 4 | 2 | 0 | 5 |
| Silverspotted sculpin | *Blepsias cirrhosus* | 10 | 0 | 8 | 2 | 0 | 0 | 10 | 0 |
| Coho salmon | *Oncorhynchus kisutch* | 8 | 0 | 2 | 3 | 3 | 0 | 1 | 4 |
| Juvenile rockfish | Scorpaenidae | 7 | 2 | 1 | 4 | 0 | 0 | 5 | 2 |
| Scalyhead sculpin | *Artedius harringtoni* | 6 | 0 | 1 | 0 | 5 | 1 | 0 | 0 |
| Juvenile lumpsucker | Cyclopteridae | 5 | 0 | 5 | 0 | 0 | 2 | 0 | 3 |
| Northern ronquil | *Ronquilus jordani* | 5 | 0 | 0 | 1 | 4 | 0 | 0 | 1 |
| Quillback rockfish | *Sebastes maliger* | 5 | 0 | 2 | 0 | 3 | 0 | 2 | 0 |
| Sockeye salmon | *Oncorhynchus nerka* | 5 | 0 | 5 | 0 | 0 | 0 | 5 | 0 |
| Northern sculpin | *Icelinus borealis* | 4 | 2 | 2 | 0 | 0 | 0 | 1 | 3 |
| Black prickleback | *Xiphister atropurpureus* | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 |
| High cockscomb | *Anoplarchus purpurescens* | 3 | 3 | 0 | 0 | 0 | 0 | 2 | 1 |
| Leister sculpin | *Enophrys lucasi* | 3 | 2 | 1 | 0 | 0 | 0 | 2 | 1 |
| Speckled sanddab | *Citharichthys stigmaeus* | 3 | 0 | 2 | 1 | 0 | 0 | 2 | 1 |
| Crested sculpin | *Blepsias bilobus* | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| Painted greenling | *Oxylebius pictus* | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 2 |
| Penpoint gunnel | *Apodichthys flavidus* | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 0 |
| Sailfin sculpin | *Nautichthys oculofasciatus* | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 2 |
| Brown Irish lord | *Hemilepidotus spinosus* | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| Buffalo sculpin | *Enophrys bison* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Red Irish lord | *Hemilepidotus hemilepidotus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Searcher | *Bathymaster signatus* | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| Slender eelblenny | *Lumpenus fabricii* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| Smallmouth ronquil | *Bathymaster leurolepis* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Smoothhead sculpin | *Artedius lateralis* | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Pacific spiny lumpsucker | *Eumicrotremus orbis* | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| Juvenile cod | Gadidae | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Juvenile gunnel | Pholidae | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Juvenile Irish lord | Cottidae | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| Total catch | | 49,060 | 4653 | 5274 | 10,176 | 28,957 | 1286 | 7819 | 10,998 |
| Number of species | | 45 | 23 | 34 | 28 | 26 | 22 | 34 | 33 |
| Number of seine hauls | | 95 | 24 | 24 | 23 | 24 | 23 | 24 | 24 |
| Median CPUE | | 43 | 28 | 41 | 57 | 73 | 7 | 188 | 44 |

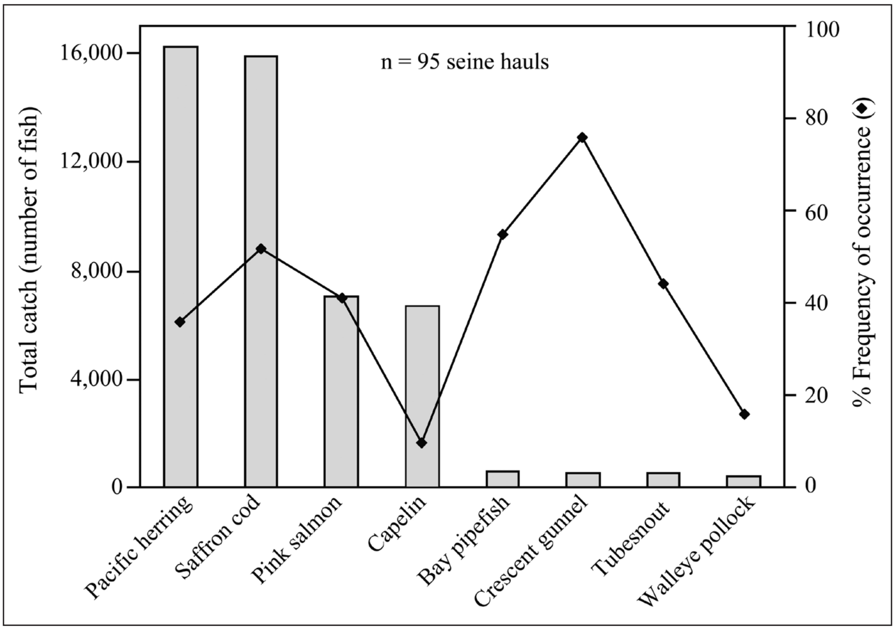


Figure 2. Total catch and frequency of occurrence of the eight most abundant fish species captured in 95 beach seine hauls in western Prince William Sound, Alaska. Fish were sampled in April, July, and September 2006, and July 2007. Percent frequency of occurrence equals the number of seine hauls with a particular species divided by the total number of seine hauls multiplied by 100. These eight species comprised 98% of the total fish catch.

