

Abstract.—Nursery areas of Pacific herring, *Clupea pallasii*, and walleye pollock, *Theragra chalcogramma*, were identified by using acoustic surveys in October 1995, and in March and July 1996 in Prince William Sound, Alaska. Pacific herring and walleye pollock were aggregated in the east-northeast and west-southwest areas. Juvenile Pacific herring spent the first two years of their lives isolated within bays. Water temperatures within bays were cooler in the summer and warmer in the winter compared with temperatures measured along coastal passages and the open coast. Although these temperature differences were small and based on point observations their accumulative effect over the season may be considerable. The school structure of juvenile Pacific herring varied seasonally. Newly recruited age-0 Pacific herring were tightly aggregated, forming a few, dense schools within a single-size cohort, in shallow water at the heads of bays in July. Age-0 Pacific herring were still aggregated within bays in shallow water in October, but the school structure was less cohesive and size cohorts began to mix. School structure and distribution completely changed in March as age-0 Pacific herring moved away from the shores into deeper water and spread out forming sparse shoals of mixed-size cohorts. Juvenile Pacific herring joined the adult schools after their second winter, leaving as new recruits entered the bays. Juvenile walleye pollock also aggregated within bays and were spatially segregated from adults. However, there appeared to be little overlap between Pacific herring and walleye pollock juveniles because they occupied different portions of the water column within these bays.

Spatial distributions of Pacific herring, *Clupea pallasii*, and walleye pollock, *Theragra chalcogramma*, in Prince William Sound, Alaska

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In Prince William Sound, Alaska, Pacific herring (*Clupea pallasii*) and walleye pollock (*Theragra chalcogramma*) support major commercial fisheries and are primary forage for marine birds, mammals and other fishes (Clausen, 1983; Hatch and Sanger, 1992; Livingston, 1993; Brown et al., 1996). Recently the abundance of both these species in Prince William Sound has fluctuated, particularly that of Pacific herring, which suffered a population crash in 1993 resulting in the closure of the commercial fisheries (bait, sac-ro, and roe on kelp)

(Meyers et al., 1994; Paine et al., 1996). Little is known of the spatial distributions and the physical and biological variables influencing Pacific herring and walleye pollock life histories in this biologically rich, high latitude ecosystem (Paine et al., 1996).

We identified Pacific herring and walleye pollock nursery areas by examining their small-scale (km) spatial distributions in Prince William Sound, Alaska. We hypothesized that juvenile Pacific herring and juvenile walleye pollock were contagiously distributed and that

their distributions varied seasonally in relation to the stage of life of fish, school structure, and coastal structure. We then examined the degree of overlap between juvenile Pacific herring and juvenile walleye pollock distributions. Further we determined if cohorts (age and size) of Pacific herring were spatially segregated. Adult Pacific herring and walleye pollock distributions were also observed; however, these fishes appeared to emigrate from Prince William Sound at certain times of the year.

Materials and methods

Prince William Sound is a large body of water separated from the Gulf of Alaska by a series of mountainous islands and deep passages (Fig. 1). The rocky coastline is highly irregular and has numerous islands, passages, bays, and deep fjords. The Sound had a semidiurnal tide with a maximum range of 4.4 m during the period of our study.

Prince William Sound coastal waters were acoustically surveyed in October 1995, and in March and July 1996 (Fig. 1). Five vessels were used during each 10-day survey (12 hours per day): three commercial seiners (≈ 16.8 m) deployed the acoustic and oceanographic equipment and fished the seines; a trawler (Alaska Department of Fish and Game RV *Pandalus*, ≈ 20 m) was used for midwater sampling; and a tour vessel (≈ 25 m) was used for processing samples. Surveys were conducted during the night (2000 to 0800 h) in October 1995 and March 1996, and during the day (0800 to 2000 h) in July 1996. Northern latitude conditions dictated this sampling design because there was little daylight in March and little darkness in July. Further, the summer cruises had to be coordinated with aerial surveys for forage fish that could only be flown during daylight (E. Brown, unpubl. data). We observed and collected both Pacific herring and walleye pollock in surface waters and near the sea floor, a range of area that coincides with the known diel distributions for these two species.

