Estuarine, Coastal and Shelf Science (2000) **51**, 45–59
doi:10.1006/ecss.1999.0615, available online at http://www.idealibrary.com on IDEAL®

Nearshore Fish Distributions in an Alaskan Estuary in Relation to Stratification, Temperature and Salinity

A. A. Abookire[a], J. F. Piatt and M. D. Robards

Alaska Biological Science Center, U.S. Geological Survey, 1011 E. Tudor Road, Anchorage, Alaska 99503, U.S.A.

Received 27 May 1999 and accepted in revised form 21 December 1999

Fish were sampled with beach seines and small-meshed beam trawls in nearshore (<1 km) and shallow (<25 m) habitats on the southern coast of Kachemak Bay, Cook Inlet, Alaska, from June to August, 1996–1998. Fish distributions among habitats were analysed for species composition, catch-per-unit-effort (CPUE) and frequency of occurrence. Two oceanographically distinct areas of Kachemak Bay were sampled and compared: the Outer Bay and the Inner Bay. Outer Kachemak Bay is exposed and receives oceanic, upwelled water from the Gulf of Alaska, whereas the Inner Bay is more estuarine. Thermohaline properties of bottom water in the Outer and Inner Bay were essentially the same, whereas the Inner Bay water-column was stratified with warmer, less saline waters near the surface.

Distribution and abundance of pelagic schooling fish corresponded with area differences in stratification, temperature and salinity. The Inner Bay supported more species and higher densities of schooling and demersal fish than the Outer Bay. Schooling fish communities sampled by beach seine differed between the Outer and Inner Bays. Juvenile and adult Pacific sand lance (*Ammodytes hexapterus*), Pacific herring (*Clupea harengus pallasi*), osmerids (Osmeridae) and sculpins (Cottidae) were all more abundant in the Inner Bay. Gadids (Gadidae) were the only schooling fish taxa more abundant in the Outer Bay. Thermohaline characteristics of bottom water were similar throughout Kachemak Bay. Correspondingly, bottom fish communities were similar in all areas. Relative abundances (CPUE) were not significantly different between areas for any of the five demersal fish groups: flatfishes (Pleuronectidae), ronquils (Bathymasteridae), sculpins (Cottidae), gadids (Gadidae) and pricklebacks (Stichaeidae).

Keywords: forage fish; nearshore (zone); stratification; temperature; salinity; distribution; estuarine habitat; Alaska

Introduction

Estuaries and sheltered coastal marine habitats are important feeding and nursery grounds for juvenile fish, and many species depend on these areas for survival (Allen, 1982; Bennett, 1989). Estuaries enhance growth and survival of juvenile fish because they provide high food availability, low predation risk, warm water temperatures and protection from adverse weather conditions (Gadomski & Caddell, 1991; Gibson, 1994). Kachemak Bay is a productive estuary within lower Cook Inlet, which is itself a large estuary in the Northern Gulf of Alaska about the same length as Chesapeake Bay (Muench *et al.*, 1978, p. 5096). Kachemak Bay supports commercial and sport fisheries (Bechtol & Yuen, 1995) and serves as an important nursery area for flatfish and groundfish (Abookire & Norcross, 1998; Norcross *et al.*, 1998).

Estuaries provide an opportunity to study the influence of thermohaline properties on fish distribution because river runoff often creates steep gradients of temperature, salinity, turbidity and nutrients in relatively small marine areas (Laevastu & Hela, 1970). Because Kachemak Bay is divided into Outer and Inner regions by the extension of Homer Spit (Figure 1), it lends itself to a study of small-scale (<10 km) nearshore fish distributions as related to localized thermohaline properties. Upwelling in lower Cook Inlet creates a cold, nutrient-rich water mass that is transported into Kachemak Bay by the northerly flow of Gulf of Alaska water through Kennedy Entrance (Muench *et al.*, 1978, p. 5097). The Outer Bay is therefore oceanic in character, well-mixed by large tidal oscillations and has limited freshwater inflow. In contrast, Inner Kachemak Bay receives freshwater from a number of large, glacially-fed rivers and develops into a well-stratified, two-layer system in late spring and summer (Science Applications, Inc., 1977). Whereas the Outer Bay is subject to greater turbulence and wave action, the Inner Bay is more sheltered and this influences nearshore habitats (Syvitski *et al.*, 1987). For example, the Outer Bay has more cobble and sand beaches while the Inner Bay is characterized by beaches with fine-grained mud (Abookire, 1997).

[a]Corresponding author: National Marine Fisheries Service, 301 Research Court, Kodiak, Alaska 99615, U.S.A. Phone: (907) 481-1735; Fax: (907) 481-1703; e-mail: alisa.abookire@noaa.gov

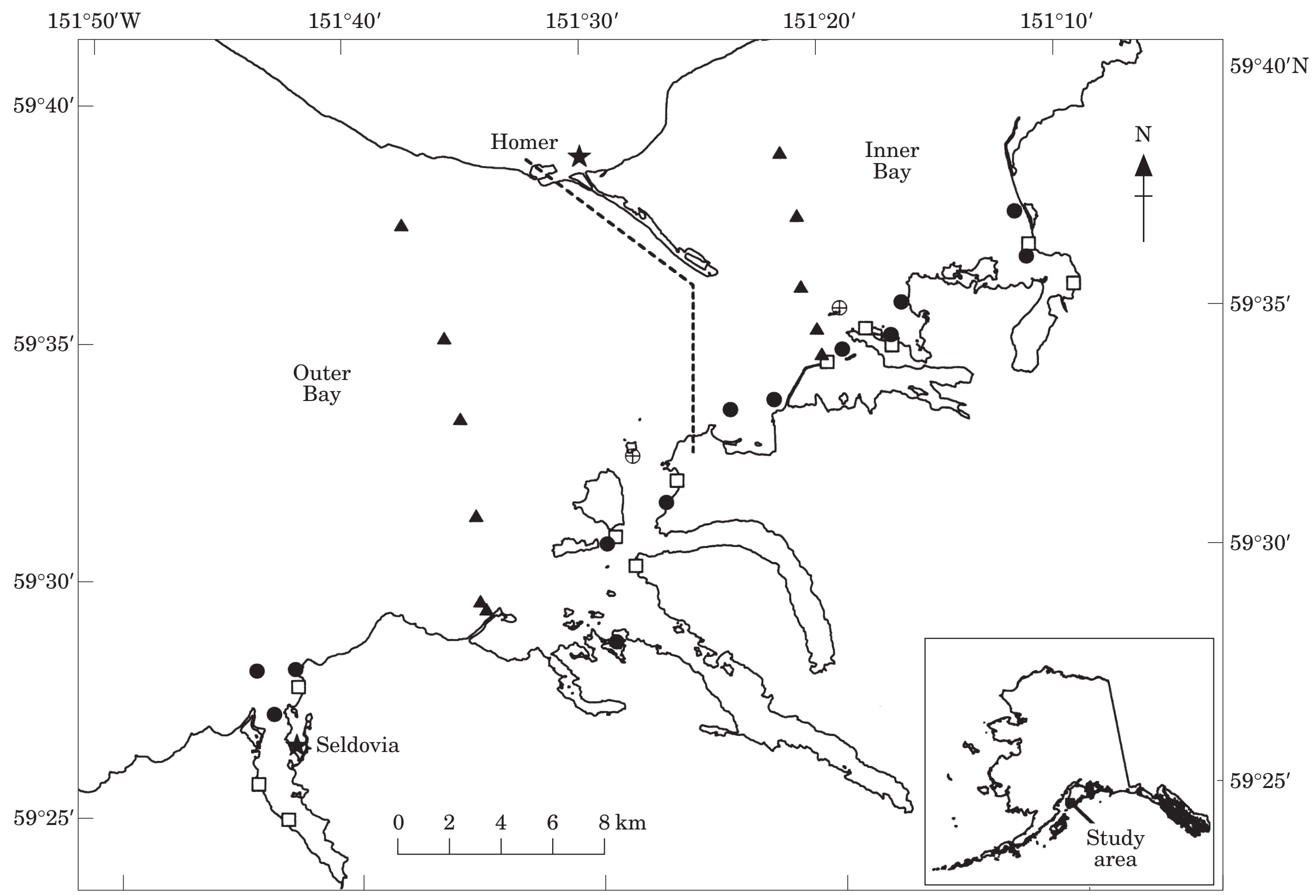

FIGURE 1. Location of sampling stations for beam trawls, beach seines, CTD transects, and surface temperature loggers in Kachemak Bay, Alaska. The Inner Bay is the area of Kachemak Bay northeast of the line from the tip of Homer Spit perpendicular to the southern shore. Filled circle: trawl; crossed circle: loggers; open square: seine; filled triangle: CTD.