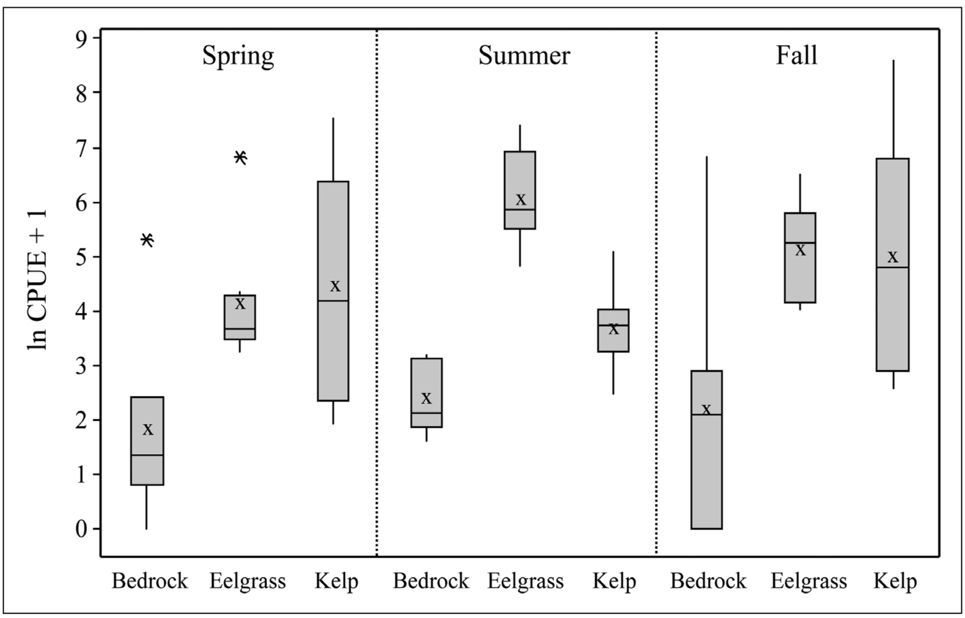


Figure 3. Box-and-whisker plots of the $\log_e$ transformed catch-per-unit-effort (CPUE + 1) by season and habitat type in western Prince William Sound, Alaska in 2006. Number of seine hauls was eight in all sampling periods and habitat types except bedrock in fall (n = 7). Bottoms of boxes: first quartile; tops of boxes: third quartile; whiskers: first quartile minus 1.5 times the interquartile range and the third quartile plus 1.5 times the interquartile range. Within boxes, crosses are means and horizontal lines are medians. Asterisks denote outliers.

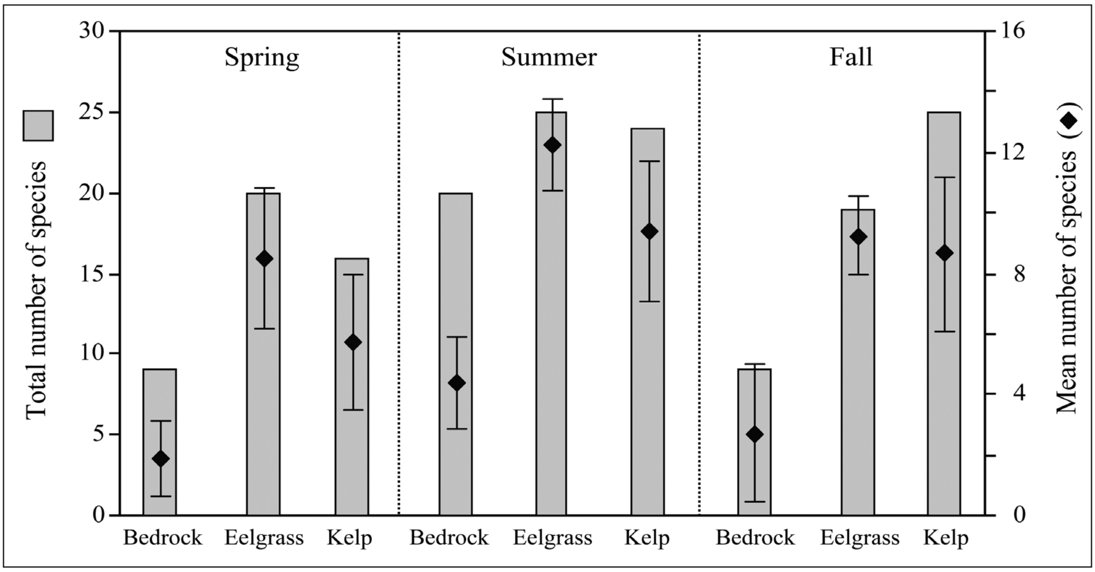


Figure 4. Total number and mean (± SD) number of fish species captured with a beach seine by season and habitat type in western Prince William Sound, Alaska in 2006. Number of seine hauls was eight in all sampling periods and habitat types except bedrock in fall (n = 7).

in kelp (Table 1). Median CPUE was 7 fish (n = 23 hauls) in bedrock, 188 fish (n = 24 hauls) in eelgrass, and 44 fish (n = 24 hauls) in kelp (Table 1). Pairwise comparisons revealed that CPUE was significantly greater ($P \leq 0.01$) in eelgrass and kelp than in bedrock. Catch did not differ significantly ($P = 0.189$) between summer 2006 and summer 2007 (28,957 fish); median CPUE was 73 fish in summer 2007 (Table 1). One seine haul in fall 2006 and two hauls in summer 2007 accounted for over 70% of the total catch of capelin, Pacific herring, and saffron cod.

Species richness differed significantly ($P < 0.001$) among seasons and habitat types in 2006 (Figure 4). Across all habitat types, the greatest number of species (34) was captured in summer, whereas 23 were captured in spring and 28 in fall (Table 1). Across all seasons, the greatest number of species (34) was captured in eelgrass, whereas 33 were captured in kelp and 22 in bedrock (Table 1). In pairwise comparisons, mean number of species captured was significantly greater ($P \leq 0.01$) in summer (8.7) than in fall (6.9) or spring (5.4), and significantly greater ($P \leq 0.01$) in eelgrass (10.0) than in kelp (7.9) or bedrock (3.0). Species richness also differed significantly ($P = 0.04$) between summer 2006 and summer 2007; mean number of species was 7.7 in 2007.

## Fish Assemblage Structure

Fish assemblages were structured mainly by habitat type and not time of sampling. Cluster and second-stage nMDS analyses based on ANOSIM $R$ values of all pairwise tests showed three groups at approximately a 50% level of similarity; a predominantly bedrock group, a predominantly kelp group, and an eelgrass group (Figure 5). Outliers were kelp in fall 2006 that had a species composition more closely linked to bedrock, and eelgrass in spring 2006 that had a species composition more closely linked to kelp (Figure 5). The fall assemblage in kelp was characterized by a seasonally high abundance of capelin; capelin were only captured in fall and mostly in kelp. The spring assemblage in eelgrass was characterized by an abundance of two resident species (crescent gunnel and bay pipefish) and a seasonally high abundance of juvenile pink salmon.

Species composition differed significantly among seasons across all habitat groups (two-way ANOSIM: Global $R = 0.318$, $P < 0.001$). All seasonal groups (spring, summer, and fall 2006, and summer 2007), differed significantly ($0.264 \leq R \leq 0.647$, $P < 0.001$) except summer 2006 versus summer 2007 ($R = 0.006$, $P = 0.417$). The spring assemblage of fish had an overall within-group Bray-Curtis similarity of 38.1%