The acoustic vessel followed a zigzag transect pattern along the shore (MacLennan and Simmonds, 1992; Gunderson, 1993) to a distance of ≈ 1 km at a speed of 14 to 17 km/h. We attempted to survey the

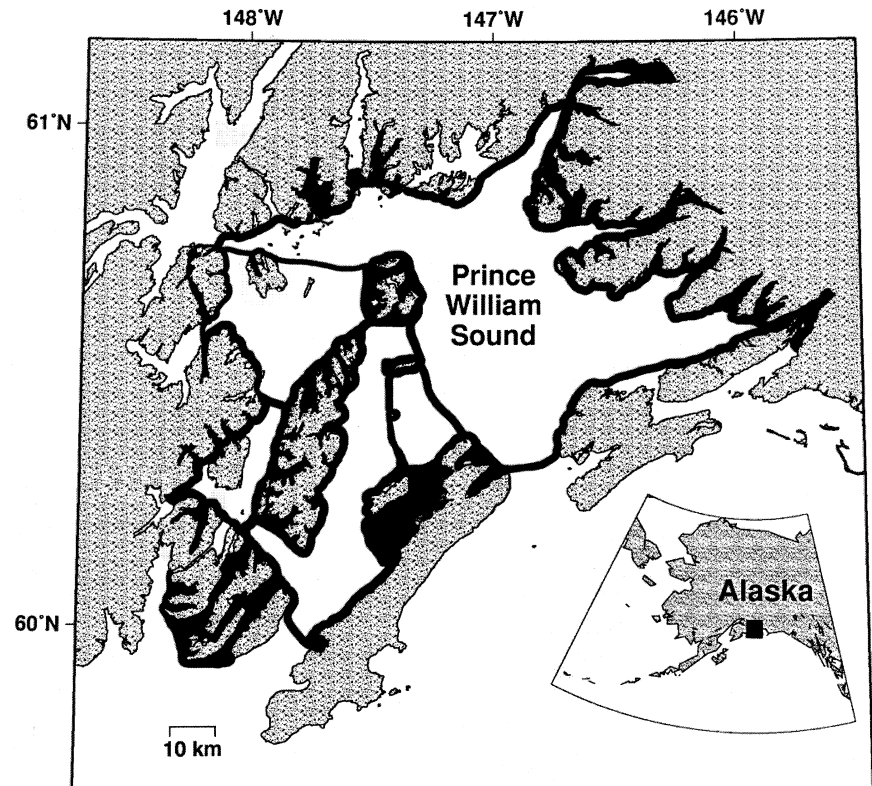


Figure 1

Location of the October 1995, March 1996, and July 1996 acoustic survey transects in Prince William Sound, Alaska. The dark areas represent the locations within which we conducted our zigzag transect survey.

same bays, passages, and open coast during all three surveys. The vessel's sonar (50 kHz, 46°) was used to locate fish schools along these transects. When a fish school was encountered, the acoustic vessel slowed to 9 to 11 km/h and completed a series of parallel transects perpendicular to shore by using a 120-kHz BioSonics 101 echosounder with a preamplified dual-beam transducer ($6^\circ \times 15^\circ$). The transducer was mounted on a BioSonics 1.2-m BioFin and towed at ≈ 1 m depth. The acoustic signals were processed in real-time with BioSonics ESP 221 Echo square integration software and ESP 281 Dual beam software, and the raw signal was stored on digital audio tape (Thorne, 1983a; 1983b; MacLennan and Simmonds, 1992). The acoustic system was calibrated before each cruise with a standard target and the source level (SL) was 225.07 dB μ Pa. Acoustic noise was well below our lowest density of interest.

Fish schools observed with the acoustic equipment were sampled to determine species composition and size structure. Fish were captured with a modified bottom trawl in deep water (1.52×2.13 m Nor'Eastern Astoria V trawl doors, 21.3-m head rope, 29.0-m, foot rope, 3×20.0 -m mouth, 10.2-cm mesh

wings, 8.9-cm middle, and a 32.0-mm codend liner), with one of two anchovy seines in surface water (250.0 × 34.0 m or 20.0 m, 25.0-mm stretch mesh), or with a small salmon fry seine in shallow water (50.0 × 8.0 m, 3.0-mm stretch mesh deployed from a 6-m skiff equipped with a 70-horsepower engine). Fish collections were directed by the acoustic survey and we attempted to sample every observed school. The catchability of the fish species sampled may vary with time of day, season, and between nets. However, we assumed that these collections reflected the actual species and age cohort ratios present within the acoustically observed fish school. A total of 220, 122, and 60 fish collections were made in 15, 29, and 28 locations in October 1995, March 1996, and July 1996, respectively. Each net collection was characterized by species, and 1000 individuals of the dominant fish species, usually Pacific herring, were randomly sampled. Fork lengths (mm) for 550 fish were measured immediately after capture, and 450 fish were frozen and later their fork length and wet weight (g) were measured in the laboratory. After subsampling the remaining fish were released unharmed from the seine.

