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Distribution of Walleye Pollock, *Theragra chalcogramma*, Spawning in Shelikof Strait, Gulf of Alaska, Based on Acoustic and Ichthyoplankton Surveys 1981, 1984 and 1985

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Acoustic and ichthyoplankton data collected from Shelikof Strait in 1981, 1984 and 1985 were examined to determine spawning ground and period of walleye pollock, *Theragra chalcogramma*. Walleye pollock in the Gulf of Alaska migrated into Shelikof Strait for spawning during late winter and early spring. They entered Shelikof Strait via the warm and saline deep layer (continental slope water mass) in the southwestern channel, and major fish schools concentrated for spawning along the deep trough (250~300 *m*) in the western part of the central strait. Peak spawning activity occurred there from late March to early April. Peak spawning time and area in Shelikof Strait varied little between years, despite difference in hydrography. Geographical advantages together with some oceanographic phenomena (reduced water transport and reduced mixed layer depth in spring) made that area an optimal spawning ground in the Gulf of Alaska during early April. After early April, spawning intensity decreased rapidly and the spawning area tended to expand to the northeast and southwest.

Introduction

The distribution and migration of marine fishes are controlled by their behavior as well as changes in environmental factors affecting them. In temperate and high latitudes, many marine fishes have well defined spawning grounds and spawning seasons (Cushing, 1975), which likely have been selected through adaptative evolutionary processes. The fish eggs and larvae produced, in general, are planktonic, and are transported from the spawning ground to nursery areas by existing current systems (Harden-Jones, 1968). However, fish eggs spawned at a fixed time and location may experience different biological and physical conditions each year, so that the distribution and survival of the early stages varies from year to year. These young stages of fish have narrow optimum ranges of temperature and salinity and are vulnerable to environmental changes (Alderdice and Forrester, 1971; Hempel, 1979). Minor changes in survival during this period may result in large differences in adult population abundance (Wooster et al., 1983; Sissenwine, 1984). Therefore, the examination of environmental conditions and fish distribution on spawning grounds will give us insight as to why fish aggregate at particular spawning grounds, and what factors influence the selection of spawning area and time. Further information about egg and larval ecology will provide a better understanding of recruitment variability.

Walley pollock, *Theragra chalcogramma,* in the Gulf of Alaska spawn in Shelikof Strait during March through May. Annual ichthyoplankton and acoustic/midwater trawl surveys have been conducted (except 1982) in the strait to determine the distribution and abundance of walleye pollock during the spawning season since the spawning ground was discovered in 1980 (Fig. 1). Acoustic/midwater trawl surveys through the most intensive spawning area several times from March to April revealed that other species amounted to only 1~2 % of total biomass in trawl samples (Nelson and Nunnallee, 1987).

Maturing walleye pollock enter Shelikof Strait via the southwestern valley between Semidi and Chirikof Islands from late winter and concentrate over the deep trough (250~300 *m*) in the western central strait before peak spawning time (Nelson and Nunnallee, 1987). Ichthyoplankton survey results support the acoustic surveys as to when and where the peak spawning aggregations occur. Bates (1987) and Dunn and Matarese (1987) found that spawning peaked in the deepest trough area near Cape Kekurnoi from late March to early April, and then declined rapidly. In this paper we analyze the distributions of spawners and eggs to examine the relationship between spatio-temporal spawning activity and the geography and oceanography of Shelikof Strait.

Materials and Methods

Geographic setting

Shelikof Strait is a long (about 340 *km*) strait between the Alaska Peninsula and several islands such as Barren, Kodiak, and Chirikof Islands, which major axis is directed from the northeast to the southwest (Fig. 1). Strait was partitioned into six subareas to study the geographical and spatial distributions of walleye pollock spawning activity: Two boundaries orthogonal to the major axis of the strait were established to define a northeastern area (north of Cape Atusagvic), a southwestern area (south of Dry Bay), and a central area in between. The major axis of the strait was used as an east-west boundary (Fig. 1). The northeastern part of the strait faces lower Cook Inlet and Stevenson Entrance, and includes two deep (about 200 *m*) and narrow troughs running NE to SW, parallel to the axis of the strait. In the central strait, bottom depth is greater than that in the northeastern strait, but the width is the same (about 50 *km*). Only one deep trough (about 300 *m*), the deepest area in Shelikof Strait, is present on the western side along the peninsula. The southwestern strait is relatively broad (about 100 *km*), and is bounded by relatively broad shallow areas to the west and south. A trough (250~300 *m*) located in the middle of this part of the strait connects with the continental slope area to the southwest.

Acoustic and oceanographic data collection

Acoustic surveys in Shelikof Strait were conducted during the walleye pollock spawning season of 1981, 1984, and 1985 from the National Oceanic and Atmospheric Administration (NOAA) R/V *Miller Freeman* using a 38 kHz echo sounder and a digital echo integrator. Details of acoustic survey method were given in Nelson and Nunnallee (1986). Sequential estimates of volumetric fish density were obtained for each of a series of preselected depth intervals from about 20 *m* to the sea bottom. Data were recorded at five-minute intervals along each of a series of systematically spaced transects throughout Shelikof Strait. Analysis of these data yielded estimates of total walleye pollock biomass, the biomass within specific depth intervals and the areal distribution of the fish stock.