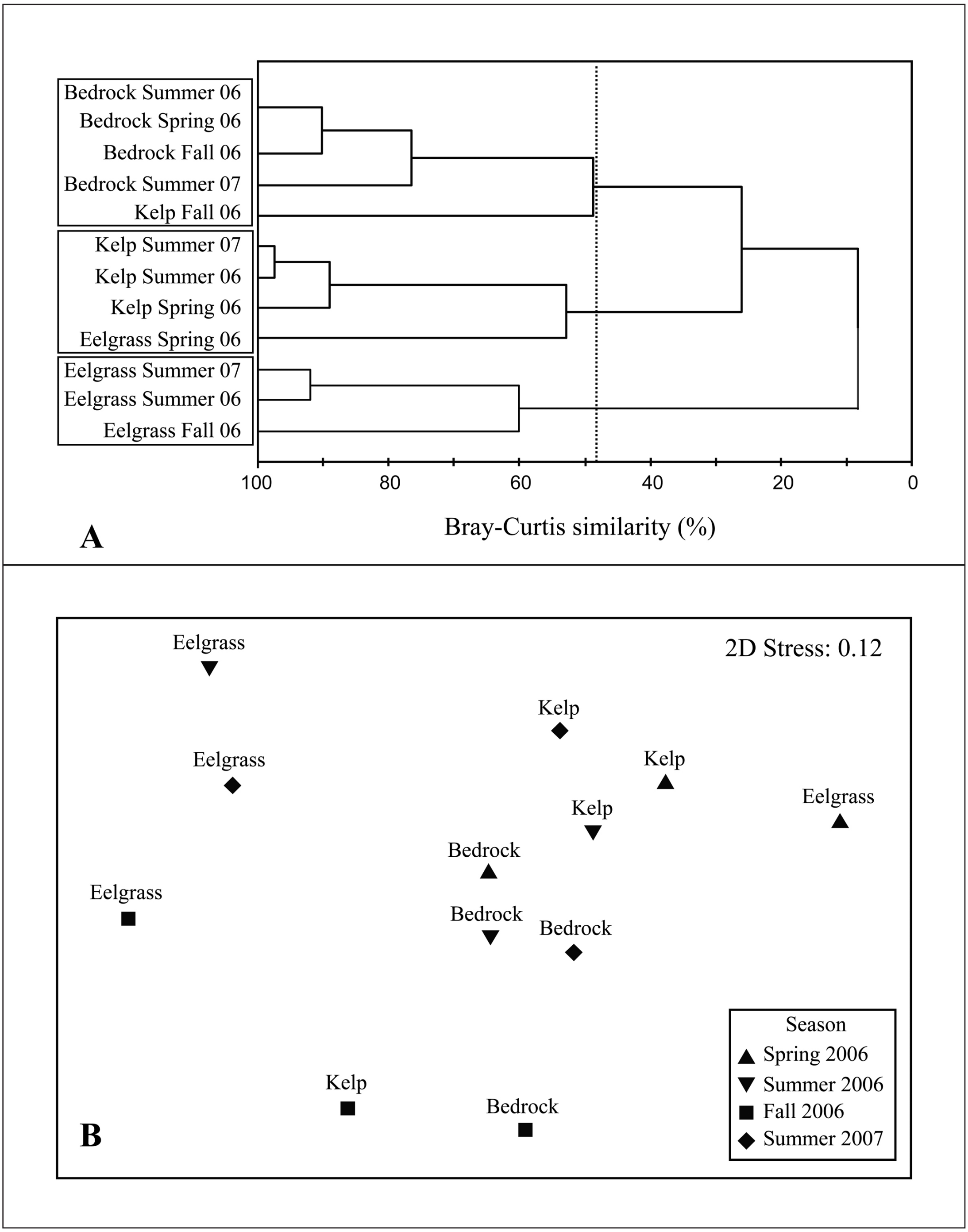


Figure 5. Similarities in fish assemblages found in nearshore habitats of western Prince William Sound, Alaska. Habitat and season were grouped for the analysis; bedrock, eelgrass, and kelp habitats were sampled in spring, summer, and fall 2006, and summer 2007. Dendrogram with group-average linking from Bray-Curtis similarity index (A), and second-stage nMDS plot showing the centroid locations of fish assemblages by season and habitat type (B).

and consisted mainly of juvenile pink salmon, crescent gunnel, bay pipefish, and Arctic shanny (*Stichaeus punctatus*), which together accounted for 84% of the cumulative within-group similarity. The summer assemblage of fish had an average within-group similarity of about 36.4% in 2006 and 2007— crescent gunnel, saffron cod, and bay pipefish in 2006, and crescent gunnel, saffron cod, and pink salmon in 2007, accounted for about 50% of the cumulative within-group similarity. The fall assemblage of fish had the highest average within-group similarity (44.5%) with saffron cod, bay pipefish, Pacific herring, crescent gunnel, capelin, and tubesnout accounting for 72% of the cumulative within-group similarity. In pairwise seasonal collections, average dissimilarity was lowest (63.2%) for summer 2006 versus summer 2007, and highest (76.8%) for spring 2006 versus fall 2006 (Table 2). Species that were good discriminators among seasonal collections

TABLE 2. Results of SIMPER analysis showing average percent dissimilarity (δ) of key fish species among seasons in western Prince William Sound, Alaska. ($\delta_i$ = average contribution of the $i^{th}$ species to the overall dissimilarity between groups, SD = standard deviation, and cum. $\delta_i$% = the cumulative contribution to the total dissimilarity; Clarke and Warwick 2001). All results are based on the 4th root transformation of catch data; nontransformed data in parentheses. (* = discriminating species).

