

Abstract—Data from ichthyoplankton surveys conducted in 1972 and from 1977 to 1999 (no data were collected in 1980) by the Alaska Fisheries Science Center (NOAA, NMFS) in the western Gulf of Alaska were used to examine the timing of spawning, geographic distribution and abundance, and the vertical distribution of eggs and larvae of flathead sole (*Hippoglossoides elassodon*). In the western Gulf of Alaska, flathead sole spawning began in early April and peaked from early to mid-May on the continental shelf. It progressed in a southwesterly direction along the Alaska Peninsula where three main areas of flathead sole spawning were identified: near the Kenai Peninsula, in Shelikof Strait, and between the Shumagin Islands and Unimak Island. Flathead sole eggs are pelagic, and their depth distribution may be a function of their developmental stage. Data from MOCNESS tows indicated that eggs sink near time of hatching and the larvae rise to the surface to feed. The geographic distribution of larvae followed a pattern similar to the distribution of eggs, only it shifted about one month later. Larval abundance peaked from early to mid-June in the southern portion of Shelikof Strait. Biological and environmental factors may help to retain flathead sole larvae on the continental shelf near their juvenile nursery areas.

Manuscript submitted 13 September 2004 to the Scientific Editor's Office.

Manuscript approved for publication 6 April 2005 by the Scientific Editor.

Fish. Bull. 103:648–658 (2005).

Temporal and spatial distribution and abundance of flathead sole (*Hippoglossoides elassodon*) eggs and larvae in the western Gulf of Alaska

Steven M. Porter

Alaska Fisheries Science Center
7600 Sand Point Way NE
Seattle, Washington 98115

Email address: steve.porter@noaa.gov

Flathead sole (*Hippoglossoides elassodon*) inhabit the continental shelf waters of the North Pacific Ocean from the northwest coast of North America to the Sea of Okhotsk in Asia (Alderdice and Forrester, 1974). The western Gulf of Alaska is an important area for adult, juvenile, and larval flathead sole. The continental shelf from the entrance to Prince William Sound to Unimak Island contains the highest relative abundance of adult flathead sole (as expressed as kg/ha) off the west coast of North America (Fig. 1; Wolotira et al.¹). Adult flathead sole are most abundant between depths of 100 and 200 m in this area (Wolotira et al.¹). During the spring adult flathead sole move from wintering grounds on the upper continental slope onto the continental shelf (Rose, 1982). Spawning flathead sole are found from February to August, and the greatest proportion of spawning fish occurs in April and May at depths between 100 and 200 m (Hirschberger and Smith²). Flathead sole eggs range in size from 2.75 to 3.75 mm (Matarese et al., 1989), and under environmental conditions similar to those they could experience in the Gulf of Alaska (temperature=5.5°C and salinity=31 PSU) it takes them about 15 days to hatch (Alderdice and Forrester, 1974). During the spring, flathead sole are the most abundant pleuronectid larvae in western Gulf of Alaska (Rugen³). Standard length at hatching is 6.89 ± 0.40 mm (95% ethanol-preserved size; S. Porter unpubl. data). Under conditions that flathead sole larvae could experience in the Gulf of Alaska, first feeding occurs about 1 week after hatching,

and in about 2 weeks the yolk is exhausted (Alderdice and Forrester, 1974). Copepod nauplii 150–350 μm in size are their predominant prey (Watts, 1988). In Auke Bay, Alaska, flathead sole larvae undertake reverse diel vertical migrations; they are concentrated near 5 m depth during the day and then disperse over a wider range of depths at night (Haldorson et al., 1993). The bays of the Alaska Peninsula and Kodiak Island provide nursery areas for juvenile flathead sole (Norcross et al., 1999).

Studies of the drift of walleye pollock (*Theragra chalcogramma*) larvae in Shelikof Strait have shown that there are physical processes that can slow the drift of these larvae out of Shelikof Strait and keep them near shore (Bailey et al., 1997). The pro-

¹ Wolotira, R. J., T. M. Sample, S. F. Noel, and C. R. Iten. 1993. Geographic and bathymetric distributions for many commercially important fishes and shellfishes off the west coast of North America, based on research survey and commercial catch data, 1912–84. NOAA Tech. Memo. NMFS-AFSC-6, 184 p. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

² Hirschberger, W. A., and G. B. Smith. 1983. Spawning of twelve groundfish species in the Alaska and Pacific coast regions, 1975–81. NOAA Tech. Memo. NMFS F/NWC-44, 50 p. Northwest and Alaska Fisheries Center, 2725 Montlake Boulevard East, Seattle, WA 98112.