A length-dependent scaling constant was used to convert estimated target strength ($TS - 10 \log_{10} w$) from units of reflected acoustic energy (dB) to units of biomass density (kg/m^3):

$$TS - 10 \log_{10} w = -6.0 \log_{10} L - 24.2 \text{ dB m}^2/\text{kg},$$

where L = the mean fork length (cm) of the fish collected in the area (Thorne, 1977; 1983a 1983b; Thorne and Thomas, 1990).

This equation differs from the more standard regression equation (Foote, 1987) because it derives the target strength as a proportion of weight. Thorne's equation was developed for echo integration primarily with Pacific herring surveys from Alaska and Puget Sound (Thorne, 1983a).

For walleye pollock, that have a physoclastic swim bladder, the standard equation:

$$TS = 20 \log_{10} x - 66.0 \text{ dB}$$

was used (Foote and Traynor, 1988).

The acoustic estimates of Pacific herring and walleye pollock school densities were derived from these target strength equations. Many physical and biological variables (including morphologic features [such as physostomic, physoclastic, fat content], the orientation of the fish, water temperature, and depth) affect target strength (Thorne, 1983b; Foote, 1987; Rose and Leggett, 1988; Thorne and Thomas, 1990; MacLennan

and Simmonds, 1992; Misund et al., 1995; Huse and Ona, 1996; McClatchie et al., 1996; Ona and Mitson, 1996; Misund, 1997; Misund et al., 1998).

Echo integration measurements were converted into data cells with lengths of 120 m, 40 m, or 20 m and width and depth of 1 m for the October 1995, March 1996, and July 1996 surveys, respectively. Cell length was determined by using the simultaneously recorded latitude and longitude from the GPS navigational system.

Species proportion and size modes per species were determined from the fish collections. The species proportions, based on the number of individuals per fish species in the random subsample, were multiplied by the echo integration densities (kg/m^3) and then converted by using length-weight regressions into the number of Pacific herring per size mode, or the number of walleye pollock. Walleye pollock were not divided into size modes because the standard deviations of the mean fork lengths of individual collections indicated that aggregations were unimodal.

A group of data cells was considered to be a fish school if the sum of the absolute differences between latitudes and longitudes of adjacent cells was $>0.009^\circ$. We concluded that cells containing the equivalent of $<0.5 \text{ fish}/\text{m}^3$ were probably zooplankton on the basis of frequency distributions of the data, and these cells were removed from the data set (MacLennan and Simmonds, 1992; Gunderson, 1993). If fish located near the bottom were difficult to distinguish acoustically, data cells for the bottom 5 m were removed.

Cohorts of Pacific herring and walleye pollock large-scale spatial distributions were examined by using circular statistics (Batschelet, 1981). The angle (0° =true north) for each data cell was determined from an origin in the center of Prince William Sound (60.6000°N , 146.9000°W). These angles represent distributions along the survey transect line and are influenced by inequalities in shoreline distance and sampling bias. Angle frequency distributions were compared with random distributions and with the distributions of other herring size modes along the same transect by using a chi-squared test at the 5% level of significance (Batschelet, 1981). Expected values were grouped according to Cochran's rule, which states that $<20\%$ of the expected frequencies should have a value <5 (Sokal and Rohlf, 1981).

Nursery areas were determined by examining the relation between juvenile fish spatial distributions and coastline structure. Bays were defined statistically from passages or open coast by calculating the sum of the three nearest shore distances ($\Sigma 3\text{NSD}$). To determine this value, first the distance between the center of each fish school and the nearest shore was measured. The second distance was determined by

moving 90° on either side of the first line, measuring the distance to shore and selecting the shorter of the two lines. The third distance was determined by moving 90° on either side of the first and second lines, measuring the distance to shore, and selecting the shorter of the two lines. These three distances were summed. This measurement was calculated at specific points inside 26 bays and outside 17 bays to verify that it accurately distinguished between bays, passages, and open coast. The Σ NSD for each fish school was compared with the same measurements from randomly selected points along the same survey transect by using a chi-squared test grouped according to Cochran's rule (Sokal and Rohlf, 1981). This technique removed sampling and shore structure discrepancies.

Differences in water conditions within bays compared with conditions in passages or along open coastline were examined. Vertical water profiles of temperature and salinity at 1-m intervals, measured with a SeaBird CTD instrument (SEACAT SBE19), were collected inside and outside bays. Differences between means were examined with a Mann-Whitney rank sum test (*U*).