| Common name | Average abundance | | | | $\delta_i$ | $\delta_i$/SD | $\delta_i$% | Cum. $\delta_i$% |
|---|---|---|---|---|---|---|---|---|
| | Spring 2006 | | Summer 2006 | | | | | |
| Pink salmon | 2.03 | (192.1) | 0.53 | (6.9) | 9.48 | 0.96* | 13.53 | 13.53 |
| Saffron cod | 0.33 | (0.8) | 1.62 | (98.3) | 5.92 | 0.97* | 8.45 | 21.98 |
| Crescent gunnel | 1.05 | (3.9) | 1.46 | (11.0) | 4.04 | 0.72 | 5.76 | 27.74 |
| Tidepool sculpin | 0.22 | (0.2) | 0.43 | (0.7) | 3.64 | 0.47 | 5.19 | 32.93 |
| Pacific herring | 0 | (0) | 0.78 | (66.0) | 3.51 | 0.61 | 5.00 | 37.93 |
| Lingcod | 0.18 | (0.2) | 0.69 | (2.7) | 3.50 | 0.82 | 4.99 | 42.92 |
| Bay pipefish | 0.99 | (6.0) | 1.04 | (9.8) | 3.24 | 0.79 | 4.63 | 47.55 |
| Arctic shanny | 0.73 | (2.4) | 0.66 | (1.4) | 3.24 | 0.62 | 4.62 | 52.17 |
| | Spring 2006 | | Fall 2006 | | | | | |
| Pink salmon | 2.03 | (192.1) | 0 | (0) | 10.55 | 1.04* | 13.74 | 13.74 |
| Pacific herring | 0 | (0) | 1.12 | (62.4) | 7.01 | 0.64 | 9.12 | 22.87 |
| Capelin | 0 | (0) | 1.19 | (290.0) | 6.26 | 0.68 | 8.15 | 31.02 |
| Saffron cod | 0.33 | (0.8) | 1.60 | (52.6) | 5.83 | 1.09* | 7.60 | 38.62 |
| Crescent gunnel | 1.05 | (3.9) | 0.85 | (2.4) | 4.27 | 0.86 | 5.56 | 44.18 |
| Padded sculpin | 0.52 | (1.2) | 0.58 | (0.9) | 4.12 | 0.74 | 5.37 | 49.55 |
| Arctic shanny | 0.73 | (2.4) | 0.21 | (0.3) | 3.59 | 0.68 | 4.68 | 54.23 |
| | Summer 2006 | | Fall 2006 | | | | | |
| Pacific herring | 0.78 | (66.0) | 1.12 | (62.4) | 7.01 | 0.77 | 10.79 | 10.79 |
| Capelin | 0 | (0) | 1.19 | (290.0) | 5.30 | 0.68 | 8.16 | 18.94 |
| Crescent gunnel | 1.46 | (11.0) | 0.85 | (2.4) | 3.98 | 0.98* | 6.13 | 25.07 |
| Saffron cod | 1.62 | (98.3) | 1.60 | (52.6) | 3.53 | 0.85 | 5.43 | 30.51 |
| Padded sculpin | 0.47 | (0.8) | 0.58 | (0.9) | 3.02 | 0.84 | 4.65 | 35.16 |
| Walleye pollock | 0.51 | (5.0) | 0.36 | (3.5) | 2.93 | 0.71 | 4.51 | 39.67 |
| Tidepool sculpin | 0.43 | (0.7) | 0.34 | (0.4) | 2.71 | 0.48 | 4.18 | 43.84 |
| Bay pipefish | 1.04 | (9.8) | 1.16 | (7.0) | 2.48 | 0.74 | 3.81 | 47.66 |
| Pink salmon | 0.53 | (6.9) | 0 | (0) | 2.46 | 0.59 | 3.78 | 51.44 |
| | Summer 2006 | | Summer 2007 | | | | | |
| Pink salmon | 0.53 | (6.9) | 1.31 | (108.9) | 6.71 | 0.73 | 10.60 | 10.60 |
| Pacific herring | 0.78 | (66.0) | 1.28 | (551.9) | 5.28 | 0.91* | 8.35 | 18.96 |
| Saffron cod | 1.62 | (98.3) | 1.80 | (513.5) | 5.17 | 0.93* | 8.17 | 27.13 |
| Crescent gunnel | 1.46 | (11.0) | 1.27 | (6.1) | 3.05 | 0.64 | 4.81 | 31.95 |
| Tidepool sculpin | 0.43 | (0.7) | 0.34 | (0.4) | 2.94 | 0.56 | 4.65 | 36.59 |
| Chum salmon | 0.51 | (2.2) | 0.33 | (0.9) | 2.89 | 0.80 | 4.56 | 41.16 |
| Pacific cod | 0.25 | (1.0) | 0.45 | (1.0) | 2.58 | 0.65 | 4.07 | 45.23 |
| Whitespotted greenling | 0.35 | (0.9) | 0.52 | (1.2) | 2.43 | 0.77 | 3.84 | 49.07 |
| Bay pipefish | 1.04 | (9.8) | 0.48 | (3.2) | 2.41 | 0.82 | 3.82 | 52.89 |

were pink salmon, saffron cod, crescent gunnel, and Pacific herring; other species contributing to dissimilarity among seasons are listed in Table 2.

Species composition differed significantly among habitat types across all seasons (two-way ANOSIM: Global $R = 0.337$, $P < 0.001$). All habitat types (bedrock, eelgrass, kelp) differed significantly ($R \geq 0.101$, $P \leq 0.021$). The fish assemblage in bedrock had the lowest average Bray-Curtis similarity (17.3%) with crescent gunnel, pink salmon, Pacific herring, and saffron cod accounting for over 72% of the cumulative within-group similarity. The fish assemblage in eelgrass had the highest average similarity (55.5%) with saffron cod, crescent gunnel, bay pipefish, and tubesnout accounting for over 62% of the cumulative within-group similarity. The fish assemblage in kelp had an average similarity of 38.1% with crescent gunnel, pink salmon, Arctic shanny, Pacific herring, and bay pipefish accounting for over 65% of the cumulative within-group similarity. In pairwise habitat collections, average dissimilarity was lowest (63.6%) for eelgrass versus kelp and highest (79.5%) for bedrock versus eelgrass (Table 3). Species that were good discriminators among habitat collections were crescent gunnel, tubesnout, bay pipefish, saffron cod, and Arctic shanny; other species contributing to dissimilarity among habitats are listed in Table 3. Based on total catch, 52% to 97% of Pacific herring, saffron cod, bay pipefish, crescent gunnel, tubesnout, and walleye pollock were captured in eelgrass; 73% and 99% of pink salmon and capelin were captured in kelp.

## Fish Size

Of the most abundant species captured (>1000 fish), most were juveniles based on estimated size at maturity (Table 4). Most Pacific herring and all pink salmon and capelin were young-of-the-year (YOY). Mean length ranged from 34 mm to 92 mm FL for Pacific herring, 69 mm to

TABLE 3. Results of SIMPER analysis showing average percent dissimilarity (δ) of key fish species among habitat types in western Prince William Sound, Alaska. ($\delta_i$ = average contribution of the $i^{th}$ species to the overall dissimilarity between groups, SD = standard deviation, and cum. $\delta_i$% = the cumulative contribution to the total dissimilarity; Clarke and Warwick 2001). All results are based on the 4$^{th}$ root transformation of catch data; nontransformed data in parentheses. (* = discriminating species).