³ Rugen, W. C. 1990. Spatial and temporal distribution of larval fish in the western Gulf of Alaska, with emphasis on the period of peak abundance of walleye pollock (*Theragra chalcogramma*) larvae. U.S. Dep. Commer., NWAFC Processed Rep. 90-01, 162 p. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

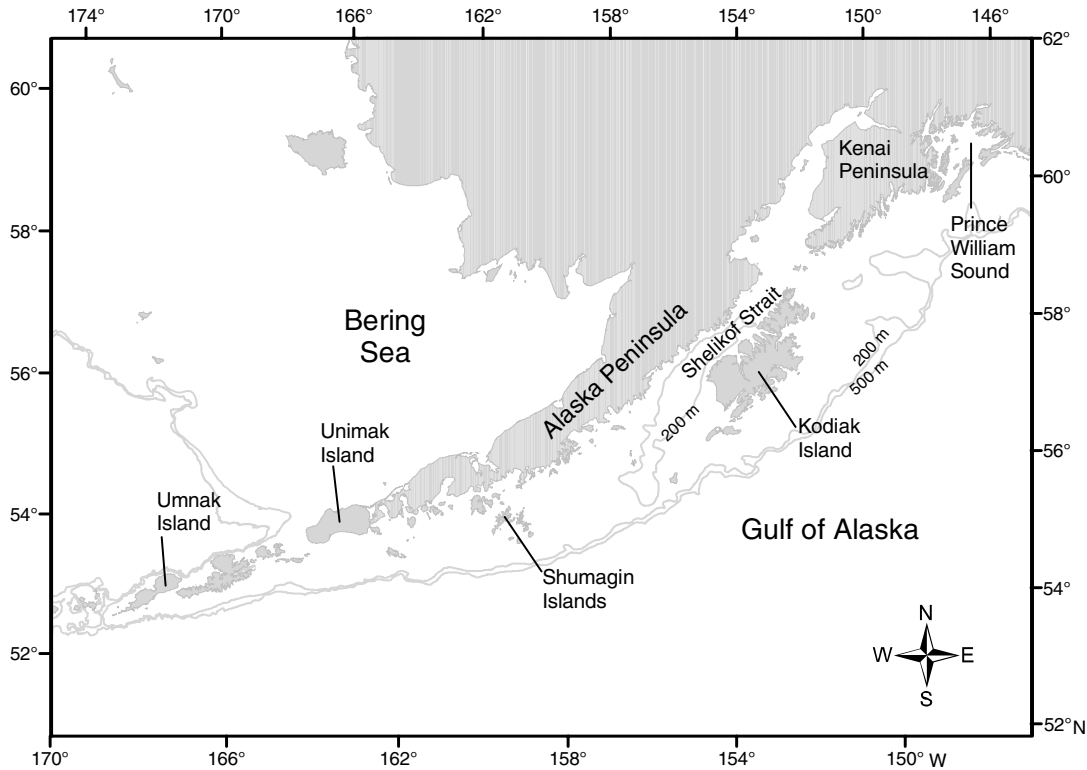


Figure 1

The western Gulf of Alaska where ichthyoplankton surveys were conducted in 1972 and from 1977 to 1999 by the Alaska Fisheries Science Center to examine the timing of spawning, geographic distribution and abundance, and vertical distribution of flathead sole (*Hippoglossoides elassodon*).

cesses that affect the drift of walleye pollock larvae may also affect the drift of flathead sole larvae in this area. For example, the drift of walleye pollock larvae in Shelikof Strait can be slowed if they become entrained in eddies that form there (Bailey et al., 1997). The Alaska Coastal Current flows southwest through Shelikof Strait and branches just south of it; one branch continues along the continental shelf, and the other heads seaward (Bailey et al., 1997). Whether larvae will stay near shore or move off shore is determined by one or other of these two branches of the current.