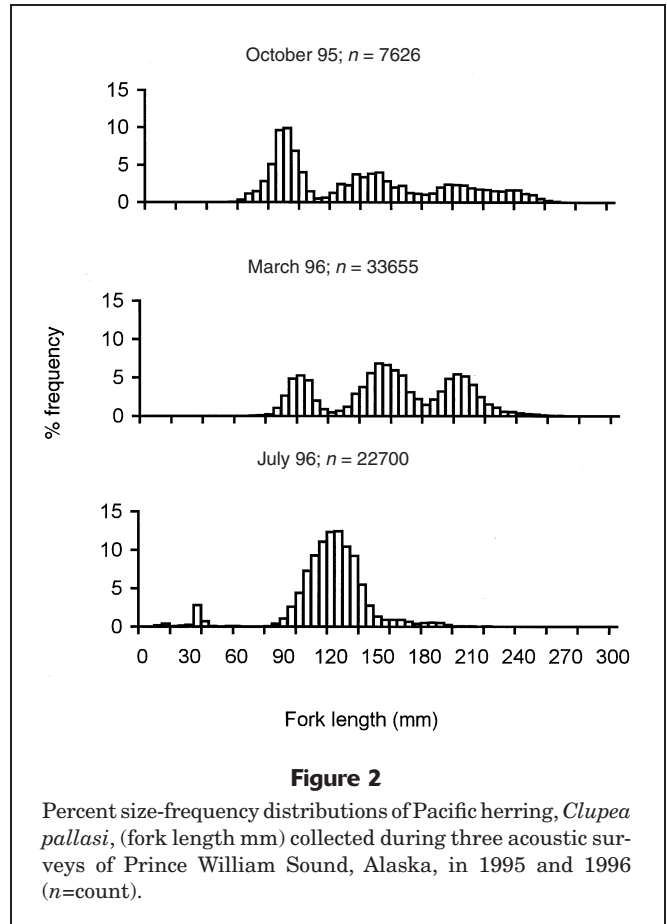
Results

Ninety-seven species of fish and macroinvertebrates were collected during the October 1995, and the March and July 1996 surveys. Pacific herring (65.0% of subsample collections) dominated the ichthyofauna followed by walleye pollock (19.2%).

Pacific herring and walleye pollock size frequencies differed. The Pacific herring population consisted of three size modes representing age-0, 1–2 year old, and adult fishes (Stokesbury et al. 1999) (Fig. 2). The walleye pollock population size distribution was bimodal, representing age-0 and adult fishes in October 1995 and March 1996, whereas only age-0 fish were collected during July 1996 (Fig. 3). Age-0 and adult pollock were always collected separately.

The proportion of Pacific herring schools consisting of a single size cohort varied among seasons. In October 1995, 49.0% of the Pacific herring schools sampled consisted of a single size class, mostly age 0. In March 1996, 38.9% of the Pacific herring schools sampled consisted of a single size, primarily 1–2 year olds. In July 1996, 83.3% of the Pacific herring schools sampled consisted of a single size, primarily 1–2 year olds.

Juvenile Pacific herring and walleye pollock were contagiously distributed in the east-northeast and the west-southwest of Prince William Sound (Fig. 4). Adult Pacific herring aggregated in the southwest



(210°–240°) in October 1995, in the south (180°) and east (90°) in March 1996, and west (240°–270°) in July 1996 (Fig. 4).

Pacific herring schools had the lowest densities in March 1996 and the highest densities in July 1996 (Table 1). Walleye pollock schools had low densities in October 1995 and March 1996 compared with very high densities in July 1996 (Table 1).

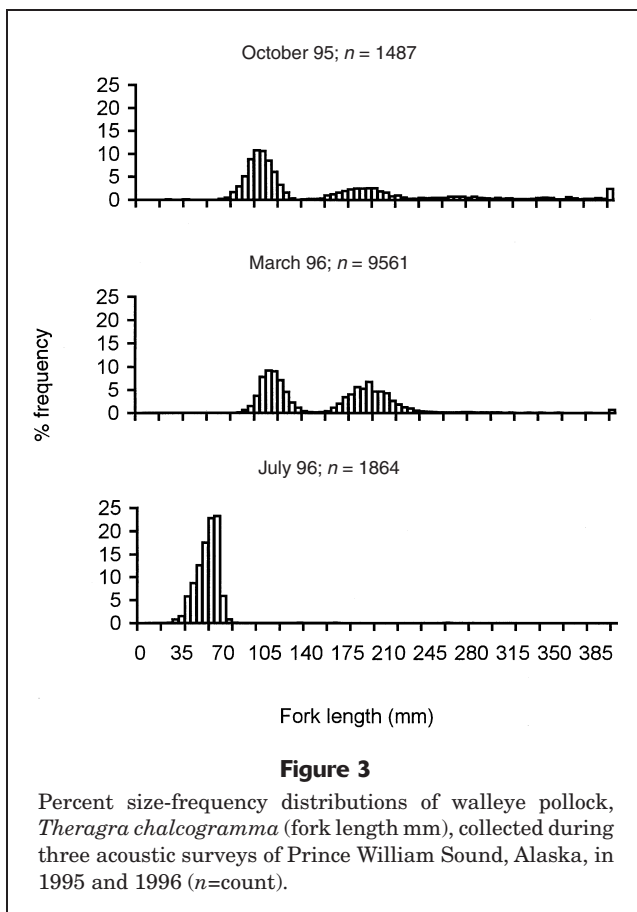
Pacific herring were deeper in the water column in March 1996 (27.0–28.9 m) than in October 1995 (15.0–20.2 m) and July 1996 (14.1–16.7 m) (Fig. 5). Walleye pollock were distributed near the bottom during all three surveys (Fig. 5).