It was assumed that acoustic survey passes conducted between 20~30 March (Table 1) represent the stabilized location for spawning since peak spawning consistently occurred during or shortly after that pariod in 1981, 1984, and 1985 (Dunn and Matarese, 1987). Surveys consisted of from 20 to 40 equally spaced zig-zag tracklines, each transect consisting of from 30 to 50 segments (Fig. 1). Each segment represents fish density distribution in the water column within preselected (10~20 *m*) depth intervals. Fish densities were expanded over volume to determine biomass at depth to show the

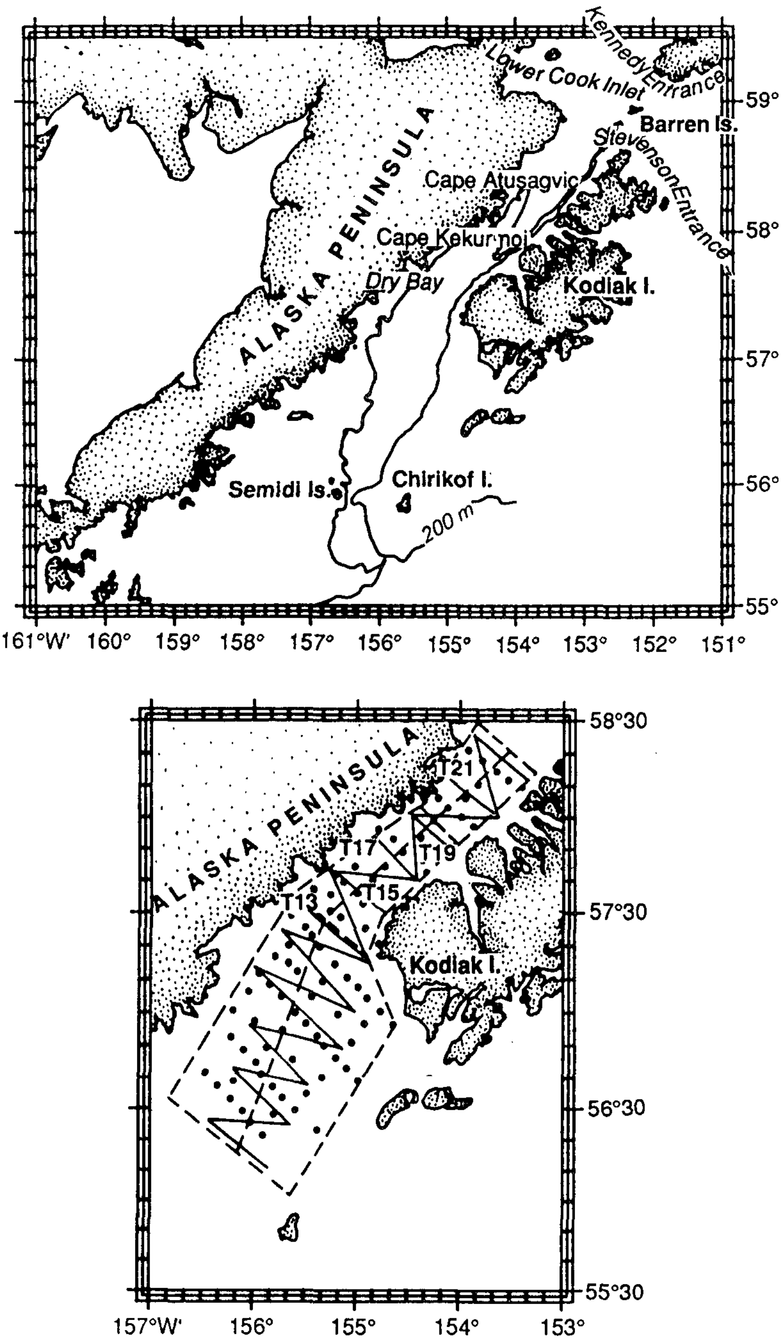

Fig. 1. Geographic setting showing (a) northern Gulf of Alaska and (b) typical ichthyoplankton sampling locations (• ; early April, 1981) and acoustic tracklines (—; late March, 1985) in Shelikof Strait with six subareas used in this paper. CTD casts were conducted at each ichthyoplankton sampling station in 1981, and on T13, T15, T17, T19, and T21 in 1985.

Table 1. Selected research cruises in Shelikof Strait during spawning time (late March-early April) of walleye pollock in 1981, 1984 and 1985.

Date	Research vessel	Main purpose
March 24~27, 1981	Miller Freeman	Acoustic survey
March 30~April 8, 1981	Miller Freeman	Egg survey
April 26~May 2, 1981	Miller Freeman	Egg and larval survey
May 20~24, 1981	Miller Freeman	Egg and larval survey
March 22~25, 1984	Miller Freeman	Acoustic survey
March 12~28, 1985	Discoverer	Hydrography survey
March 21~28, 1985	Miller Freeman	Acoustic survey
April 2~11, 1985	Miller Freeman	Egg survey

general pattern of the vertical distribution of spawners. Fish trawlings also were conducted to examine some biological characteristics at the several locations of fish school (Nelson and Nunnallee, 1986). Note that age 1 fish biomass (< 0.024 % of the total walleye pollock biomass in Shelikof Strait in 1981~1984; Nelson and Nunnallee, 1986) was included in 1981 and 1984 data. Age 2 and older fish biomass was used for 1985.

In 1985, 19 conductivity-temperature versus depth (CTD) casts were made on five cross-strait tracklines in the central and the northeastern strait to investigate the relationship between fish aggregation and their abiotic environment (Fig. 1). The CTD recorded temperature and salinity information at 1 *m* intervals from the surface to the near bottom. To examine the environmental factors affecting to the distribution of walleye pollock, contours of fish density with depth were superimposed over the temperature distribution in the strait, and volumetric fish density at each sampling depth interval (10 *m*) was allocated according to temperature and salinity categories. In addition to 1985 CTD data, several data sets from the 1981 survey were selected for comparison in cases when fish density data collections from acoustic surveys and CTD casts during the ichthyoplankton surveys occurred at nearly the same location within a two day span, assuming no significant changes in water properties within two days. A CTD data set collected on the NOAA vessel *Discoverer* during March 1985 was used for determining the characteristics of water masses in Shelikof Strait for that year.