Within estuarine environments, the influence of small-scale (<10 km) variability in water temperature and salinity on nearshore fish distributions is poorly understood. At larger spatial scales, it is known that water temperature and salinity can affect fish distribution and community composition over seasonal (Pearcy, 1978; Blackburn, 1979; Allen, 1982; Nash & Gibson, 1982; Nash, 1988) and decadal (Beamish, 1995; and refs therein) time-periods. Whereas large-scale distributions have been described for Pacific herring *Clupea harengus pallasi* (Carlson, 1980; Zebdi & Collie, 1995), capelin *Mallotus villosus* (Frank *et al.*, 1996), and gadids (Shimada & Kimura, 1994; Quinn & Niebauer, 1995), investigations of small-scale distributions are uncommon, with the exception of Pacific sand lance *Ammodytes hexapterus* (McGurk & Warburton, 1992) and juvenile salmonids *Oncorhynchus* spp. (Macdonald *et al.*, 1987).

Previous studies in Kachemak Bay have examined fish communities on broad temporal (Bechtol, 1997; Robards *et al.*, 1999) and spatial scales (Blackburn, 1979; Norcross *et al.*, 1998), but little is known about either small-scale fish distributions within Kachemak Bay or environmental factors which influence these distributions. Our overall objective was to determine if fish distribution and abundance was influenced by stratification, temperature, or salinity in Kachemak Bay. Specific objectives of this study were to: (a) determine whether water temperature and salinity differed by area; (b) compare how nearshore fish species were distributed in the two areas (by percent community composition and frequency of occurrence); and (c) compare the relative abundance (catch-per-unit-effort, CPUE) of nearshore fish in the Outer and Inner Bay.

Materials and methods

Temperature and salinity

A conductivity, temperature, and density (CTD) recorder (Seabird Electronics Inc, SBE-19 SEACAT profiler) was used to collect vertical temperature and salinity profiles. Collections were made on 10 August 1996; 7 June, 13 July and 19 August 1997; and 9 June, 16 July and 16 August 1998, at six stations in the Outer Bay and five stations in the Inner Bay (Figure 1). When surface thermohaline data are presented, values represent an average of about 12 data points collected in 30 s between the surface and 5 m depth. The only exception is temperature data collected in June and July of 1996 with a temperature logger (ONSET Electronics StowAway). The logger was stationed 5 m below the surface in the Outer and Inner Bays (Figure 1) where it continuously collected temperature data at hourly intervals. The CTD was also deployed at all beam trawl locations (Figure 1) prior to each fishing effort, and these data were used for comparisons of bottom water temperature and salinity. When bottom thermohaline data are presented, values represent an average of about 12 data points collected in 30 s within the deepest 5 m of water.

Spatial comparisons of average thermohaline properties were tested for significance with a Student *t*-test (*t*-test) or a Mann–Whitney Rank Sum Test (MW). Interannual and seasonal thermohaline comparisons were made using one-way Analysis of Variance (ANOVA) or Kruskal–Wallis one-way ANOVA on ranks. Averaged thermohaline data are presented as mean $\pm$ 1 SE. August temperature and salinity vertical profiles were plotted using a minimum curvature programme (Surfer Golden Software, 1995).

Fish collections

Beach seines were conducted with a 44 m wide net that was 4 m deep with a 3 mm mesh in the centre. The net was set 25 m from shore with an inflatable skiff, and we seined within 1 h of low tide during daylight. Twenty stations were sampled, eight stations on five beaches in the Inner Bay and 12 stations on six beaches in the Outer Bay (Figure 1). When two stations were located on the same beach, they were separated by at least 30 m. Seines were conducted about every two weeks in June, July and August for a total of 88 seines in 1996, 116 seines in 1997, and 110 seines in 1998. All fishes were identified, counted, and a subsample (<100 individuals) were retained for lengths and weights. Additionally, Pacific sand lance were measured, weighed, and classified as juvenile or adult based on length (Robards *et al*., pers. comm.). The catch-per-unit-effort (CPUE) was calculated as the total number of fish captured per seine for all fish, or by species groups. Fishes captured in beach seines were grouped into eight subsets: juvenile sand lance, adult sand lance, Pacific herring, salmonids (Salmonidae), gadids (Gadidae), osmerids (Osmeridae), sculpins (Cottidae) and other fishes (Table 1).

Bottom trawls were conducted on 7–9 August 1996; 3, 14 July and 6–14 August 1997; and 1–2, 18 July, and 14 August 1998, at six stations in the Outer Bay and seven stations in the Inner Bay (Figure 1). Stations were chosen such that depth ranges 8–10, 10–15, 15–20 and 20–25 m were represented proportionately between areas. Standard tow duration was 5 min, and station depth did not exceed 25 m. A 3·05 m plumbstaff beam trawl equipped with a double tickler chain was towed (Gunderson & Ellis, 1986). Net body was 7 mm square mesh with a 4 mm mesh codend liner. All fishes were identified to species, counted and measured to the nearest mm fork length. Data was analysed only for demersal fishes with fork length less than 150 mm because beam trawls of this size select for small fishes. Fish data were standardized to CPUE for an area of 1000 m^2. The area towed was calculated as the effective width of net (0·74; Gunderson & Ellis, 1986), multiplied by the width of our trawl (3·05 m), multiplied by tow length as determined by Global Positioning System data. Fishes captured in beam trawls were grouped into six subsets: flatfishes (Pleuronectidae), ronquils (Bathymasteridae), sculpins (Cottidae), gadids (Gadidae), pricklebacks (Stichaeidae), and other fish (Table 1).

Statistical analyses of fish data

Shannon–Wiener Index of Diversity (Krebs, 1989) and species richness (the total number of species) were calculated for beach seine and trawl data by year and area. To test for differences among areas in the species composition of fish groups, Likelihood Ratio Chi-Square Tests (G-tests) were calculated with SAS (SAS Institute Inc., 1996). If the overall model was significant, we calculated individual G values for each factor. Significance was assumed at $P<0·05$ for all statistics.

All CPUE data were ranked or log (x+1) transformed to correct for heterogeneity of variance. A multiple analysis of variance (MANOVA) was calculated on CPUE of the eight beach seine fish groups with SAS using area (Inner and Outer Bay) and year (1996–1998) as factors. For bottom trawl catches, separate Mann–Whitney Rank Sum Tests (MW) were performed on each month–year combination to test for differences in CPUE by area (Inner and Outer Bay). Separate ANOVAs were run for interannual and seasonal comparisons of bottom trawl data because

TABLE 1. Mean catch of fishes captured per seine or per trawl in Outer and Inner Kachemak Bay from June to August, 1996–1998. Sample size is given in parentheses. CPUE numbers have been rounded, and 'a' denotes values less than 1