The 26 locations within bays had a mean Σ NSD value of 3.8 km (SD=2.45), significantly smaller than 9.8 km (SD=6.69) for the 17 locations within passages and along the open coast ($t=-3.61$, $df=41$, $P<0.001$). The water conditions within these bays generally differed from conditions in passages and open coast (Table 2). The surface water temperatures (0–30 m) were cooler inside than outside the bays by 0.32°C and 0.20°C in October 1995 and July 1996, respectively. The surface water inside the bays was also less saline in October 95 but was similar inside

Table 1

Means and standard deviations (SD) of densities (fish/m³) for the three Pacific herring, *Clupea pallasii*, size modes and for walleye pollock, *Theragra chalcogramma*, aggregations observed during three acoustic surveys of Prince William Sound, Alaska, in 1995 and 1996 (n =number of schools observed).

	October 1995 fish/m ³			March 1996 fish/m ³			July 1996 fish/m ³		
	n	mean	SD	n	mean	SD	n	mean	SD
Herring									
age-0	137	2.52	8.36	179	0.91	2.84	8	2.67	5.46
age 1–2	126	0.51	1.10	223	0.81	0.95	42	9.15	15.75
adult	54	1.35	3.21	147	0.51	0.95	32	3.62	0.86
Pollock	119	3.14	8.68	148	4.20	14.59	31	267.87	72.05



and outside the bays in deeper water (31–60 m) and throughout the water columns in July 1996 (Table 2). Deeper waters, where Pacific herring were aggregated, inside the bays were warmer than outside the bays, 0.28°C (31–60 m) in March 1996.

Pacific herring and walleye pollock Σ 3NSD distributions differed from randomly calculated Σ 3NSD distributions during all three surveys (Table 3; Fig. 6). In October 1995, age-0 and 1–2 year old Pacific

herring aggregated at the heads of bays with Σ 3NSD values <3 km (Fig. 6). Adult Pacific herring were aggregated in passages or along the open coast (Fig. 6). Walleye pollock distribution was also significantly aggregated within bays but not as tightly as age-0 and 1–2 year old Pacific herring (Table 3; Fig. 6). In March 1996, all size modes of Pacific herring and walleye pollock had greater than expected Σ 3NSD values, ranging between 4 and 10 km (Table 3; Fig. 6). In July 1996, age-0 Pacific herring were highly aggregated at the heads of bays (57.1% of Σ 3NSD <1 km; Fig. 6). Age 1–2 year old Pacific herring were also aggregated at the head of bays (<2 km). Adult Pacific herring were aggregated within bays (<2 km), but more than expected had Σ 3NSD values of 6 to 7 km (Fig. 6). In July 1996, walleye pollock were aggregated within bays and the majority of Σ 3NSD values were <3 km (Table 3; Fig. 6).

Discussion

Pacific herring was the most abundant fish aggregating in the east-northeast and west southwest areas of Prince William Sound. Bays appeared to be nursery areas for age-0 and 1–2 year old Pacific herring. Water conditions within bays fluctuated less than conditions within passages and along the open coast. In October 1995 and July 1996 water temperatures in the upper 30 m were cooler inside these bays than within passages or along the open coast. In March this pattern was reversed and deeper waters, where the Pacific herring were aggregated, were warmer within the bays than within passages or along the open coast. Although, these fluctuations were small, they may have affected juvenile Pacific herring metabolic rates. Temperature and length of winter are critical factors in determining juvenile Pacific herring growth and over-winter survival (Paul and Paul, 1998; Paul et al., 1998; Foy and Paul, 1999).