| Common name | Average abundance | | | | $\delta_i$ | $\delta_i$/SD | $\delta_i$% | Cum. $\delta_i$% |
|---|---|---|---|---|---|---|---|---|
| | Bedrock | | Eelgrass | | | | | |
| Saffron cod | 0.35 | (2.1) | 2.79 | (491.7) | 10.35 | 1.30* | 13.02 | 13.02 |
| Bay pipefish | 0.17 | (0.3) | 1.72 | (16.3) | 7.56 | 1.48* | 9.51 | 22.53 |
| Crescent gunnel | 0.60 | (1.1) | 1.70 | (12.8) | 6.05 | 1.51* | 7.60 | 30.13 |
| Tubesnout | 0.15 | (0.8) | 1.41 | (13.4) | 5.67 | 1.49* | 7.14 | 37.27 |
| Pacific herring | 0.57 | (32.9) | 0.94 | (461.2) | 5.06 | 0.63 | 6.37 | 43.64 |
| Pink salmon | 0.81 | (77.1) | 0.70 | (32.8) | 4.69 | 0.71 | 5.89 | 49.53 |
| Padded sculpin | 0.19 | (0.2) | 0.67 | (1.3) | 3.49 | 0.98 | 4.39 | 53.92 |
| | Bedrock | | Kelp | | | | | |
| Pink salmon | 0.81 | (77.1) | 1.43 | (116.3) | 9.89 | 0.87 | 13.41 | 13.41 |
| Crescent gunnel | 0.60 | (1.1) | 1.13 | (3.4) | 5.59 | 1.11* | 7.59 | 21.01 |
| Saffron cod | 0.35 | (2.1) | 0.75 | (3.6) | 4.85 | 0.97 | 6.58 | 27.58 |
| Arctic shanny | 0.16 | (0.2) | 0.70 | (1.1) | 4.84 | 1.03* | 6.56 | 34.15 |
| Bay pipefish | 0.17 | (0.3) | 0.74 | (2.3) | 4.36 | 0.83 | 5.92 | 40.07 |
| Pacific herring | 0.57 | (32.9) | 0.83 | (17.3) | 4.35 | 0.74 | 5.90 | 45.97 |
| Padded sculpin | 0.19 | (0.2) | 0.48 | (0.9) | 3.16 | 0.74 | 4.29 | 50.26 |
| | Eelgrass | | Kelp | | | | | |
| Saffron cod | 2.79 | (491.7) | 0.75 | (3.6) | 7.50 | 1.19* | 11.80 | 11.80 |
| Pink salmon | 0.70 | (32.8) | 1.43 | (116.3) | 4.63 | 0.79 | 7.28 | 19.08 |
| Pacific herring | 0.94 | (461.2) | 0.83 | (17.3) | 4.46 | 0.75 | 7.02 | 26.10 |
| Bay pipefish | 1.72 | (16.3) | 0.74 | (2.3) | 4.06 | 1.21* | 6.39 | 32.49 |
| Tubesnout | 1.41 | (13.4) | 0.48 | (1.9) | 3.93 | 1.27* | 6.19 | 38.67 |
| Padded sculpin | 0.67 | (1.3) | 0.48 | (0.9) | 2.74 | 1.07 | 4.30 | 42.97 |
| Crescent gunnel | 1.70 | (12.8) | 1.13 | (3.4) | 2.55 | 1.21* | 4.01 | 46.99 |
| Arctic shanny | 0.69 | (2.3) | 0.70 | (1.1) | 2.50 | 1.01 | 3.93 | 50.92 |

TABLE 4. Mean length (fork length or total length (mm) depending on species) and range of the most abundant species captured by beach seine in western Prince William Sound, Alaska in 2006 and 2007. Based on size range of fish captured and estimated size at maturity (mm in parentheses) from FishBase (2010), <1.0% of Pacific herring and saffron cod, and no pink salmon and capelin were mature. Only those species with more than 1000 fish captured are listed. (n = number measured, SD = standard deviation).

| | Pacific herring (161) | | | | Saffron cod (287) | | | | Pink salmon (420) | | | | Capelin (106) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | n | $\bar{x}$ | ±SD | Range | n | $\bar{x}$ | ±SD | Range | n | $\bar{x}$ | ±SD | Range | n | $\bar{x}$ | ±SD | Range |
| Spring 2006 | | | | | | | | | | | | | | | | |
| Bedrock | | | | | | | | | 59 | 32.5 | ± 1.4 | 29-35 | | | | |
| Eelgrass | | | | | 7 | 136.3 | ±37.9 | 115-221 | 89 | 34.1 | ± 2.9 | 26-43 | | | | |
| Kelp | | | | | 1 | 134.9 | ±14.5 | 119-165 | 218 | 33.8 | ± 2.8 | 29-54 | | | | |
| Summer 2006 | | | | | | | | | | | | | | | | |
| Bedrock | 5 | 33.5 | ± 2.4 | 30-38 | 20 | 74.8 | ± 5.3 | 67-87 | 3 | 68.3 | ± 7.4 | 60-74 | | | | |
| Eelgrass | 97 | 68.4 | ±33.2 | 34-125 | 476 | 103.5 | ±53.7 | 46-335 | 4 | 64.5 | ± 4.5 | 59-70 | | | | |
| Kelp | 3 | 79.9 | ±25.3 | 35-105 | 5 | 163.1 | ±79.0 | 58-304 | 77 | 67.3 | ± 6.2 | 50-78 | | | | |
| Fall 2006 | | | | | | | | | | | | | | | | |
| Bedrock | 36 | 53.3 | ±12.2 | 34-98 | | | | | | | | | 8 | 41.0 | ±7.6 | 31-49 |
| Eelgrass | | | | | 406 | 131.6 | ±47.5 | 88-340 | | | | | | | | |
| Kelp | 48 | 40.8 | ± 9.2 | 29-91 | 51 | 155.0 | ±54.3 | 97-272 | | | | | 96 | 46.4 | ±4.7 | 36-58 |
| Summer 2007 | | | | | | | | | | | | | | | | |
| Bedrock | 2 | 91.6 | ±49.3 | 32-203 | 42 | 69.4 | ±36.3 | 47-254 | 41 | 77.4 | ±12.9 | 42-123 | | | | |
| Eelgrass | 239 | 47.9 | ±27.0 | 30-121 | 477 | 102.6 | ±58.4 | 47-308 | 64 | 61.3 | ± 6.6 | 43-83 | | | | |
| Kelp | 31 | 61.6 | ±37.6 | 31-135 | 37 | 113.1 | ±78.8 | 52-341 | 56 | 79.1 | ±16.9 | 45-123 | | | | |

163 mm TL for saffron cod, 33 mm to 79 mm FL for pink salmon, and 41 mm to 46 mm FL for capelin (Table 4). Species captured with the greatest estimated proportion of adults were bay pipefish (65%; based on our own observations of gravid fish and total length), Arctic shanny (48%), and tubesnout (44%) (FishBase 2010); none of these species are important in sport or commercial fisheries.

### Temperature and Salinity

Water temperatures followed a similar seasonal pattern at all thermograph locations (Figure 6), whereas salinity varied widely among sample sites depending on seasonal rainfall and proximity to freshwater streams. Mean monthly water temperatures were highest in July or August (13-14 °C) and lowest in March (3-4 °C) (Figure 6). Inclusive of all sampling periods, mean surface salinity was 22 PSS and ranged from 5 to 33 PSS. Catch-per-unit-effort (all species) was not significantly correlated ($P > 0.173$) with water temperature or salinity. Species richness, however, was positively correlated ($P = 0.005$) with water temperature, but not salinity ($P = 0.068$).