				Beach seine		Beam trawl	
Scientific name	Common name	Seine group	Trawl group	Outer Bay (n=156)	Inner Bay (n=158)	Outer Bay (n=33)	Inner Bay (n=47)
Ammodytes hexapterus	Pacific sand lance	sand lance	other	165	871	0	5
Clupea harengus pallasi	Pacific herring	herring	other	10	405	0	0
Oncorhynchus gorbuscha	Pink salmon	salmon	other	16	11	0	0
Oncorhynchus keta	Chum salmon	salmon	other	a	1	0	0
Oncorhynchus nerka	Sockeye salmon	salmon	other	a	4	0	0
Oncorhynchus tshawytscha	Chinook salmon	salmon	other	1	1	0	0
Salvelinus malma	Dolly varden	salmon	other	13	3	0	0
Gadus macrocephalus	Pacific cod	gadid	gadid	10	12	4	25
Microgadus proximus	Pacific tomcod	gadid	gadid	1	a	0	0
Eleginus gracilis	Saffron cod	gadid	gadid	17	7	a	12
Theragra chalcogramma	Walleye pollock	gadid	gadid	a	2	1	9
Hypomesus pretiosus pretiosus	Surf smelt	osmerid	other	a	1	0	0
Mallotus villosus	Capelin	osmerid	other	5	14	0	0
Thaleichthys pacificus	Eulachon	osmerid	other	0	a	0	0
Spirinchus thaleichthys	Longfin smelt	osmerid	other	0	a	0	0
Artedius fenestralis	Padded sculpin	sculpin	sculpin	a	a	0	0
Artedius harringtoni	Scalyhead sculpin	sculpin	sculpin	a	0	0	4
Asemichthys taylori	Spinynose sculpin	sculpin	sculpin	0	0	a	12
Blepsias cirrhosus	Silverspotted sculpin	sculpin	sculpin	a	1	a	10
Enophrys bison	Buffalo sculpin	sculpin	sculpin	a	a	a	7
Enophrys lucasi	Leister sculpin	sculpin	sculpin	0	0	a	9
Gymnocanthus galeatus	Armorhead sculpin	sculpin	sculpin	a	a	a	9
Gymnocanthus pistilliger	Threaded sculpin	sculpin	sculpin	0	0	0	4
Gymnocanthus spp.	Gymnocanthus spp.	sculpin	sculpin	0	0	a	4
Hemilepidotus hemilepidotus	Red Irish lord	sculpin	sculpin	a	0	1	4
Hemilepidotus jordani	Yellow Irish lord	sculpin	sculpin	a	a	1	4
Icelinus borealis	Northern sculpin	sculpin	sculpin	a	a	1	4
Leptocottus armatus	Pacific staghorn sculpin	sculpin	sculpin	a	a	0	0
Myoxocephalus polyacanthocephalus	Great sculpin	sculpin	sculpin	2	4	0	9
Myoxocephalus spp.	Myoxocephalus spp.	sculpin	sculpin	0	0	1	7
Myoxocephalus verrucosus	Warty sculpin	sculpin	sculpin	0	a	0	0
Nautichthys oculofasciatus	Sailfin sculpin	sculpin	sculpin	0	0	0	6
Nautichthys pribilovius	Eyeshade sculpin	sculpin	sculpin	0	0	1	8
Oligocottus maculosus	Tidepool sculpin	sculpin	sculpin	0	a	0	12
Psychrolutes paradoxus	Tadpole sculpin	sculpin	sculpin	0	0	0	7
Radulinus asprellus	Slim sculpin	sculpin	sculpin	0	0	0	4
Rhamphocottus richardsoni	Grunt sculpin	sculpin	sculpin	0	0	a	4
Triglops macellus	Roughspine sculpin	sculpin	sculpin	0	0	1	9
Triglops pingeli	Ribbed sculpin	sculpin	sculpin	0	a	2	4
Atheresthes stomias	Arrowtooth flounder	other	flatfish	0	0	0	5
Citharichthys sordidus	Pacific sanddab	other	flatfish	0	0	a	6
Errex zachirus	Rex sole	other	flatfish	0	0	0	5
Hippoglossoides elassodon	Flathead sole	other	flatfish	a	a	0	8
Hippoglossus stenolepis	Pacific halibut	other	flatfish	a	a	3	12
Microstomus pacificus	Dover sole	other	flatfish	0	a	a	5
Platichthys stellatus	Starry flounder	other	flatfish	a	a	0	0
Pleuronectes asper	Yellowfin sole	other	flatfish	a	a	2	6
Pleuronectes bilineatus	Rock sole	other	flatfish	4	4	13	21
Pleuronectes isolepis	Butter Sole	other	flatfish	a	0	0	5
Pleuronectes vetulus	English sole	other	flatfish	a	0	0	5
Psettichthys melanostictus	Sand sole	other	flatfish	a	0	0	0
Bathymaster signatus	Searcher	other	ronquil	0	0	a	8
Ronquilus jordani	Northern ronquil	other	ronquil	0	0	2	8
Anoplarchus purpurescens	High cockscomb	other	prickleback	a	a	0	0

TABLE 1. *Contnued*

Scientific name	Common name	Seine group	Trawl group	Beach seine: Outer Bay (n=156)	Beach seine: Inner Bay (n=158)	Beam trawl: Outer Bay (n=33)	Beam trawl: Inner Bay (n=47)
Lumpenus fabricii	Slender eelblenny	other	prickleback	a	10	0	9
Lumpenus maculatus	Daubed shanny	other	prickleback	0	a	0	5
Lumpenus sagitta	Pacific snake prickleback	other	prickleback	1	2	0	6
Lumpenus spp.	Lumpenus spp.	other	prickleback	a	7	0	0
Sitchaeus punctatus	Arctic shanny	other	prickleback	a	a	2	7
Gasterosteus aculeatus	Threespine stickleback	other	other	a	a	0	0
Trichodon trichodon	Pacific sandfish	other	other	a	a	0	0
Pholis laeta	Crescent gunnel	other	other	a	1	a	5
Pholis ornata	Saddleback gunnel	other	other	0	a	0	0
Zaprora silenus	Prowfish	other	other	0	a	0	0
Anoplopoma fimbria	Sablefish	other	other	0	a	0	0
Hexagrammos lagocephalus	Rock greenling	other	other	a	a	a	4
Hexagrammos decagrammus	Kelp greenling	other	other	a	1	0	4
Hexagrammos octogrammus	Masked greenling	other	other	a	a	0	5
Hexagrammos stelleri	White-spotted greenling	other	other	1	2	a	4
Ophiodon elongatus	Lingcod	other	other	1	1	a	4
Sebastes polyspinis	Northern rockfish	other	other	0	a	0	0
Sebastes spp.	Rockfishes	other	other	a	0	a	5
Sebastes reedi	Yellowmouth rockfish	other	other	0	0	0	12
Anoplagonus inermis	Smooth alligatorfish	other	other	0	a	a	9
Pallasina barbata	Tubenose poacher	other	other	a	a	0	8
Podothecus acipenserinus	Sturgeon poacher	other	other	a	a	a	4
Hypsagonus quadricornis	Fourhorn poacher	other	other	0	0	a	8
Sarritor frenatus	Sawback poacher	other	other	0	0	0	8
Asterotheca infraspinata	Spinycheek starsnout	other	other	0	0	0	9
Aptocyclus ventricosus	Smooth lumpsucker	other	other	0	a	0	0
Liparis spp.	Snailfishes	other	other	a	a	a	8
Syngnathus griseolineatus	Pipefish	other	other	a	0	0	0
Shannon–Wiener Diversity				1·37	1·00	2·13	3·91
Species richness				49	55	34	56

collections in 1996 occurred only in August, and a two-way ANOVA was performed on year (1997 and 1998) and date (early July, mid July and August). Separate tests were performed for total catch and for specific fish groups.

Frequency of occurrence is expressed as a percent, and is defined as (100 times) the number of tows with the fish present divided by the total number of tows conducted. Comparisons of frequency of occurrence by area, year, and month were calculated with logistic regressions on presence/absence data for each fish group. A model with all two-way interactions was run, followed by a simpler model with insignificant interaction terms removed. Although the logistic regression tests may seem redundant, when results from both quantitative and binary datasets concur we gain confidence in our findings and can overcome the uncertainty that accompanies the high variances in fish catch data.

Results

Temperature and salinity

The water-column in the Inner Bay was stratified in all years. Temperature and salinity profiles illustrate stratification of the water-colmn with horizontal isotherm and isohaline gradients (Figures 2 and 3) ranging from depths of 0 to 10 m. Horizontal isotherms were more clearly defined in the Inner Bay than in the Outer Bay in all years. We chose to plot August data because surface salinities were highest in June ($30{\cdot}4 \pm 0{\cdot}2$), lowest in July ($26{\cdot}3 \pm 0{\cdot}7$), and at intermediate levels during August ($28{\cdot}4 \pm 0{\cdot}4$; ANOVA, $F{=}36{\cdot}15_{[62,2]}$, $P{<}0{\cdot}001$).