Ichthyoplankton sampling

Four ichthyoplankton surveys were conducted from mid March to late May on the *Miller Freeman* in 1981 (Table 1). Sampling was done with 60 *cm* bongo nets (mesh: 0.505 *mm*), making double oblique hauls from 200 *m* to the surface. No data were available for 1982~1984 because no ichthyoplankton surveys were conducted during the main spawning season in 1982 and 1983, and the shallow sampling strategy used in 1984 was inadequate for the density estimate of walleye pollock eggs in Shelikof Strait. In 1985, sampling was conducted to within about 10 *m* of the bottom. Egg catch samples were subsampled to determine egg developmental stage (A. C. Matarese, Alaska Fisheries Science Center, 7600, Sand Point Way, NE, Seattle, WA 98115, pers. comm.). If catches exceeded 200, only 100 eggs were identified for developmental stage, but all eggs were staged for catches less than 100 eggs. Only the abundances of eggs in the cell stage (i.e., less than one day old) were chosen to determine the exact location and intensity of spawning, because the daily egg advection was an order of 2~3 *km* in Shelikof Strait (Kendall and Kim, 1989). Egg concentration at each station was standardized to number of eggs sampled per m^2 surface area (Smith and Richardson, 1977) to examine the differences in spawning activity. A 3-dimensional construction model was used for the estimation of egg abundance within specific subareas (Kim and Gunderson, 1989).

Results

In general, adult walleye pollock occupied the same areas before peak spawning time each year, although spawner densities in Shelikof Strait have decreased continuously since 1981 (Fig. 2). The spatial distribution of spawning aggregations formed on elliptical shape. Their presence at the southwest and northeast entrances of Shelikof Strait was minimal. Each year the highest fish densities were located in the deep portion (> 200 *m* of the narrow trough in the central strait near Cape Kekurnoi. The second highest densities were found in the middle of the southwestern part of the strait during each of the subject years. Mean density of spawners in each subarea is presented in Table 2. Fish densities varied between the years, but distribution patterns were similar. The highest densities were found in the western part of the central strait, and the lowest was in the eastern part of the northeastern strait. Results of an ANOVA test (Rubin, 1982) for the homogeneity of fish density revealed that there were significant differences in

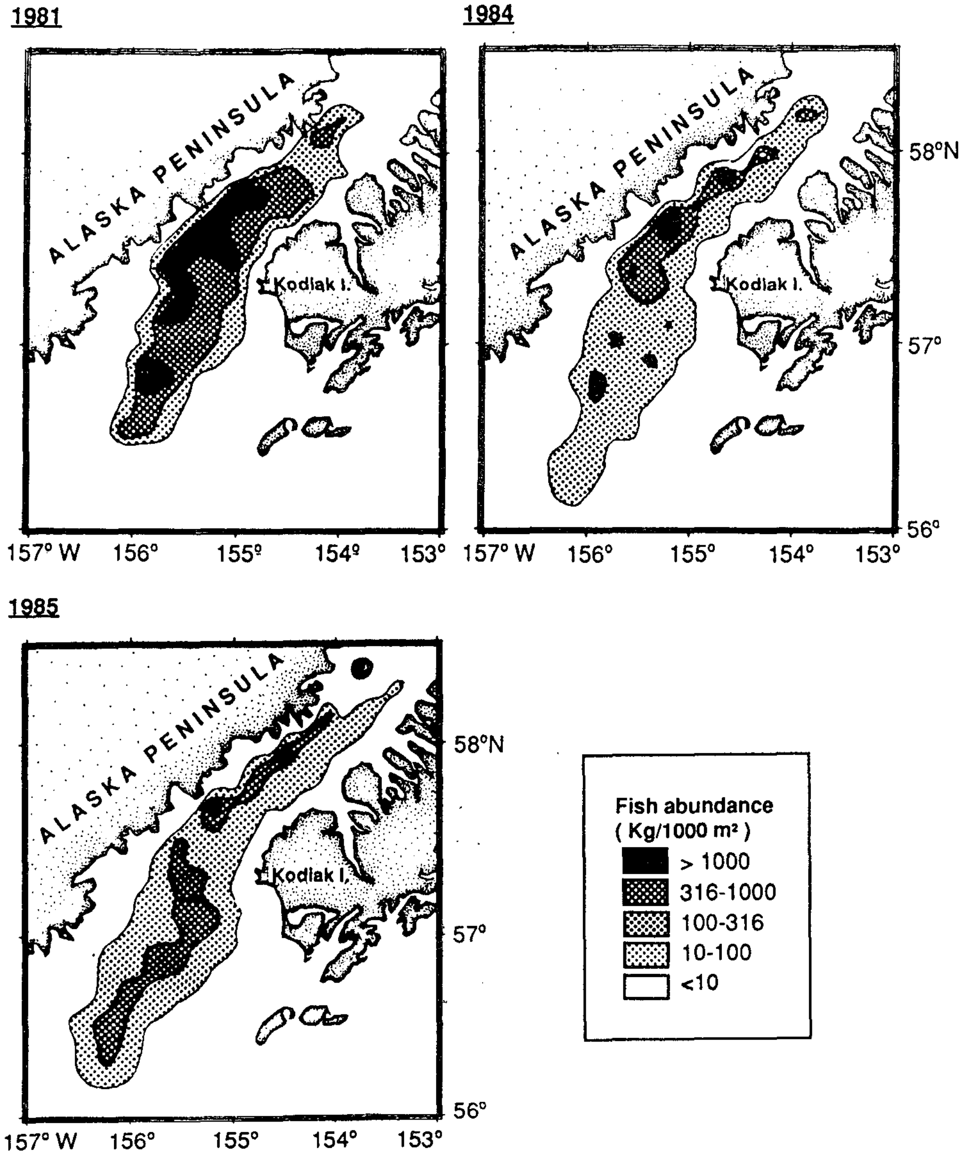

Fig. 2. Spatial distribution of walleye pollock in Shelikof Strait during the late March 1981, 1984, and 1985. Note that small amounts of age 1 fish were included in 1981 and 1984 distribution, but not for 1985.