## Discussion

Nearshore fish assemblages in western PWS are dominated by a few species (e.g., bay pipefish, crescent gunnel, tubesnout) that are present from at least April to September, and seasonal pulses of juvenile pink salmon in April, Pacific herring and saffron cod in July, and capelin in September. Wertheimer and Celewycz (1996) also reported peak abundance of juvenile pink salmon in spring followed by declines through early summer in western PWS. Juvenile Pacific herring that we captured likely arrived from other areas via larval dispersal (e.g., Montague Island; Norcross et al. 2001) as there are no major Pacific herring spawning areas in western PWS (Cooney 2007). Capelin spawn in June and July in PWS, and larvae move inshore from July to October (Brown 2002); this explains the high abundance of YOY capelin that we observed in September. Although capelin were the fourth most abundant species based on total catch, infrequent catches (FO = 10%, all sampling periods) suggest limited or patchy distribution. Crescent gunnel, tubesnout, and sculpins (Cottidae) may reside in the nearshore throughout the year in western PWS; these species were captured with a

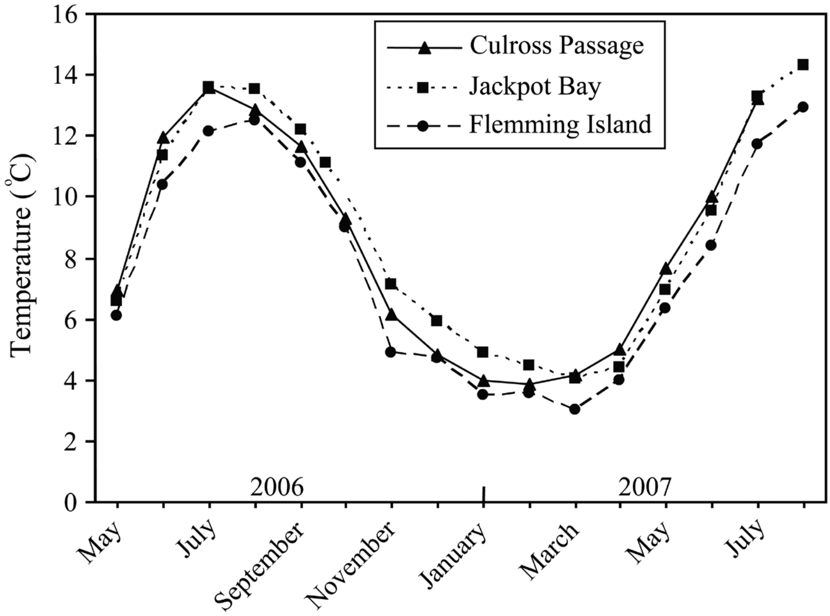


Figure 6. Mean monthly water temperatures at three locations in western Prince William Sound, Alaska in 2006 and 2007. See Figure 1 for thermograph locations.

beach seine in February and March in southeastern Alaska (Thedinga et al. 2006).

In many other nearshore studies, fish abundance and species richness were higher in summer, when water temperatures were warmer, than other times of the year (Allen and Horn 1975, Lazzari et al. 1999, Methven et al. 2001, Pihl and Wennhage 2002, Masuda 2008). Our results followed this seasonal pattern of species richness but not fish abundance; we found that CPUE (all species) was similar among seasons, largely the result of the transition from one seasonally abundant species to another. For example, as pink salmon abundance declined from spring to summer, abundance of Pacific herring and saffron cod increased. In addition, variability in catch among seasons was high and strongly influenced by the schooling behavior and infrequent but large catches of some species (e.g., capelin in fall).

We observed greater abundance and number of species in eelgrass and kelp habitats than in bedrock habitats, most likely related to habitat type. In addition, some species were largely restricted to one vegetation type; for example, 97% of the total catch of saffron cod in 2006 was in eelgrass. Similarly at Kodiak Island, Alaska, saffron cod were almost exclusively restricted to eelgrass (Laurel et al. 2007). Eelgrass and kelp provide increased structure and complexity versus bare or sparsely vegetated habitats (Heck and Orth 1980, Hamilton and Konar 2007). Higher abundance and species richness of fish in vegetated versus sparsely vegetated habitats has been reported elsewhere (Sogard and Able 1991, Franco et al. 2006). Bedrock outcrops may be an example of a transitional habitat; our catches were usually lowest in this habitat type possibly from stronger currents and limited cover. Low catches of fish in bedrock habitats has also been reported in the Aleutian Islands (Thedinga et al. 2008). All nearshore habitats in western PWS, however, have ecological value. Bedrock habitats may be used only short-term as fish migrate from sheltered bays toward the Gulf of Alaska (Wertheimer and Celewycz 1996), whereas eelgrass and kelp may be used for several weeks as foraging areas (Johnson et al. 2008).

The summer fish assemblage in nearshore waters of western PWS appears to have changed over the last 20 years. In our study, species that dominated the summer fish assemblage were crescent gunnel, saffron cod, pink salmon, and bay pipefish, whereas in the 1990s, the dominant nearshore species reported in SCUBA surveys were juvenile Pacific cod, pricklebacks (mostly Arctic shanny), gunnels (mostly crescent gunnels), greenlings (Hexagrammidae), and sculpins (Cottidae) (Dean et al. 2000). In particular, the low abundance of juvenile Pacific cod in eelgrass was unexpected in our study, as was the high abundance of saffron cod. Saffron cod were not mentioned in the suite of species captured or observed in any earlier nearshore studies in PWS (Laur and Haldorson 1996, Wertheimer and Celewycz 1996, Dean et al. 2000). Whether saffron cod was misidentified as another gadid (e.g., Pacific tomcod) in earlier studies or is a relatively new inhabitant in western PWS is unknown. Johnson et al. (2009) describe in detail the recent invasion of saffron cod into nearshore habitats of western PWS and possible ecological implications. Bay pipefish were likely present but missed in earlier SCUBA surveys in PWS; their slender, green bodies can make them difficult to see, especially in eelgrass meadows. Bay pipefish were captured in eelgrass with a beach seine in western PWS in 1989 (Orsi et al. 1991).

Although we captured many species in small or incidental numbers, they are important from an ecosystem perspective. Some of these species included crescent gunnel, Arctic shanny, and a variety of sculpins; these species are important members of the food web. For example, crescent gunnel was the most frequently encountered species in our study (FO = 76%, all sampling periods) and is prey for river otter (*Lutra canadensis*), pigeon guillemot (*Cepphus columba*), and other fishes (Golet et al. 2000, Jewett et al. 2002) including the commercially important lingcod (Beaudreau and Essington 2007).