In all months and years (1996–1998), surface waters in the Inner Bay had higher temperatures and lower salinities than in the Outer Bay (Table 2). Bottom temperatures did not vary between Inner and

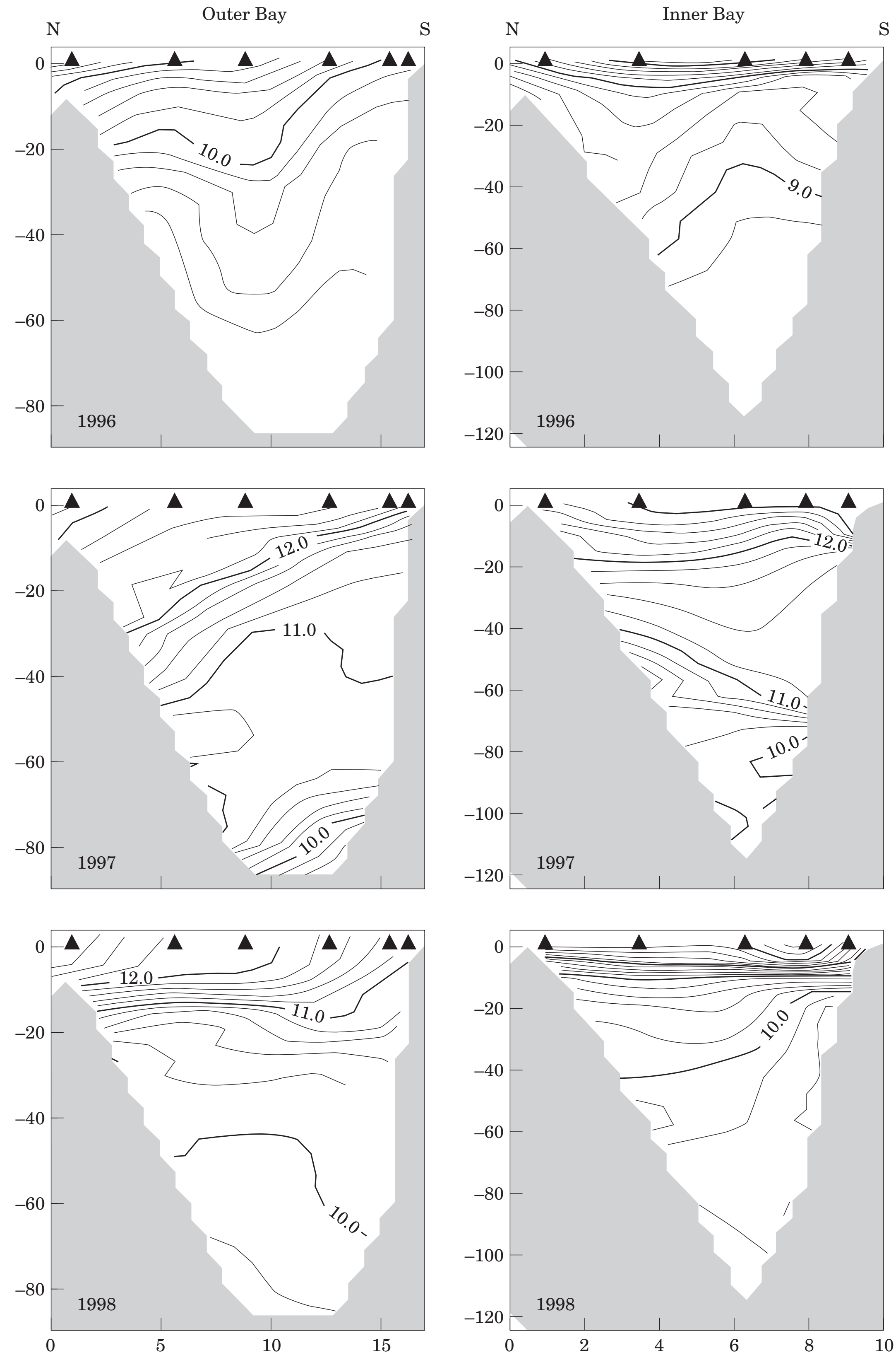

FIGURE 2. Vertical temperature profiles from CTD data collected in August 1996–1998 at six stations in the Outer Bay and five stations in the Inner Bay. Station locations are denoted with a triangle, and north (N) and south (S) directions are indicated. Distance along the x-axis is 15·3 km in the Outer Bay and 8·0 km in the Inner Bay; depth (m) is on the y-axis. Temperature isotherms are plotted in increments of 0·2 °C, and every 1 °C isotherm has a thicker line.

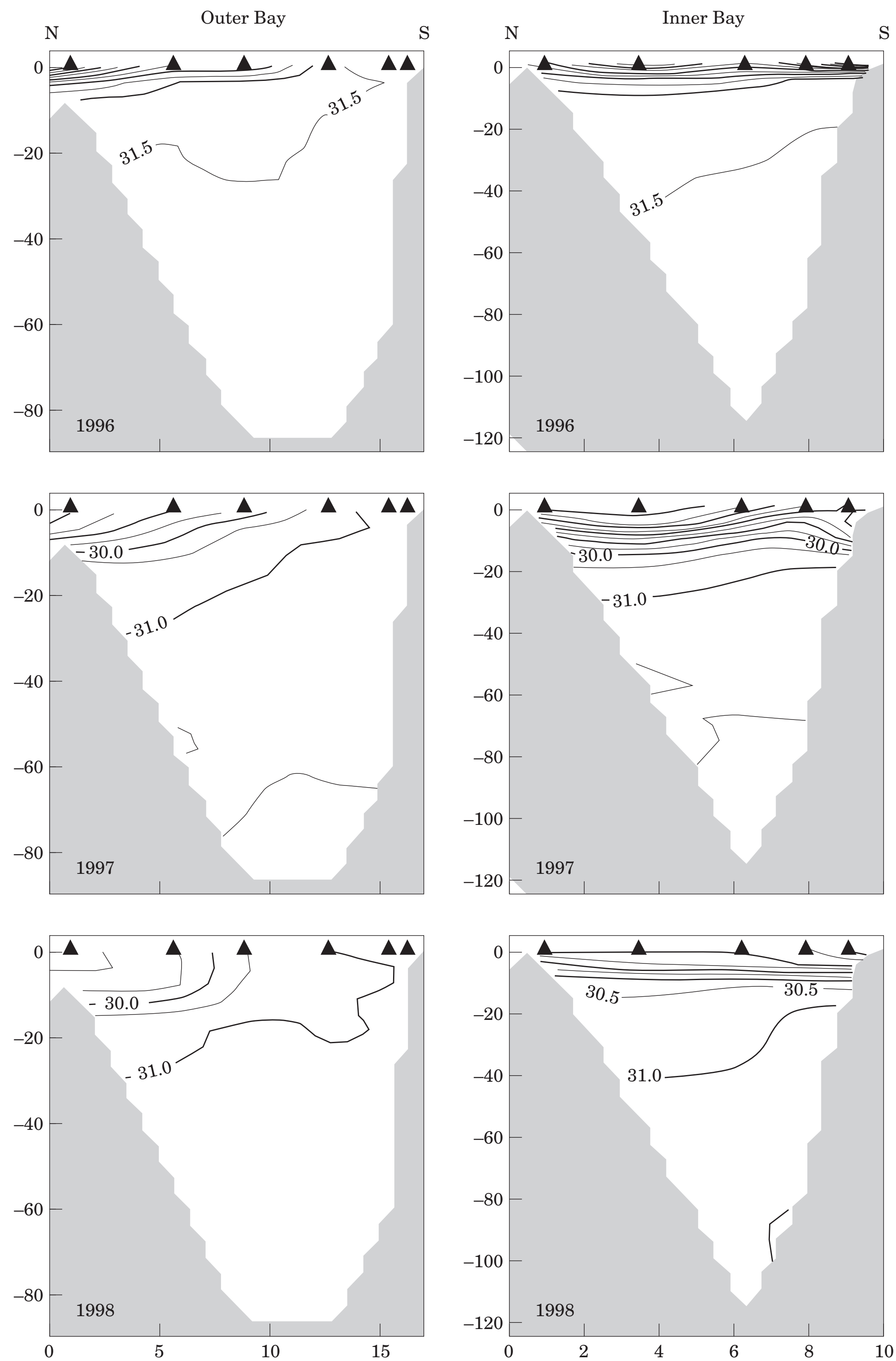

FIGURE 3. Vertical salinity profiles from CTD data collected in August 1996–1998 at six stations in the Outer Bay and five stations in the Inner Bay. Station locations are denoted with a triangle, and north (N) and south (S) directions are indicated. Distance along the x-axis is 15·3 km in the Outer Bay and 8·0 km in the Inner Bay; depth (m) is on the y-axis. Salinity isohaline contours are plotted in increments of 0·5, and thicker lines represent whole number salinity data.