When larval Pacific herring metamorphose into juveniles, they develop the ability to form and maintain schools (Blaxter, 1985; Gallego and Heath, 1994). Schooling behavior is the juvenile herring's primary defense against predation (Blaxter and Hunter, 1982). School structure results from the dynamic interaction of several variables causing opposing behaviors, primarily the availability of food, the physical size and condition of the fish, and the threat of predation (for a review see Pitcher, 1986). Newly recruited age-0 Pacific herring were tightly aggregated in shallow water at the heads of bays in July. These herring formed a few dense schools of a single-size cohort near the surface. This distribution possibly resulted from a high threat of predation (Stokesbury et al.¹), coupled with an abundance of food as indicated by the fullness of herring stomachs (Foy and Norcross, 1999) and from zooplankton samples (Foy²).

Age-0 Pacific herring were aggregated within bays near the surface, in October. However, the number of schools increased, schools became less cohesive, and size cohorts began to mix in contrast to the highly aggregated unimodal schools observed in July. The distribution observed in October may have resulted from a decrease in food abundance, a decrease in the threat of predation, or both (Foy and Norcross, 1999, Stokesbury et al.¹).

Age-0 Pacific herring school structure and distribution completely changed in March. These herring had just survived the winter when prey abundance is minimal and the risk of starvation is great (Paul and Paul, 1998; Paul et al., 1998; Foy and Paul, 1999). Herring moved away from the shores into deeper water and spread out forming sparse (<1 fish/m³) shoals of mixed-size cohorts. Distance between fish within schools increases with hunger, reducing cohesion, and causing lower mean densities (Pitcher and Partridge, 1979; Robinson, 1995). This independent segregating behavior reduces competition for food and increases the chance of encountering food by

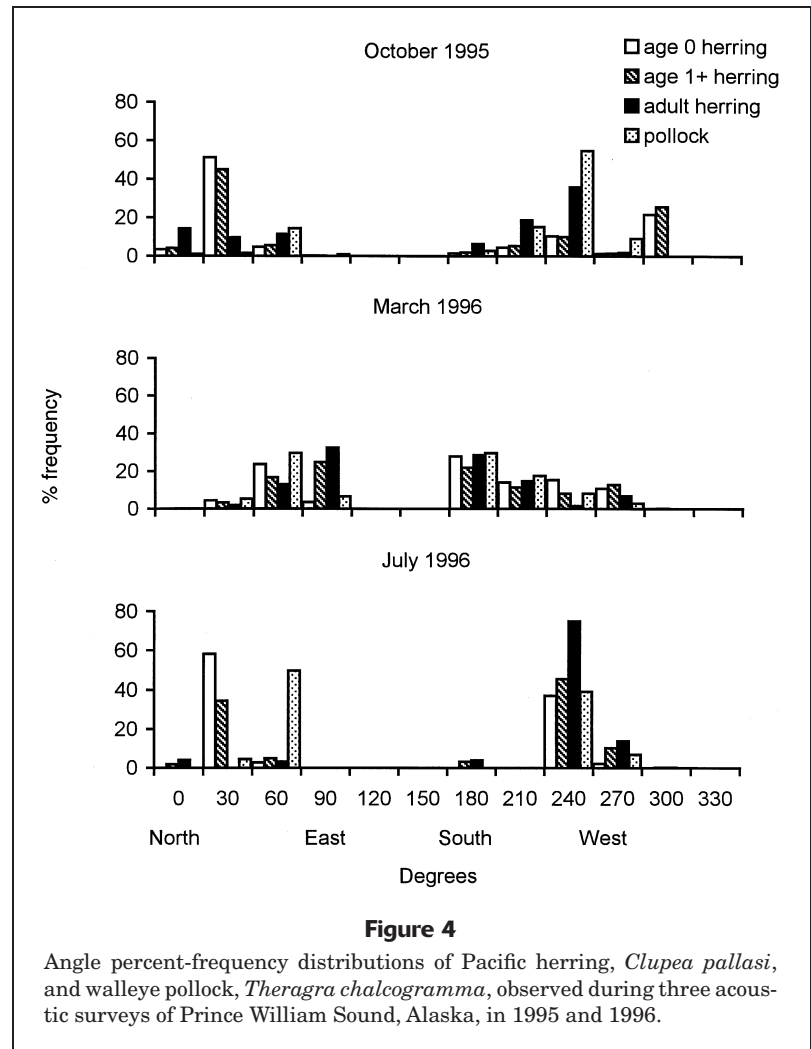


Figure 4

Angle percent-frequency distributions of Pacific herring, *Clupea pallasii*, and walleye pollock, *Theragra chalcogramma*, observed during three acoustic surveys of Prince William Sound, Alaska, in 1995 and 1996.