fish density along-strait ($P<0.01$ in 1981 and 1985, and $P<0.02$ in 1984) and across-strait ($P<0.01$ in 1981, 1984, and 1985). Negligible amounts of fish (mostly immature) were in the upper 100 *m* of the water column, and fish biomass and density tended to increase with depth (Fig. 3). About 60~80 % of the total biomass was found below 200 *m*, and the highest densities were found at 220~260 *m*. In the deepest depth intervals (below 260 *m*), biomass amounted to only a small portion of the total due to the small volume of water represented, and densities were low except in 1981. Low densities in 1984 and 1985 were due to the lower fish density at this depth in the southwestern part of the strait (Fig. 2).

Based on cross-strait acoustic tracklines in late March 1985 most walleye pollock resided within about 50 *m* of the bottom (Fig. 4). The species showed a relatively continuous distribution across the strait in the south (T13, see Fig. 1), while they concentrated in the deep trough of the western strait in the central region (T17, Fig. 1). Toward the northeast portion of the strait, where bathymetry is generally shallower, the fish were less dense, and were found mainly in the troughs on the Alaska Peninsula side and the Kodiak Island side (T21, Fig. 1). East-west differences in mean density with depth for 1985 were tabulated in Table 3. As expected, the greatest concentrations were located below 220 *m* in the western strait. Only fish densities

Table 2. Abundances (kg/m^2) of spawning walleye pollock in six subareas of Shelikof Strait during late March 1981, 1984, and 1985. Numbers indicate mean ± standard deviation, with sample size (acoustic transect segments) in parentheses.

		Northeast	Central	Southwest
1981				
	East	0.03 ± 0.06 (43)	0.27 ± 0.21 (103)	0.14 ± 0.12 (185)
	West	0.25 ± 0.28 (40)	1.15 ± 1.60 (98)	0.43 ± 0.59 (180)
1984				
	East	0.01 ± 0.01 (19)	0.05 ± 0.05 (69)	0.06 ± 0.06 (203)
	West	0.56 ± 1.09 (19)	0.44 ± 0.54 (69)	0.09 ± 0.18 (202)
1985				
	East	0.03 ± 0.03 (67)	0.05 ± 0.04 (99)	0.08 ± 0.06 (239)
	West	0.08 ± 0.30 (64)	0.26 ± 0.40 (95)	0.08 ± 0.07 (238)

Table 3. The relative volumetric densities of walleye pollock by depth from an acoustic survey in late March 1985. Five tracklines which are perpendicular to the along-strait axis in the central strait were chosen, and divided into the eastern and the western strait regions. Data are mean ± standard deviation, with sample size (acoustic transect segments) in partentheses.

Depth interval(*m*)	Cross strait			
	West		East	
120~140	438 ± 668	(146)	489 ± 683	(140)
140~160	615 ± 637	(145)	703 ± 898	(136)
160~180	1,354 ± 1,605	(140)	942 ± 1,159	(128)
180~200	2,082 ± 10,897	(134)	3,010 ± 3,707	(114)
200~220	4,355 ± 10,897	(122)	3,892 ± 3,617	(64)
220~240	10,979 ± 35,955	(104)	5,147 ± 3,714	(25)
240~260	21,704 ± 51,199	(81)		
260~280	22,478 ± 29,374	(50)		
280~300	20,137 ± 30,831	(22)		

found between 120 and 200 *m* were examined for adult density differences in mid-water with respect to water column depth and east-west location, because much of the walleye pollock found at shallower depths were juvenile. Fish densities in mid-water (i.e., 120~200 *m*) tended to increase with depth (ANOVA test, $P<0.01$), and increments of relative fish density with depth were similar in the eastern and the western parts of the strait (ANOVA test, $P>0.95$). This result implies that the increase in fish biomass with depth in mid-water is similar in both eastern and western regions. Only the deepest trough area in the western region of the central strait had very heavy concentrations