Using identical methods, fish catch (CPUE), species richness, and composition of the most abundant species varied between western PWS and other regions of Alaska. For example, median CPUE (all species) and total species richness were 41 fish and 34 species in July 2006, and 73 fish and 26 species in July 2007 in western PWS, versus 151 fish and 28 species in the Aleutian Islands in June 2005 (Thedinga et al. 2008), and 1091 fish and 37 species at The Brothers Islands, southeastern Alaska (July 2001, 2002, and 2003; Thedinga et al. 2006, NOAA Fisheries 2009a). Dominant species identified in the Aleutian Islands were Pacific sand lance, juvenile gadids, pink salmon, and Pacific sandfish (*Trichodon trichodon*), whereas in southeastern Alaska, dominant species were walleye pollock, Pacific herring, Pacific sand lance, and Pacific cod (Thedinga et al. 2006, 2008). Use of the nearshore by many commercially important and forage fish species over spatially large areas of Alaska emphasizes the importance of managing and protecting coastal areas from shoreline disturbance.

Our capture of mostly juvenile capelin, Pacific herring, pink salmon, and saffron cod supports the importance of shallow, nearshore areas as juvenile habitat in western PWS. The use of nearshore areas as nursery and juvenile habitat is well documented (Beck et al. 2003, Spalding et al. 2003, Johnson and Thedinga 2005). Previous studies in PWS have reported that YOY Pacific herring and capelin enter nursery bays and fiords in summer and early fall; both species likely use the same areas to overwinter (Stokesbury et al. 1999, Brown 2002, Cooney 2007). Although mostly deeper water in embayments have been identified as nursery habitat (Brown 2002), our study identifies the importance of shallow-water habitats (<5 m deep, <20 m from shore) within embayments to juvenile fishes. These "edge" habitats (e.g., eelgrass, kelp) are extremely vulnerable to shoreline development and oil spills. Spatially explicit data on the distribution and habitat use of nearshore fishes in this study is included in an online database (NOAA Fisheries 2009a) that provides resource managers with a baseline to track long-term and large-scale changes in the nearshore ecosystem.

Nearshore habitats in western PWS support a diverse and dynamic fish assemblage characterized by resident species and the seasonal recruitment of mostly YOY fishes. Many species are important commercially or as forage fish in the diet of higher-level predators. The nearshore fish assemblage in western PWS has changed over the last 20 years and may see further change in the future with a warming climate and the predicted northward redistribution of some species (Lubchenco et al. 1993) with unknown consequences to existing stocks and food webs. Climate change and the vulnerability of shallow-water habitats to shoreline development or an oil spill justifies the need to better understand, protect, and manage these valuable nearshore habitats.

## Acknowledgments

We thank the crews of the RV *Solstice* and RV *Pandalus* for their invaluable support at sea. We would especially like to thank Matthew Eagleton of the NMFS regional office in Anchorage for providing logistical support. We also thank Dugan Greenwell, Kris Holderied, John Hudson, Sarah Lyn McConahay, John Moran, Sue Saupe, Fletcher Sewall, and Ashwin Sreenivasan for help with field and laboratory work. Funding for this research was provided by the North Pacific Research Board (Publication 249) and the NOAA Fisheries Essential Fish Habitat Program. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

## Literature Cited

Allen, L. G., and M. H. Horn. 1975. Abundance, diversity, and seasonality of fishes in Colorado Lagoon, Alamitos Bay, California. Estuarine and Coastal Marine Science 3:371-380.

Beaudreau, A. H., and T. E. Essington. 2007. Spatial, temporal, and ontogenetic patterns of predation on rockfishes by lingcod. Transactions of the American Fisheries Society 136:1438-1452.

Beck, M. W., K. L. Heck, Jr., K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. S. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2003. The role of nearshore ecosystems as fish and shellfish nurseries. Issues in Ecology 11:1-12.

Brown, E. D., T. T. Baker, J. E. Hose, R. M. Kocan, G. D. Marty, M. D. McGurk, B. L. Norcross, and J. Short. 1996. Injury to the early life history stages of Pacific herring in Prince William Sound after the *Exxon Valdez* oil spill. *In* S. D. Rice, R. B. Spies, D. A. Wolfe, and B. A. Wright (editors), Proceedings of the *Exxon Valdez* Oil Spill Symposium. American Fisheries Society, Symposium 18, Bethesda, MD. Pp. 448-462.

Brown, E. D. 2002. Life history, distribution, and size structure of Pacific capelin in Prince William Sound and the northern Gulf of Alaska. ICES Journal of Marine Science 59:983-996.

Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E: Plymouth, UK.

Conover, W. J. 1980. Practical nonparametric statistics. John Wiley & Sons, New York.

Cooney, T. 2007. Pacific herring. *In* R. B. Spies (editor), Long-term Ecological Change in the Northern Gulf of Alaska. Elsevier Publications. Pp. 81-85.

Dean, T. A., L. Haldorson, D. R. Laur, S. C. Jewett, and A. Blanchard. 2000. The distribution of nearshore fishes in kelp and eelgrass communities in Prince William Sound, Alaska: associations with vegetation and physical habitat characteristics. Environmental Biology of Fishes 57:271-287.

FishBase. A global information system on fishes. 2010. Available online at http://www.fishbase.org/ (accessed 18 May 2010).

Franco, A., P. Franzoi, S. Malavasi, F. Riccato, and P. Torricelli. 2006. Fish assemblages in different shallow water habitats of the Venice Lagoon. Hydrobiologia 555:159-174.

Golet, G. H., K. J. Kuletz, D. D. Roby, and D. B. Irons. 2000. Adult prey choice affects chick growth and reproductive success in pigeon guillemots. The Auk 117:82-91.

Hamilton, J., and B. Konar. 2007. Implications of substrate complexity and kelp variability for south-central Alaskan nearshore fish communities. Fishery Bulletin 105:189-196.

Heard, W. R., and A. M. Andersen. 1999. Alaska salmon. *In* Our Living Oceans. Report on the Status of U.S. Living Marine Resources. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-F/SPO-41. Pp. 157-166.

Heck, K. L., and R. J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. *In* V. S. Kennedy (editor), Estuarine Perspectives—Proceedings of the 1979 Biennial Meeting of the Estuarine Research Federation. Academic Press, New York. Pp. 449-464.

Jewett, S. C., T. A. Dean, B. R. Woodin, M. K. Hoberg, and J. J. Stegeman. 2002. Exposure to hydrocarbons 10 years after the *Exxon Valdez* oil spill: evidence from cytochrome P4501A expression and biliary FACs in nearshore demersal fishes. Marine Environmental Research 54:21-48.

Johnson, S. W., M. G. Carls, R. P. Stone, C. C. Brodersen, and S. D. Rice. 1997. Reproductive success of Pacific herring *Clupea pallasii*, in Prince William Sound, Alaska, six years after the *Exxon Valdez* oil spill. Fishery Bulletin 95:748-761.

Johnson, S. W., M. L. Murphy, D. J. Csepp, P. M. Harris, and J. F. Thedinga. 2003. A survey of fish assemblages in eelgrass and kelp habitats of southeastern Alaska. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-139.