Table 2. Median surface temperature and salinity values by month and year. Results from thermohaline comparisons between areas are given: *t*-tests (*t*) or Mann–Whitney Rank Sum Tests (T) are presented with sample size (*n*) and *P*-values. When significant, surface temperatures were higher and surface salinities were lower in the Inner Bay for all month and year combinations

		June					July					August				
Factor	Year	Outer Bay	Inner Bay	test	*n*	*P*	Outer Bay	Inner Bay	test	*n*	*P*	Outer Bay	Inner Bay	test	*n*	*P*
Temp.	1996	7·7	8·8	T=1323·0	30	<0·001	9·3	10·1	T=755·0	31	0·002	11·5	12·0	*t*=5·4	12	<0·001
Temp.	1997	7·9	8·9	*t*= − 14·8	11	<0·001	9·5	10·2	*t*= − 9·1	11	<0·001	11·7	12·1	*t*= − 5·4	11	<0·001
Temp.	1998	7·9	8·8	T=41·0	11	0·052	11·1	12·8	*t*=6·9	11	<0·001	11·8	12·9	*t*=3·6	11	0·006
Salinity	1996	—	—	—		—	—	—	—		—	30·3	26·9	T=42	12	0·004
Salinity	1997	31·3	30·3	*t*= − 3·5	11	0·006	27·1	23·1	*t*= − 3·6	11	0·006	29·9	26·6	*t*=4·6	11	0·001
Salinity	1998	30·3	29·3	T=20·0	11	0·082	30·0	23·9	*t*= − 11·6	11	<0·001	30·3	27·6	*t*= − 6·4	11	<0·001

Outer Kachemak Bay, except in August 1997 when the Outer Bay was warmer (Table 3). Bottom salinities were similar between Inner and Outer Kachemak Bay, except in mid-July of 1998 when they were higher in the Outer Bay.

Beach seines

We caught 259 811 fish in 314 beach seines from June to August 1996–1998. Composition of beach seine catches was 63% sand lance, 26% herring, 4% salmonids, 3% gadids, 1% osmerids, 1% sculpins and 2% other fish. The index of species diversity was higher in Outer Kachemak Bay, but species richness was higher in the Inner Bay (Table 1). Fish communities differed between areas (G-test, G=29159·8, df=7, P=0·001; Table 4). Adult sand lance (48%), herring (29%), and juvenile sand lance (15%) dominated the Inner Bay fish community, whereas adult sand lance (45%), juvenile sand lance (19%), salmonids (14%), and gadids (13%) dominated the Outer Bay fish community (Table 1).

Mean catch in beach seines was greater in Inner Kachemak Bay than Outer Kachemak Bay (ANOVA, $F=29{\cdot}68_{[1,312]}$, $P<0{\cdot}001$; Figure 4). CPUE of the eight main fish groups differed by area (MANOVA, $F=12{\cdot}18_{[8,297]}$, $P<0{\cdot}001$). Juvenile and adult sand lance, herring, and osmerids were all more abundant (Table 5) and captured more frequently (Table 6) in the Inner Bay. Relative abundance (CPUE) of sculpins was also greater in the Inner Bay, but their frequency of occurrence did not differ between areas. Only gadids were significantly more abundant in the Outer Bay (Table 5; Figure 4), but they were distributed evenly between areas, as their frequency of occurrence was not greater in the Outer Bay (Table 6).

Beam trawls

We caught 5437 fish in 80 beam trawls from 1996 to 1998. Composition of beam trawl catches was 37% flatfishes, 33% gadids (23% Pacific cod, *Gadus macrocephalus*; 5% walleye pollock, *Theragra chalcogramma*; 5% saffron cod, *Eleginus gracilis*), 14% sculpins, 5% ronquils, 5% pricklebacks, and 6% other (Table 1). Both indices of species diversity and species richness were higher in the Inner Bay than the Outer Bay.

Demersal fish communities in the Outer and Inner Bay had different percentages of the same main fish groups. Overall demersal fish community composition differed between areas (G-test, G=284·7, df=5, P=0·001): Inner Bay fish composition was primarily 34% flatfish and 38% gadids while the Outer Bay was primarily 47% flatfish and 21% sculpins (Table 1). Percent composition varied between areas for flatfish, gadids, and sculpins (Table 4). Differences in relative abundances (CPUE) were small between areas and were not significantly different for any of the trawl fish groups; however, total trawl CPUE was higher in the Inner Bay for all years and months combined (Table 7).

In August 1996–1998, the total catch was higher in the Inner Bay (ANOVA, $F=4{\cdot}95_{[1,35]}$, $P=0{\cdot}033$) than the Outer Bay (Figure 5). In 1997 and 1998, total catch was higher in the Inner Bay (ANOVA, $F=4{\cdot}99_{[1,68]}$, $P=0{\cdot}029$), did not differ between years (ANOVA, $F=1{\cdot}48_{[1,68]}$, $P=0{\cdot}228$), and was higher in August than early or late July (ANOVA, $F=5{\cdot}97_{[2,67]}$, $P=0{\cdot}004$). Frequency of occurrence for demersal fish was not different between Inner and Outer Bays (Table 6). Thus, bottom fish were distributed similarly among Outer and Inner Bay sites, but overall abundance was higher in the Inner Bay.

Discussion

Spatial differences were found in pelagic fish communities that correspond with spatial differences in water stratification, temperature and salinity. Schooling pelagic fish (mostly sand lance and juvenile herring) were five times more abundant in habitats that were well-stratified with warmer, less-saline surface waters. In contrast, demersal fish abundance (mostly flatfish, gadids and sculpins) varied little among the Outer and Inner Bays, presumably because bottom waters were similar among areas. Others have found that larger temperature and salinity gradients can influence the distribution of demersal fish such as juvenile flatfish (Henderson & Seaby, 1994; Norcross *et al.*, 1997), larval pricklebacks (*Stichaeus punctatus* and *Lumpenus* spp. and gadids (*Boreogadus saida*; Laprise & Pepin, 1995, p. 88).