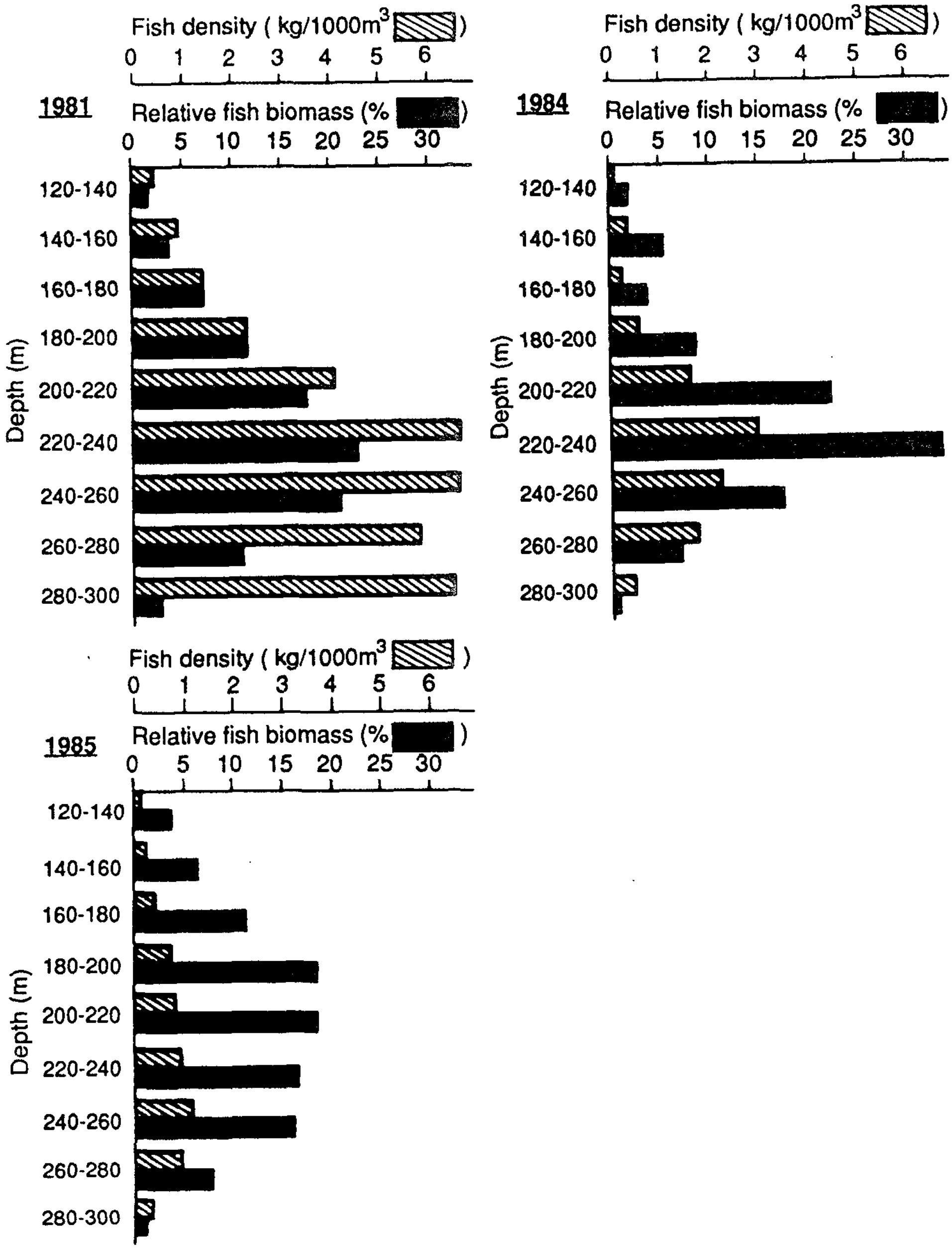

Fig. 3. Mean density and relative biomass of walleye pollock in each depth stratum of Shelikof Strait during late March 1981, 1984, and 1985. Note that age 1 fish were included in 1981 and 1984, but not for 1985.

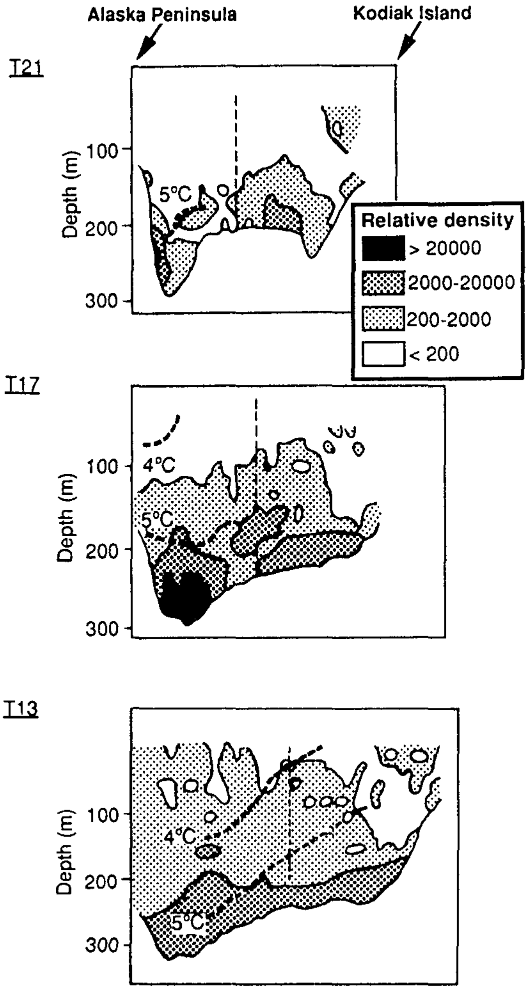

Fig. 4. Continuous contourings of relative fish density in selected cross-strait trackline shown in Fig. 1, late March 1985. The difference between each density concentration contour is a factor of ten. Four and five degree isotherms are superimposed, and the east-west separation is indicated by the vertical bar in each profile.

of spawning walleye pollock.