Johnson, S. W., and J. F. Thedinga. 2005. Fish use and size of eelgrass meadows in southeastern Alaska: A baseline for long-term assessment of biotic change. Northwest Science 79:141-155.

Johnson, S. W., J. F. Thedinga, and K. M. Munk. 2008. Distribution and use of shallow-water habitats by Pacific sand lances in southeastern Alaska. Transactions of the American Fisheries Society 137:1455-1463.

Johnson, S. W., J. F. Thedinga, and A. D. Neff. 2009. Invasion by saffron cod *Eleginus gracilis* into nearshore habitats of Prince William Sound, Alaska, USA. Marine Ecology Progress Series 389:203-212.

Laur, D., and L. Haldorson. 1996. Coastal habitat studies: The effect of the *Exxon Valdez* oil spill on shallow subtidal fishes in Prince William Sound. *In* S. D. Rice, R. B. Spies, D. A. Wolfe, and B. A. Wright (editors), Proceedings of the *Exxon Valdez* Oil Spill Symposium. American Fisheries Society, Symposium 18, Bethesda, MD. Pp. 659-670.

Laurel, B. J., A. W. Stoner, C. H. Ryer, T. P. Hurst, and A. A. Abookire. 2007. Comparative habitat associations in juvenile Pacific cod and other gadids using seines, baited cameras, and laboratory techniques. Journal Experimental Marine Biology and Ecology 351:42-55.

Lazzari, M. A., S. Sherman, C. S. Brown, J. King, B. J. Joule, S. B. Chenoweth, and R. W. Langton. 1999. Seasonal and annual variations in abundance and species composition of two nearshore fish communities in Maine. Estuaries 22:636-647.

Lubchenco, J., S. A. Navarrete, B. N. Tissot, and J. C. Castilla. 1993. Possible ecological responses to global climate change: nearshore benthic biota of Northeastern Pacific coastal ecosystems. *In* H. A. Mooney, E. R. Fuentes, and B. I. Kronberg (editors), Earth System Responses to Global Change. Academic Press, San Diego, CA. Pp. 147-166.

Masuda, R. 2008. Seasonal and interannual variation of subtidal fish assemblages in Wakasa Bay with reference to the warming trend in the Sea of Japan. Environmental Biology of Fishes 82:387-399.

Methven, D. A., R. L. Haedrich, and G. A. Rose. 2001. The fish assemblage of a Newfoundland estuary: diel, monthly, and annual variation. Estuarine, Coastal and Shelf Science 52:669-687.

NOAA (National Oceanic and Atmospheric Administration) Fisheries. 2009a. Nearshore fish atlas of Alaska. Available online at www.fakr.noaa.gov/habitat/fishatlas/ (accessed 15 December 2009).

NOAA (National Oceanic and Atmospheric Administration) Fisheries. 2009b. Alaska ShoreZone coastal mapping and imagery. Available online at http://www.alaskafisheries.noaa.gov/habitat/shorezone/szintro.htm (accessed 15 December 2009).

Norcross, B. L., and M. Frandsen. 1996. Distribution and abundance of larval fishes in Prince William Sound, Alaska, during 1989 after the *Exxon Valdez* oil spill. *In* S. D. Rice, R. B. Spies, D. A. Wolfe, and B. A. Wright (editors), Proceedings of the *Exxon Valdez* Oil Spill Symposium. American Fisheries Society, Symposium 18, Bethesda, MD. Pp. 463-486.

Norcross, B. L., E. D. Brown, R. J. Foy, M. Frandsen, S. M. Gay, T. C. Kline Jr., D. M. Mason, E. V. Patrick, A. J. Paul, and K. D. E. Stokesbury. 2001. A synthesis of the life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. Fisheries Oceanography 10 (Suppl. 1):42-57.

Orsi, J. A., R. K. Gish, and B. L. Wing. 1991. Northern range extension of four nearshore marine fishes in Alaska. The Canadian Field-Naturalist 105:82-86.

*Received 20 April 2009*
*Accepted for publication 26 May 2010*

Ostrand, W. D., S. Howlin, and T. A. Gotthardt. 2004. Fish school selection by marbled murrelets in Prince William Sound, Alaska: responses to changes in availability. Marine Ornithology 32:69-76.

Pihl, L., and H. Wennhage. 2002. Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish west coast. Journal of Fish Biology 61:148-166.

Pollard, D. A. 1984. A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. Aquatic Botany 18:3-42.

Robards, M. D., J. F. Piatt, and G. A. Rose. 1999. Maturation, fecundity, and intertidal spawning of Pacific sand lance in the northern Gulf of Alaska. Journal of Fish Biology 54:1050-1068.

SigmaStat. 1997. SigmaStat statistical software. SPSS Inc., Chicago.

Sogard, S. M., and K. W. Able. 1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. Estuarine, Coastal and Shelf Science 33:501-519.

Spalding, M., M. Taylor, C. Ravilious, F. Short, and E. Green. 2003. The distribution and status of seagrasses. *In* E. P. Green, and F. T. Short (editors), World Atlas of Seagrasses. UNEP World Conservation Monitoring Center, University of California Press, Berkeley. Pp. 5-26.

Stokesbury, K. D. E., R. J. Foy, and B. Norcross. 1999. Spatial and temporal variability in juvenile Pacific herring, *Clupea pallasii*, growth in Prince William Sound, Alaska. Environmental Biology of Fishes 56:409-418.

Thedinga, J. F., S. W. Johnson, and D. J. Csepp. 2006. Nearshore fish assemblages in the vicinity of two Steller sea lion haul-outs in southeastern Alaska. *In* A. W. Trites, S. K. Atkinson, D. P. DeMaster, L. W. Fritz, T. S. Gelatt, L. D. Rea, and K. M. Wynne (editors). Sea Lions of the World. Alaska Sea Grant College Program, University of Alaska, Fairbanks. Pp. 269-284.

Thedinga, J. F., S. W. Johnson, A. D. Neff, and M. R. Lindeberg. 2008. Fish assemblages in shallow nearshore habitats of the Bering Sea. Transactions of the American Fisheries Society 137:1157-1164.

Weingartner, T. 2007. The physical environment of the Gulf of Alaska. *In* R. B. Spies (editor), Long-term Ecological Change in the Northern Gulf of Alaska. Elsevier Publications. Pp. 12-17.

Wertheimer, A. C., and A. G. Celewycz. 1996. Abundance and growth of juvenile pink salmon in oiled and non-oiled locations of western Prince William Sound after the *Exxon Valdez* oil spill. *In* S. D. Rice, R. B. Spies, D. A. Wolfe, and B. A. Wright (editors), Proceedings of the *Exxon Valdez* Oil Spill Symposium. American Fisheries Society, Symposium 18, Bethesda, MD. Pp. 518-532.