Oceanographic differences between areas

There is a two-layered pattern of water circulation in the Inner Bay (Burbank, 1977). Increased insolation during late spring and summer increases freshwater runoff and raises surface water temperatures, which results in a well-stratified water column in the Inner Bay (Figures 2 and 3; Science Applications, Inc., 1977, p. 24). Inner Bay surface waters are characterized by lower salinity and warmer temperatures, and are largely unaffected by intrusion of Outer Bay water. Below the pycnocline, bottom waters in the Outer and Inner Bay are essentially homogeneous and are not

Table 3. Median bottom temperature and salinity values by month and year, as collected with CTDs at beam trawl stations. Results from thermohaline comparisons between areas are given: *t*-tests (*t*) or Mann–Whitney Rank Sum Tests (T) are presented with sample size (*n*) and *P*-values

		Early July					Mid-July					August				
Factor	Year	Outer Bay	Inner Bay	test	*n*	*P*	Outer Bay	Inner Bay	test	*n*	*P*	Outer Bay	Inner Bay	test	*n*	*P*
Temp.	1996	—	—	—	—	—	—	—	—	—	—	9·8	9·6	$t = -1·8$	11	0·111
Temp.	1997	7·5	7·0	T=20·0	10	0·517	8·2	7·6	$t = -1·8$	10	0·116	11·3	10·5	$t = -3·1$	13	0·011
Temp.	1998	8·2	7·7	t=1·9	10	0·088	9·1	8·8	T=52·0	14	0·414	10·1	10·3	$t = -0·5$	14	0·632
Salinity	1996	—	—	—	—	—	—	—	—	—	—	31·4	31·4	$t = -0·6$	11	0·561
Salinity	1997	32·4	32·3	t=0·3	10	0·741	32·5	32·3	$t = -1·1$	9	0·300	31·5	31·8	T=32·0	13	0·181
Salinity	1998	31·2	31·0	t=1·8	10	0·103	31·3	30·9	t=2·5	14	0·028	31·1	31·0	T=54·0	14	0·282

TABLE 4. Composition of fish groups compared betwen Outer and Inner Bays. Individual G and *P*-values for factors in two Likelihood Ratio Chi-Square tests (G-tests) are presented. Beach seine and beam trawl data are for all years (1996–1998) combined

Seine group	G	*P*	Trawl group	G	*P*
Juvenile sand lance	322·66	<0·001	Flatfish	46·74	<0·001
Adult sand lance	71·42	<0·001	Ronquil	3·21	0·073
Herring	8681·50	<0·001	Sculpin	55·89	<0·001
Salmon	11 104·90	<0·001	Gadid	155·87	<0·001
Gadid	11 316·10	<0·001	Prickleback	1·64	0·200
Osmerid	247·74	<0·001	Other fish	0·12	0·729
Sculpin	15·70	<0·001			
Other fish	197·26	<0·001			

influenced by river runoff and insolation above the thermocline. Accordingly, we detected little or no difference in bottom water temperatures or salinities between areas.

These oceanographic differences between areas probably account for most of the observed spatial differences in fish distribution. Nearshore fish abundance was higher in the Inner Bay than the Outer Bay, as indicated by total catch in beach seines and beam trawls. Higher fish abundance in the Inner Bay may be because stratification promotes stability of surface waters and often enhances primary production (Harrison *et al.*, 1991, p. 303), and higher production often occurs at river outflows (Grimes & Finucane, 1991, p. 113; St. John *et al.*, 1992, p. 153). Stratification combined with the input of river nutrients may explain the extraordinarily high primary production in Inner Kachemak Bay (Science Applications, Inc., 1977, p. 25). In addition, nutrients upwelled from depth may concentrate in stratified waters (Harrison *et al.*, 1991, p. 301), thereby increasing production (Grimes & Finucane, 1991, p. 110). When physical and nutrient dynamics support high primary and secondary production, appropriately-adapted fish species may be able to gain a trophic advantage (Fielder & Bernard, 1987; Grimes & Finucane, 1991, p. 117; Grimes & Kingsford, 1996, p. 202). This may explain the much higher abundance of certain fishes in Inner Bay habitats.

TABLE 5. Average beach seine catches (CPUE) compared between areas (Outer and Inner Bays) and years (1996–1998). Individual 2-way ANOVAs were run for each fish group, and values of $F_{[df]}$ and *P*-value are listed. The overall MANOVA model was significant

Beach seine fish group	Area		Year	
	$F_{[1,312]}$	*P*	$F_{[2,311]}$	*P*
Juvenile sand lance	16·10	<0·001	1·93	0·147
Adult sand lance	10·93	0·001	5·07	0·007
Herring	32·69	<0·001	5·75	0·004
Salmon	2·85	0·092	1·05	0·350
Gadid	4·91	0·027	0·50	0·604
Osmerid	13·53	<0·001	11·22	<0·001
Sculpin	7·81	0·006	1·72	0·180
Other fish	21·30	<0·001	5·10	0·007

Species accounts

Juvenile sand lance (McGurk & Warburton, 1992, p. 306) and osmerids (St. John *et al.*, 1992, p. 160) often concentrate and feed on zooplankton within estuaries, and both are well adapted to benefit from high food concentrations at oceanographic features like estuarine plumes and their associated fronts (Fortier *et al.*, 1992, p. 215). In the Port Moller estuary, larval sand lance have a dispersal strategy in which they move 20 km from the location of egg hatch to a deep, stratified basin, possibly to enhance growth by feeding on a more abundant zooplankton community (McGurk & Warburton, 1992, p. 317–318). Likewise, juvenile and adult sand lance were present throughout Kachemak Bay, but were more abundant in the surface waters of the stratified Inner Bay. Osmerids were also more abundant in the warmer, less saline Inner Bay habitat. Similarly, large capelin larvae are more abundant in the warmer, less saline waters of both Hudson Bay (Ponton *et al.*, 1993, p. 324) and Conception Bay (Laprise & Pepin, 1995, p. 86).

Pacific herring spawn in estuaries, and larvae remain in the estuarine nursery grounds through their juvenile stage (Hourston, 1958; Boehlert & Morgan, 1985, p. 162). Larval Pacific herring that hatch in Lamber Channel in the Strait of Georgia, British Columbia, quickly disperse into Baynes Sound, a stable area which is strongly stratified through

TABLE 6. Outer and Inner Bay frequency of occurrence (%) for beach seine and beam trawl fish groups by area. Logistic regression *P*-values for beach seine and beam trawl fish groups compared by area (Outer and Inner Bays), among years (1996–1998) and months (June–August). Sampling dates for trawl data are early July, mid July, and August. A (—) indicates that no interactions (Year * Area; Month * Area) were significant and a simpler model was run with interaction terms removed

Beach seine fish group	Outer Bay freq. (%)	Inner Bay freq. (%)	Area (df=1)	Year (df=2)	Month (df=2)	Year * area (df=2)	Month * area (df=2)	Beam trawl fish group	Outer Bay freq. (%)	Inner Bay freq. (%)	Area (df=1)	Year (df§2)	Date (df=2)
Juv. sand lance	27	43	0·001	0·739	0·000	—	—	Flatfish	68	74	0·503	0·339	0·897
Adult sand lance	41	56	0·001	0·079	0·599	0·015	—	Ronquil	41	48	0·466	0·814	0·214
Herring	15	35	0·000	0·004	0·011	—	—	Sculpin	72	75	1·000	0·336	0·480
Salmon	72	68	0·139	0·022	0·000	—	—	Gadid	48	57	0·307	0·696	0·007
Gadid	56	45	0·549	0·123	0·167	—	0·020	Prickleback	38	40	0·751	0·287	0·999
Osmerid	7	22	0·000	0·004	0·187	—	—	Other fish	57	62	0·806	0·003	0·944
Sculpin	74	80	0·236	0·515	0·200	—	—						
Other fish	78	85	0·030	0·144	0·147	—	—						

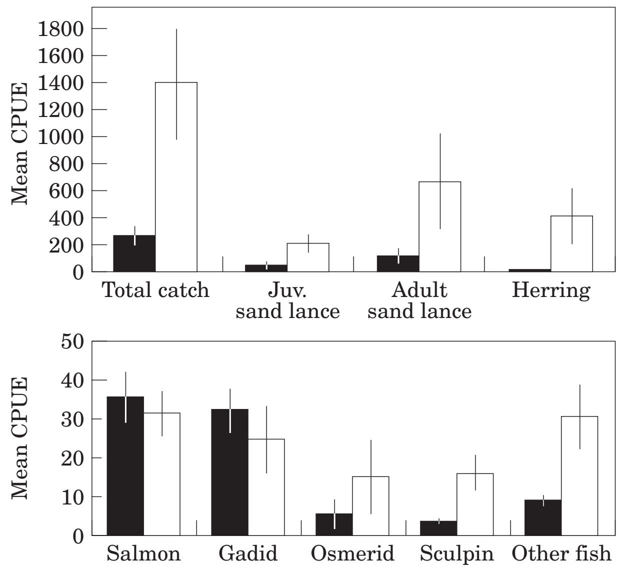

FIGURE 4. Mean (±SE) beach seine CPUE for total catch and each fish group in the Outer and Inner Bays (1996–1998 data combined). Relative abundances were significantly different between areas for total catch and all fish groups, excluding salmon. The two graphs have different y-axis scales, and the number of seine sets conducted in each area is given in parentheses. Filled bars: Outer Bay (156); open bars: Inner Bay (158).