Plots of water temperature superimposed on depth distributions of fish density indicated that 1985 spawners stayed in the warm bottom waters (>5 ℃) and avoided cold regions (<4 ℃) (Fig. 4). The surveyed area had a temperature range of 1~6 ℃ and salinity range of 31~34 ‰ in March 1985 (Kim, 1987). Relative volumetric fish density superimposed on a temperature-salinity diagram showed clearly that the highest densities of mature fish were found in warmer (>5.05 ℃) and saltier (>32.45 ‰) waters and that densities decreased with lower temperature or salinity, and the ranges of temperature and salinity that fish occupied in 1981 were narrower compared to those in 1985 (Fig. 5). Water properties in Shelikof Strait varied among years due to the global changes in environmental conditions. For example, mean temperature at 162~216 *m* in the main spawning area of the strait was 5.7 ℃, 5.2 ℃, 5.6 ℃ and 4.2 ℃ in 1977, 1981, 1985, and 1986, respectively (Kim, 1987). However, regardless of interannual changes in water properties, we can define three water masses in Shelikof Strait (Mysak et al., 1981; Reed et al., 1987): A small amount of cold and low saline surface water along the Alaska Peninsula originates from land runoff through lower Cook Inlet, and flows southwestwardly. Below this southwestern drift, the Alaskan Coastal Current (ACC), which enters Shelikof Strait via Kennedy Entrance, occupies the middle layer of the water column along the peninsula and the surface layer of the eastern side of the strait and flows southwestwardly. Those two water masses, bounded on the northwest by the Alaska peninsula coast, form wave-like structures in the surface as they travel downstrait. On the other hand, a warm and saline water mass occupies the rest of strait at depths greater than 150~200 *m*. This bottom water mass comes from the conntinental slope area via the southwestern valley of the strait between the Semidi Islands and Chirikof Island, and flows slowly toward the northeast (Fig. 6).

Changes in the location and intensity of spawning in Shelikof Strait during April~May were indicated by changes in mean density of young eggs in each subarea during 1981 (Table 4). Spawning activity generally peaked in the western side of the central strait during early April. In late April, however, the spawning intensity was less and no significant difference in egg densities among subareas was found. In late May, spawning activity was very weak throughout the entire strait and the relative abundances (%) of eggs released in each subarea showed an expansion of spawning activity toward the northeast and southwest (Fig. 7). An east-west difference in spawning intensity also was evident in early April (i.e., 96 % of total spawning was in the

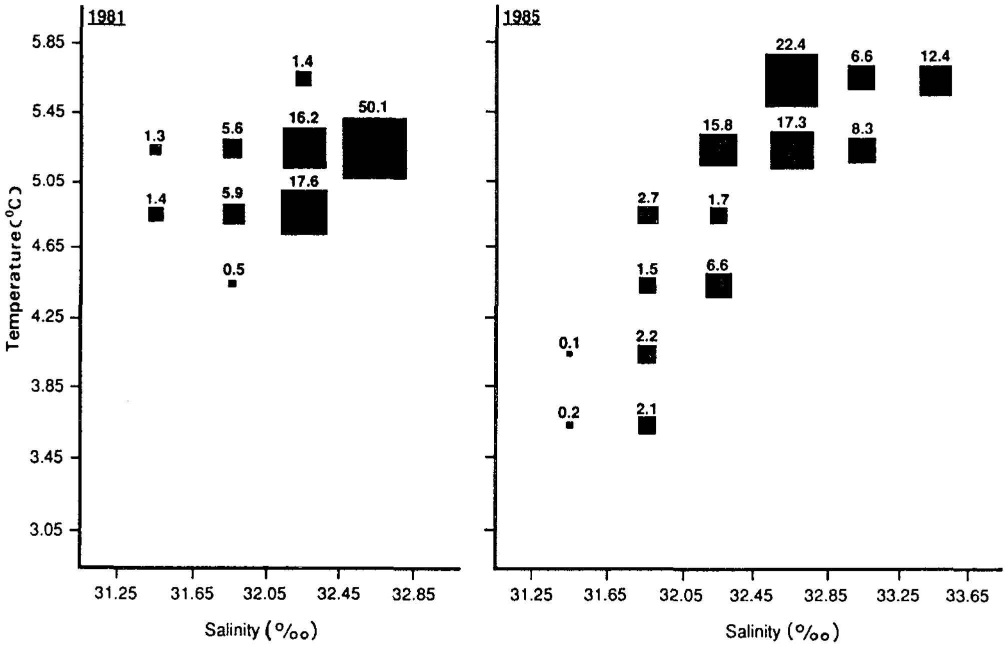

Fig. 5. The distributions of fish density observed at selected ranges of temperature and salinity in April 1981 and 1985. Numbers indicate the volumetric fish density in relative scale each year.

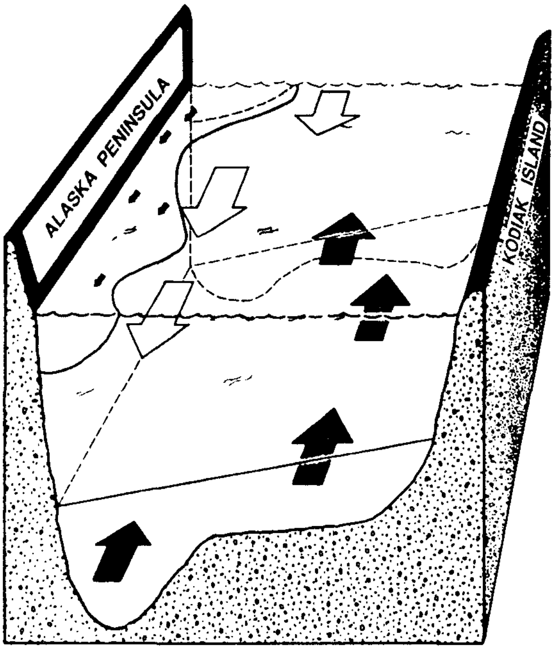

Fig. 6. Schematic features of three water masses in Shelikof Strait. Large dark arrows: northeastward bottom water mass; white arrows: southwestward Alaskan Coastal Current; small dark arrows: southwestward coastal drift from lower Cook Inlet.

west), but the difference became small or negligible later.

Our ANOVA test rejected the null hypothesis of spatially homogeneous spawning activity during late March (for acoustic data) and early April (for ichthyoplankton data). However, the Newman-Keuls multiple range test (Zar, 1974) revealed another feature of spawning activity. The spawning intensity in the western part of the central strait was always

Table 4. The spatio-temporal changes in young egg density (eggs/m^2) of walleye pollock eggs in the six subareas of Shelikof Strait during the 1981 spawning season.