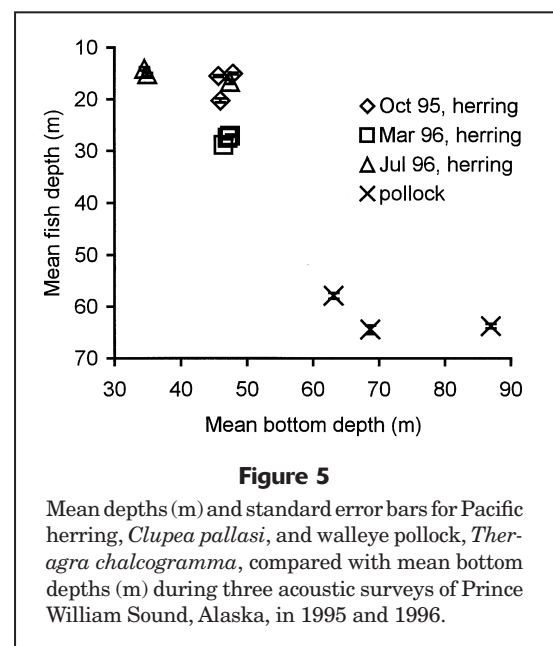


Figure 5

Mean depths (m) and standard error bars for Pacific herring, *Clupea pallasii*, and walleye pollock, *Theragra chalcogramma*, compared with mean bottom depths (m) during three acoustic surveys of Prince William Sound, Alaska, in 1995 and 1996.

¹ Stokesbury, K. D. E., J. Kirsch, and B. L. Norcross. 1999. Mortality estimates of juvenile Pacific herring (*Clupea pallasii*) in Prince William Sound, Alaska. Unpubl. manuscript.

² Foy, W. 1996–1998. Unpubl. data. Institute of Marine Science, Industrial Technology Center, University of Alaska, Fairbanks, 118 Trident Way, Kodiak, AK 99614-7401.

Table 2

Means and standard deviations (SD) of water conditions inside bays and outside bays in passages and along open coast during three surveys of Prince William Sound, Alaska, in 1995 and 1996 (n =count; Mann-Whitney rank sum test= U).

Water depth (m)	n	Temperature ($^{\circ}\text{C}$)		Salinity (‰)				
		mean	SD	mean	SD			
October 1995								
0–30	inside	146	9.34	0.626	$U=16135$	28.77	1.111	$U=18583$
0–30	outside	180	9.66	0.821	$P<0.001$	29.29	1.063	$P<0.001$
31–60	inside	71	7.95	2.06	$U=4212$	30.62	0.749	$U=8610$
31–60	outside	186	9.87	0.393	$P<0.001$	30.36	0.21	$P=0.303$
March 1996								
0–30	inside	667	4.14	0.437	$U=281130$	31.65	0.225	$U=305280$
0–30	outside	509	4.06	0.357	$P<0.001$	31.66	0.219	$P=0.320$
31–60	inside	416	4.53	0.521	$U=228192$	31.83	0.106	$U=209925$
31–60	outside	512	4.25	0.344	$P<0.001$	31.80	0.106	$P<0.001$
July 1996								
0–30	inside	688	10.93	1.984	$U=291730$	28.98	1.772	$U=287935$
0–30	outside	480	11.10	1.569	$P=0.049$	29.09	1.642	$P=0.194$
31–60	inside	453	6.45	1.084	$U=192162$	31.02	0.479	$U=213780$
31–60	outside	492	6.94	1.238	$P<0.001$	31.08	0.265	$P=0.911$

Table 3

Chi-squared analysis in which the percent frequency distributions of the sum of the three near shore distances (Σ3NSD) for Pacific herring, *Clupea pallasii*, and walleye pollock, *Theragra chalcogramma*, aggregations were compared with values generated from a random distribution during three acoustic surveys in Prince William Sound, Alaska (Fig. 6 in main text); * = $P<0.05$, ** = $P<0.01$, df = degrees of freedom.

	October 1995		March 1996		July 1996	
	df	χ^2	df	χ^2	df	χ^2
Herring						
age-0	12	55.30**	9	53.68**	8	182.17**
age 1–2	12	51.41**	9	58.40**	8	59.29**
adult	12	123.26**	9	84.55**	8	52.18**
Pollock						
	12	25.16*	9	63.60**	8	64.46**