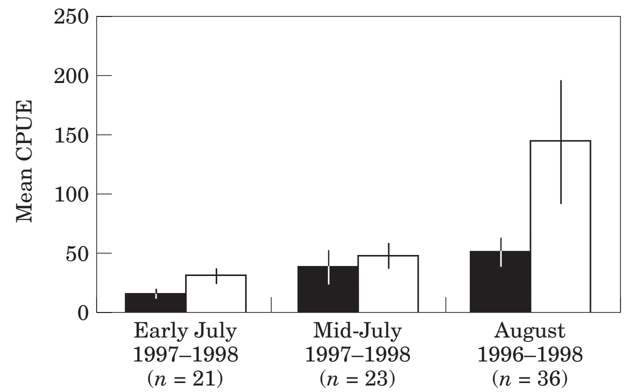

FIGURE 5. August mean (±SE) beam trawl catch in Outer and Inner Kachemak Bay for all years combined. Mean beam trawl catch (±SE) in the Outer and Inner Bay for all months sampled (1997 and 1998 combined). In both cases, relative abundances were significantly higher in the Inner Bay. The total number of trawls conducted in each sampling period is given in parentheses. Filled bars: Outer Bay; open bars: Inner Bay.

TABLE 7. Mean bottom trawl catches (CPUE) compared between Outer and Inner Bays for all months and years combined. Individual Mann–Whitney Rank Sum Tests were run; T and *P*-values are listed. Mean total catch in beam trawls was higher in the Inner Bay

Beam trawl fish group	Outer Bay mean ± SE	Inner Bay mean ± SE	T (df=1)	*P*
Flatfish	17·7 ± 5·7	28·8 ± 8·2	1249·0	0·256
Ronquil	2·1 ± 0·8	3·7 ± 1·0	1274·0	0·369
Sculpin	7·9 ± 1·8	10·2 ± 2·3	1294·0	0·478
Gadid	5·6 ± 2·5	32·4 ± 22·9	1249·0	0·256
Prickleback	1·5 ± 0·5	4·2 ± 1·3	1298·5	0·504
Other fish	2·9 ± 0·7	6·3 ± 1·4	1231·0	0·192
Total catch	37·7 ± 6·9	85·6 ± 24·1	1124·0	0·021

freshwater input (Robinson, 1988). Our results indicate a similar distribution, as juvenile herring were higher in abundance, constituted a higher percentage of the fish community, and were more frequently captured in the more stratified Inner Bay. Juvenile herring may also be attracted to the Inner Bay by feeding opportunities. Because juvenile herring feed at a greater rate under moderate suspensions of fine-grained sediment (Boehlert & Morgan, 1985, p. 161; St. John *et al.*, 1992, p. 154), and much of the freshwater input in the Inner Bay contains sediment and glacial silt (Burbank, 1977), these suspensions may promote feeding aggregations by providing visual contrast of prey items while reducing predation (Boehlert & Morgan, 1985, p. 167).

Anadromous salmonids use estuaries as nursery zones along the north Pacific coast (Macdonald *et al.*, 1987, p. 1233), and salinity gradients are thought to provide an orientation mechanism for outmigrating salmonids (McInerney, 1964). The low-salinity surface waters in the Inner Bay may reduce stress and lower mortality rates of juvenile salmonids as they acclimatize to a high-salinity marine environment (St. John *et al.*, 1992, p. 160). Therefore, we expected to find more juvenile salmonids in the Inner Bay, but we did not detect a difference in their relative abundance between areas.

The only schooling fish more abundant in the Outer Bay were gadids, and this was only in nearshore seine catches. Trawl catches of gadids at depths ranging from 10 to 25 m were not significantly different between areas (although catch variability was quite high). At small spatial scales, catches of juvenile Atlantic cod (*Gadus morhua*) are also highly variable (Methven, 1995, p. 47), reflecting their patchy distribution and the difficulty in sampling. Our understanding of the distribution of gadids in Kachemak Bay remains ambiguous. Temperature and salinity can influence gadid distribution at larger scales. For example, Arctic cod (*Boreogadus saida*) larvae are much more abundant in colder waters with salinities >25, but occur regularly in small numbers in warmer, lower salinity waters (Ponton *et al.*, 1993, p. 324). Studies along the English, Welsh and Norwegian coasts have shown age-0 Atlantic cod are abundant in low-salinity, sheltered sites, but in Finnmark and Norway, age-0 Atlantic cod are found at the entrances of larger fiords, with reduced abundance inside the fiords (in Methven, 1995, p. 40).

Acknowledgements

We thank Captains Mike Geagel and Greg Snedgen and all who assisted with fish collections: Yumi Arimitsu, David Black, Elizabeth Chilton, Brian Duggan, Jared Figurski, Roman Kitaysky, Mike Litzow, April Nielson, and Brian Smith. Special thanks to Jared Figurski for assistance with processing fish samples. Statistical advice was provided by Franz Müter and Mike Litzow. Gary Drew kindly provided the study area map. We thank Professor Brenda Norcross (Institute of Marine Science, University of Alaska Fairbanks) for use of the beam trawl gear. Additionally, we thank Mike Litzow and two anonymous reviewers for comments on the manuscript. This project was funded by The Exxon Valdez Oil Spill Trustee Council (Restoration Project 99163M), the Minerals Management Service and the U.S. Geological Survey.

References

Abookire, A. A. 1997 *Environmental Factors Affecting Seasonal Habitat and Distribution of Flathead Sole and Rock Sole in Kachemak Bay, Alaska*. M.S. Thesis, University of Alaska, Fairbanks, Alaska, 87 pp.

Abookire, A. A. & Norcross, B. L. 1998 Depth and sediment as determinants of juvenile flathead sole (*Hippoglossoides elassodon*) and rock sole (*Pleuronectes bilineatus*) distribution in Kachemak Bay, Alaska. *Journal of Sea Research* **39,** 113–123.

Allen, L. G. 1982 Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Newport Bay, California. *Fisheries Bulletin, U.S.* **80,** 769–790.

Beamish, R. J. (ed.) 1995 Climate change and Northern fish populations. *Canadian Special Publication of Fisheries and Aquatic Sciences* No. 121, 739 pp.

Bechtol, W. R. 1997 Changes in Forage Fish Populations in Kachemak Bay, Alaska, 1976–1995. In *Forage Fishes in Marine Ecosystems: Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems* (Mecklenburg, C. W., ed.) Alaska Sea Grant College Program Report No. 97–01, University of Alaska, Fairbanks, Alaska, pp. 441–456.

Bechtol, W. R. & Yuen, H. 1995 Abundance and composition of flatfish in Kachemak Bay, Alaska. In *Proceedings of the International Symposium on North Pacific Flatfish* (Baxter, B., ed.). Alaska Sea Grant College Program Report No. 95–04, University of Alaska, Fairbanks, Alaska, pp. 497–521.

Bennett, B. A. 1989 The fish community of a moderately exposed beach on the southwestern Cape Coast of South Africa and an assessment of this habitat as a nursery for juvenile fish. *Estuarine, Coastal and Shelf Science* **28,** 293–305.

Blackburn, J. E. 1979 Pelagic and demersal fish assessment in the lower Cook Inlet estuary system. In *Environmental Assessment of the Alaskan Continental Shelf: Annual Reports of the Principal Investigators for the year ending March 1979*. Vol. 4: Receptors—Fish, Littoral, Benthos. Alaska Department of Fish and Game, Kodiak, Alaska, pp. 289–446.

Boehlert, G. W. & Morgan, J. B. 1985 Turbidity enhances feeding abilities of larval Pacific herring, *Clupea harengus pallasi. Hydrobiologia* **123,** 161–170.