	Northeast	Central	Southwest
Early April			
East	5.4	7.7	14.8
West	7.1	1,127.2	49.4
Late April			
East	5.9	6.3	8.1
West	6.5	4.1	9.4
Late May			
East	0.0	0.4	0.5
West	1.2	0.5	0.4

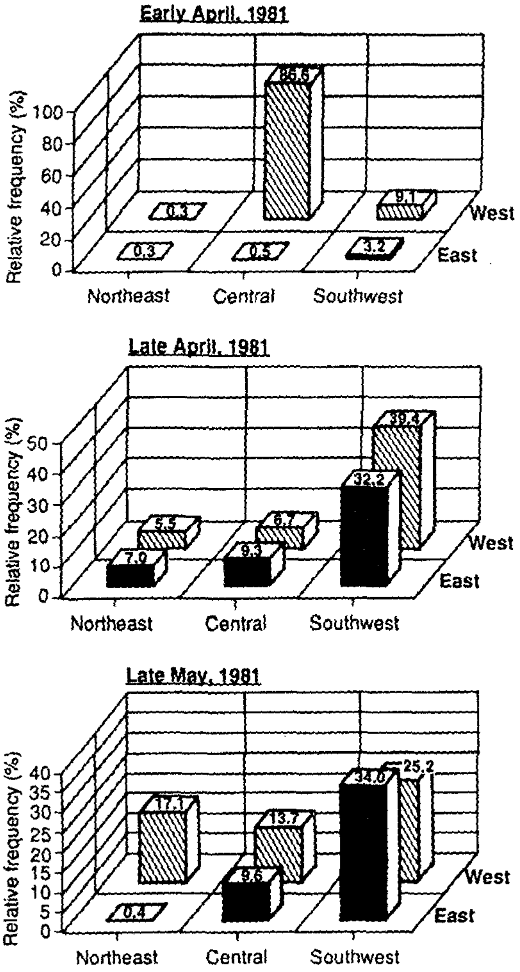

Fig. 7. The relative frequency (%) distribution of spawning products from each subarea during three surveys in 1981: (a) early April, (b) late April, and (c) late May.

significantly higher than other areas (Fig. 8). Spawning intensity throughout the other areas of the strait was statistically similar except for some minor exceptions in the 1981 and 1984 acoustic data.

Discussion

The assumption of major spawning locations based on areas of high fish density in late March may not be valid during some years, because spawners apparently moved between areas inside Shelikof Strait between the timing of the acoustic and ichthyoplankton surveys (A. W. Kendall Jr., Alaska Fisheries Science Center, 7600, Sand Point Way, NE, Seattle, WA 98115, pers. comm.). Even though there is a difficulty for comparing two data sets (i. e., acoustic and ichthyoplankton data) due to the different collecting and organizing methods, the tendency of aggregation could be inferred; the range of highest to lowest walleye pollock abundance in late March 1981 was a factor of about 30~40 (Table 2). One week later, however, the ratio of the highest to lowest egg concentrations in the same regions was over 200 (Table 4), implying that fish formed heavier aggregations in the main spawning area as they approached the peak in spawning activity.

Within this context of water masses, we might describe what influences the distribution of walleye pollock during peak spawning time. Figures 2 through 5 indicate that most walleye pollock stay in the bottom layer of Shelikof Strait, no matter how water proprties change from year to year. Because the structure and location of water masses in Shelikof Strait during spring is a quasi-permanent feature, the main influencing factor of spawner distribution seems to be seabed topography (i.e., the deepest trough in the western side of the central strait) instead of the specific ranges of water properties. The geographical spawning area of walleye pollock in Shelikof Strait appears to be relatively consistent.

Even though we concluded that conservative water properties such as temperature and salinity do not have major roles in influencing the spawning areas of walleye pollock, the non-conservative dissolved oxygen (DO) concentration might influence small scale movement and schooling behavior inside Shelikof Strait. McFarland and Moss (1967) argued that temperature is too homogenous in marine environments to be responsible for the continuous changes observed in behavior of fish, but found positive correlation between oxygen gradients within schools and modifications in school structure. In Shelikof Strait, the extremely high concentration of fish and low rate of water transport in the bottom layer may accelerate depletion of DO. Evidence for oxygen depletion was found in the large variance in DO concentration at 200 *m* in March 1981 (Kim, 1987). If walleye pollock tend to avoid low oxygen as shown by other fish (e.g., Whitmore et al., 1960), the oxygen gradients could possible result in small scale movements in Shelikof Strait.

The geographic, meteorologic, and oceanographic characteristics of Shelikof Strait interact to make the area an optimal spawning ground for walleye pollock during early April. The environment is favorable for spawners as well as eggs and larvae. Adult walleye pollock can access the area easily (i.e., no geographical or environmental barriers), and the chance of survival of offspring is good. Mature walleye pollock enter lower Shelikof Strait from the continental slope through a deep interconnecting trough. In general, they follow the intrusion of slope water to near the deep, central part of the strait where inflow current is minimal. The bulk of spawning activity occurs in this area. Spawned eggs experience little water transport until they approach hatching. At that time they rise through the water column into the surface layer where they encounter a southwesterly flow that transports the early larval stages into bays/shallows to the west of the strait, and many young walleye pollock reside in these nursery areas along the peninsula for much of their first year of life (Walters et al., 1985). In addition, the spawning time of walleye pollock is the transition period for the abiotic environment. Reduced precipitation and river runoff as well as weak wind strength during the spring (March~May) in the northern Gulf of Alkaska result in reduced baroclinic water transport and current speed in the upper layer in Shelikof Strait (Schumacher and Reed, 1980). Also, beginning in April, as the days lengthen, the photic zone deepens, the mixed layer depth becomes shallower and the sur-