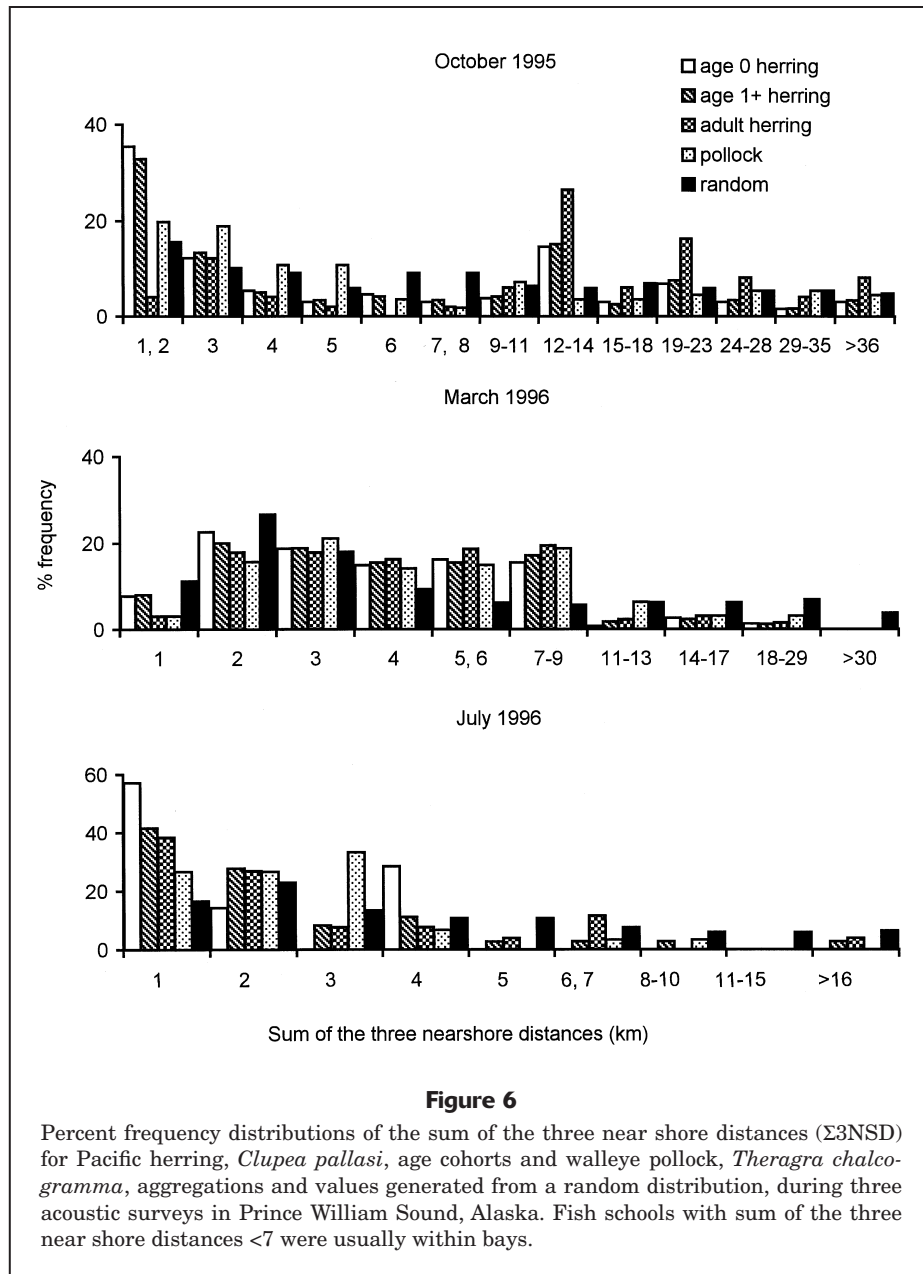
increasing the foraging area (Robinson and Pitcher, 1989; Robinson, 1995).

Age-1 Pacific herring repeated this contraction-expansion pattern of school structure and distribution during the year. After their second winter, herring appeared to join the adult schools, leaving as new recruits entered the bays.

Pacific herring and walleye pollock geographic distributions were roughly similar within Prince William Sound. Walleye pollock distribution was bimodal with aggregations in the east-northeast and the west-southwest areas. However, there appeared to be little spatial overlap between these species because they occupied different portions of the water column. Juvenile walleye pollock were highly aggregated, forming a few, very dense schools in July within bays. Juve-

nile walleye pollock distribution may be influenced by the cannibalistic behavior of adult walleye pollock (Livingston, 1993). Adult walleye pollock were primarily aggregated in the southern portion of Prince William Sound, although a smaller school was evident in the east-northeast.

Bays within Prince William Sound appear to be nursery areas for both Pacific herring and walleye pollock juveniles. Data presented here and growth studies suggest that these nursery areas are isolated (Stokesbury et al., 1999). This finding differs from that for other herring species distributions where juveniles from different populations appear to share a common nursery and feeding areas, separating only when adults begin to spawn (Blaxter and Hunter, 1982; Iles and Sinclair, 1982; Sinclair et



al., 1985; Sinclair, 1988). Future work should focus on determining the physical and biological variables influencing juvenile Pacific herring and walleye pollock within these bays to estimate population fluctuations that are critical for ecosystem models and effective fisheries management.

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