Burbank, D. C. 1977 Circulation studies in Kachemak Bay and lower Cook Inlet. In *Environmental Studies of Kachemak Bay and Lower Cook Inlet, Volume III* (Trasky, L. L., Flagg, L. B. & Burbank, D. C., eds). Alaska Department of Fish and Game, Anchorage, Alaska, pp. 22–181.

Carlson, H. R. 1980 Seasonal distribution and environment of Pacific Herring near Auke Bay, Lynn Canal, Southeastern Alaska. *Transactions of American Fisheries Society* **109,** 71–78.

Fielder, P. C. & Bernard, H. J. 1987 Tuna aggregation and feeding near fronts observed in satellite imagery. *Continental Shelf Research* **7,** 871–881.

Fortier, L., Levasseur, M. E., Drolet, R. & Therriault, J. C. 1992 Export production and the distribution of fish larvae and their prey in a coastal jet frontal region. *Marine Ecology Progress Series* **85,** 203–218.

Frank, K. T., Carscadden, J. E. & Simon, J. E. 1996 Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. *Canadian Journal of Fisheries and Aquatic Sciences* **53,** 1473–1486.

Gadomski, D. M. & Caddell, S. M. 1991 Effects of temperature on early-life-history stages of California halibut *Paralichthys californicus*. *Fisheries Bulletin, U.S.* **89,** 567–576.

Gibson, R. N. 1994 Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Netherlands Journal of Sea Research* **32,** 191–206.

Grimes, C. B. & Finucane, J. H. 1991 Spatial distribution and abundance of larval and juvenile fish, chlorophyll and macrozooplankton around the Mississippi River discharge plume, and the role of the plume in fish recruitment. *Marine Ecological Progress Series* **75,** 109–119.

Grimes, C. B. & Kingsford, M. J. 1996 How do riverine plumes of different sizes influence fish larvae: Do they enhance recruitment? *Marine Freshwater Research* **47,** 191–208.

Gunderson, D. R. & Ellis, I. E. 1986 Development of a plumb staff beam trawl for sampling demersal fauna. *Fisheries Research (Amsterdam)* **4,** 35–41.

Harrison, P. J., Clifford, P. J., Cochlan, W. P., Yin, K., St. John, M. A., Thompson, P. A., Sibbald, M. J. & Albright, L. J. 1991 Nutrient and plankton dynamics in the Fraser River plume, Strait of Georgia, British Columbia. *Marine Ecology Progress Series* **70,** 291–304.

Henderson, P. A. & Seaby, R. M. H. 1994 On the factors influencing juvenile flatfish abundance in the lower Severn Estuary, England. *Netherlands Journal of Sea Research* **32,** 321–330.

Hourston, A. S. 1958 Population studies on juvenile Pacific herring in Barkley Sound, British Columbia. *Journal of Fisheries Research Board of Canada* **15,** 909–960.

Krebs, C. J. 1989 *Ecological Methodology*. Harper & Row, New York.

Laevastu, T. & Hela, I. 1970 *Fisheries Oceanography*. Fishing News (Books) Ltd, London.

Laprise, R. & Pepin, P. 1995 Factors influencing the spatio-temporal occurrence of fish eggs and larvae in a northern, physically dynamic coastal environment. *Marine Ecology Progress Series* **122,** 73–92.

Macdonald, J. S., Birtwell, I. K. & Kruzynski, G. M. 1987 Habitat utilization by juvenile salmonids in Campbell River estuary. *Canadian Journal of Fisheries and Aquatic Sciences* **44,** 1233–1246.

McGurk, M. D. & Warburton, D. H. 1992 Pacific sand lance of the Port Moller estuary, southeastern Bering Sea: an estuarine-dependent early life history. *Fisheries Oceanography* **1,** 306–320.

McInerney, J. E. 1964 Salinity preference: An orientation mechanism in salmon migration. *Journal of Fisheries Research Board of Canada* **21,** 995–1018.

Methven, D. A. 1995 Early life history of juvenile cod (*Gadus morhua*): Spatial and temporal variability and variability due to gear. Ocean Sciences Centre, Memorial University of Newfoundland, St. John's. *Final Report Department of Fisheries and Oceans*, 132 pp.

Muench, R. D., Mofjeld, H. O. & Charnell, R. L. 1978 Oceanographic conditions in lower Cook Inlet: spring and summer 1973. *Journal of Geophysical Research* **83,** 5090–5098.

Nash, R. D. M. 1988 The effects of disturbance and severe seasonal fluctuations in environmental conditions on North Temperate shallow-water fish assemblages. *Estuarine, Coastal and Shelf Science* **26,** 123–135.

Nash, R. D. M. & Gibson, R. N. 1982 Seasonal fluctuations and compositions of two populations of small demersal fishes on the West coast of Scotland. *Estuarine, Coastal and Shelf Science* **15,** 485–495.

Norcross, B. L., Holladay, B. A., Abookire, A. A. & Dressel, S. C. 1998 Defining habitats for juvenile groundfishes in southcentral Alaska, with emphasis on flatfishes. Volume I. *Final Report, OCS Study MMS 97–0046*. Coastal Marine Institute, University of Alaska, Fairbanks, AK, 131 pp.

Norcross, B. L., Müter, F. J. & Holladay, B. A. 1997 Habitat models for juvenile pleuronectids around Kodiak Island, Alaska. *Fishery Bulletin* **95,** 504–520.

Pearcy, W. G. 1978 Distribution and abundance of small flatfishes and other demersal fishes in a region of diverse sediments and bathymetry off Oregon. *Fisheries Bulletin, U.S.* **76,** 629–640.

Ponton, D., Gagné, J. A. & Fortier, L. 1993 Production and dispersion of freshwater, anadromous, and marine fish larvae in and around a river plume in subarctic Hudson Bay, Canada. *Polar Biology,* **13,** 321–331.

Quinn, T. J. & Niebauer, H. J. 1995 Relation of eastern Bering Sea walleye pollock (*Theragra chalcogramma*) recruitment to environmental and oceanographic variables. In *Climate Change and Northern Fish Populations* (Beamish, R. J., ed.), Canadian Special Publication of Fisheries and Aquatic Sciences No. 121, pp. 497–507.

Robards, M. D., Piatt, J. F., Kettle, A. B. & Abookire, A. A. 1999 Temporal and geographic variation in fish communities of Lower Cook Inlet, Alaska. *Fisheries Bulletin, U.S.* **97,** 962–977.

Robinson, S. M. C. 1988 *Early Life History Characteristics of Pacific Herring, Clupea harengus pallasi Valenciennes 1847, in the Strait of Georgia, British Columbia: Hydrodynamics, Dispersal, and Analysis of Growth Rates*. (Ph.D. Thesis). University of British Columbia, Vancouver, British Columbia, 141 pp.

SAS Institute Inc. 1996 *SAS User's Guide: Statistics, Version 6.11 Edition*. SAS Institute Inc., Cary, North Carolina.

Science Applications, Incorporated 1977 *Environmental Assessment of the Alaskan Continental Shelf: Interim Lower Cook Inlet Synthesis Report*. National Oceanic and Atmospheric Administration, Boulder, 169 pp.

Shimada, A. M. & Kimura, D. K. 1994 Seasonal movements of Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea and adjacent waters based on tag-recapture data. *Fisheries Bulletin, U.S.* **92,** 800–816.

St. John, M. A., Macdonald, J. S., Harrison, P. J., Beamish, R. J. & Choromanski, E. 1992 The Fraser River plume: some preliminary observations on the distribution of juvenile salmon, herring, and their prey. *Fisheries Oceanography* **1,** 153–162.

Surfer Golden Software 1995 *Surfer User's Guide, Version 6.0*. Golden Software, Inc., Golden, Colorado.

Syvitski, J. P. M., Burell, D. C. & Skei, J. M. 1987 *Fjords: Processes and Products*. Springer-Verlag, New York.

Zebdi, A. & Collie, J. S. 1995 Effect of climate on herring (*Clupea pallasi*) population dynamics in the Northeast Pacific ocean. In *Climate Change and Northern Fish Populations* (Beamish, R. J., ed.), Canadian Special Publication of Fisheries and Aquatic Sciences, No. 121, pp. 277–290.