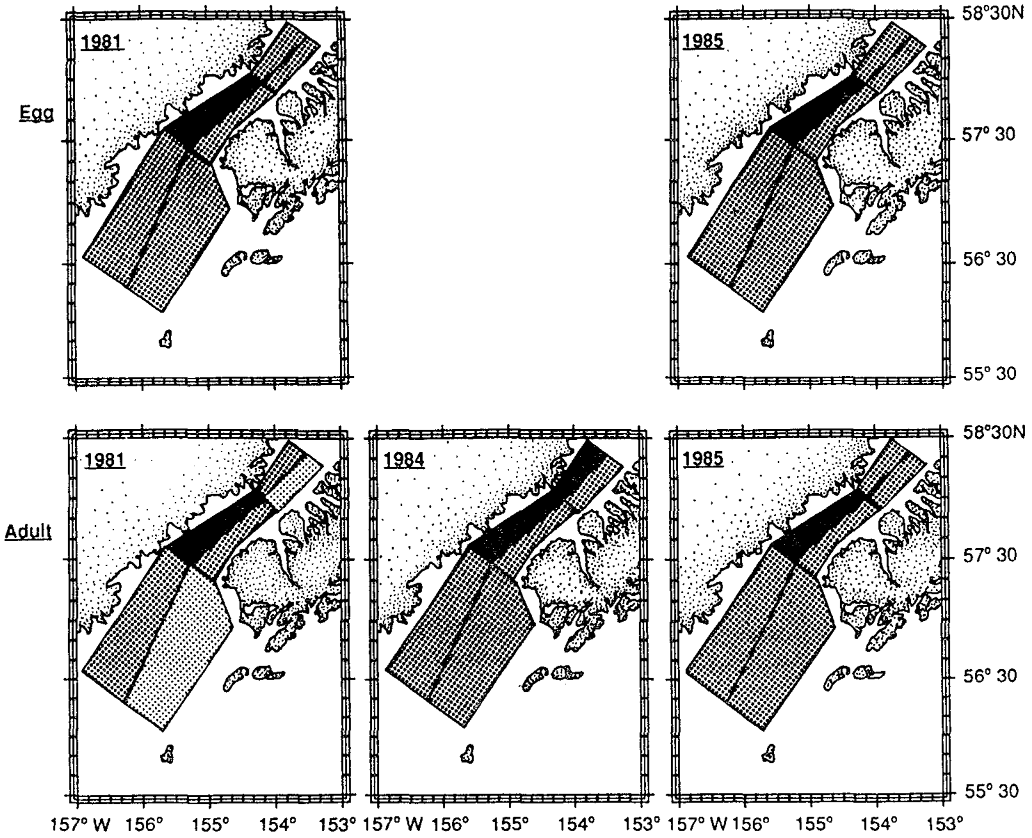

Fig. 8. The spawning area separation that shows statistically significant difference in spawning intensity based on (a) acoustic survey data and () ichthyoplankton survey data. The order of strength of spawning activity is indicated by black (strongest), gridding, and stippling (most weak).

face layer warms up. These are basic conditions for the spring phytoplankton bloom, that is, when the critical depth is equal to the mixed layer depth or mixed layer depth becomes shallower than critical depth, the spring bloom commences (Sverdrup, 1953), which in turn, provides the basis for zooplankton production. Haldorson et al. (1989) recently observed the coincidence of spawning time of walleye pollock and the spring bloom in Auke Bay, Alaska. They argued that the spawning of walleye pollock might use light reduction as a spawning cue, and rapid light reduction due to phytoplankton bloom is the strongest environmental signal for demersal fish. If everything goes normally, such physical and biological changes in the environment are beneficial to the early life stages of walleye pollock spawned at this time, since they can avoid being flushed out of the strait, and can find food easily. Therefore, from an ecological point of view, the spawning time and location of walleye pollock is well adapted to average oceanic transport processes and larval feeding conditions in Shelikof Strait.

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알라스카만 쉘리코프 해협에서 산란하는 명태, *Theragra chalcogramma*,의 분포에 대하여: 1981, 1984~85년의 음향학적 조사 및 난치자어 조사

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쉘리코프 해협에서 산란하는 명태의 정확한 산란장소 및 시기를 조사하기 위하여 1981년, 1984년, 1985년에 음향학적 조사 및 난치자어 조사를 하였다. 알라스카만의 명태는 산란하기 위하여 늦겨울 내지 초봄에 쉘리코프 해협으로 이동한다. 명태는 대륙사면으로부터 따뜻하고 염분도가 높은 해수를 이용하여 해협 남동쪽 입구의 바닥을 타고 들어와 중앙부의 서쪽면에 있는 깊은(>200 *m*) 곳에 모여들고, 3월부터 산란을 한다. 최대산란은 이곳에서 3월 하순부터 4월 초순에 걸쳐 일어나고, 해협내 수괴의 성질(해수온, 염분도, 밀도 등)은 해마다 다르지만 산란시기 및 장소는 거의 변함이 없다. 이 해역은 어류의 산란장이 보육장과 가까이 있다는 지리적 이점 이외에도 해마다 이 시기에는 해수의 이동량이 최저치로 내려가고 식물플랑크톤 번식의 핵심요소인 해수의 표면 혼합층이 최소로 된다는 해양학적 현상 때문에 알라스카만 명태의 최적합 산란장이 되어왔다고 추측된다. 4월 초순 이후, 산란행위는 급격히 감소하며 산란장은 북동쪽과 남서방향으로 약간 확장됨을 보여준다.