Information about the early life history of flathead sole in the Gulf of Alaska is lacking. Data from ichthyoplankton surveys conducted in the western Gulf of Alaska were used to examine the timing of spawning, geographic distribution and abundance, and the vertical distribution of flathead sole eggs and larvae. The purpose of this study was to give a general overview of flathead sole egg and larval distribution and abundance in the Gulf of Alaska during the calendar year.

Materials and methods

The study area covered the continental shelf (approximately 300 m depth and less) of the western Gulf of

Alaska from the Kenai Peninsula southwest along the Alaska Peninsula to Umnak Island (Fig. 1). Also covered was the east side of Kodiak Island out to the continental shelf break (Fig. 1). The Alaska Stream and the Alaska Coastal Current are two major surface currents that flow through the study area. Both currents flow southwesterly: the Alaska Stream along the shelf break and the Alaska Coastal Current through Shelikof Strait (Kendall et al., 1996).

A series of ichthyoplankton surveys were conducted in 1972 and from 1977 to 1999 (no data were collected in 1980) by the Alaska Fisheries Science Center (NOAA, NMFS) in the western Gulf of Alaska (Tables 1 and 2). Data were used from 75 surveys. Surveys were conducted from February to November; the most intensive sampling was in April and May. Not all months were sampled every year, and not all cruises surveyed the same area. A 60-cm diameter bongo sampler with a net mesh size of 333 or 505 μm was towed in a double oblique fashion (from the surface to near bottom and back to the surface) to collect samples used to examine the geographic distribution and abundance of eggs and larvae. Interannual variability in the abundance of eggs and larvae in the Shelikof Strait spawning area can vary as much as tenfold (S. Porter, unpubl. data), but to increase sampling coverage of the study area,

Table 1

The number of stations used each year to assess monthly flathead sole (*Hippoglossoides elassodon*) egg distribution in the western Gulf of Alaska.

Cruise year	Feb	Mar	Apr 1-15	Apr 16-30	May 1-15	May 16-31	Jun 1-15	Jun 16-30	Jul	Aug	Sep	Oct	Nov
1972	— ¹	—	—	27	40	—	—	—	—	—	—	—	—
1977	—	—	—	—	—	—	—	—	—	—	—	11	48
1978	—	23	61	2	—	—	—	69	20	—	57	67	118
1979	48	40	—	—	—	58	—	—	—	—	18	—	—
1981	—	190	61	123	16	136	—	—	—	—	—	—	—
1982	—	—	55	28	—	62	—	—	—	—	—	—	—
1983	—	—	—	—	1	67	—	—	—	—	—	—	—
1984	—	2	63	66	28	—	—	—	—	—	—	—	—
1985	—	109	87	28	62	135	54	—	—	—	—	—	—
1986	—	11	185	34	89	19	—	—	—	—	—	—	—
1987	—	—	177	83	—	59	—	15	4	—	—	—	—
1988	—	102	228	64	13	4	1	—	—	—	—	—	—
1989	—	—	128	69	132	47	1	—	—	—	—	—	—
1990	—	—	107	—	88	70	78	—	—	—	6	—	—
1991	—	—	90	150	119	97	—	—	—	—	—	—	—
1992	—	—	94	—	158	136	—	—	—	—	—	—	—
1993	—	—	96	—	141	90	24	—	—	—	—	—	—
1994	—	10	9	—	88	133	6	—	—	—	—	—	—
1995	1	5	—	—	—	98	—	—	—	—	—	—	—
1996	—	—	—	59	269	130	—	—	—	—	—	—	—
1997	—	—	—	—	—	100	—	—	—	—	—	—	—
1998	—	—	—	—	72	128	—	26	—	—	—	—	—
1999	—	—	—	—	2	233	83	—	—	—	—	—	—
Total	49	492	1436	733	1320	1803	247	110	24	0	81	78	166

¹ No stations.

years were pooled for each month. Abundance did not appear to affect the spatial distribution of eggs or larvae; their distribution patterns were similar no matter whether abundance was high or low. Months of highest abundance (April, May, and June) were divided into early to mid-month (days 1–15) and mid- to late month (days 16–31). The area covered by the cruises was divided into 50 × 50 km grid cells. Mean catch per cell was calculated for each grid cell, averaging over all stations falling within the cell. For the areas other than Shelikof Strait, the number of stations per cell ranged from 1 to 10. The most intensive sampling was conducted in the Shelikof Strait area, south to approximately 56°N latitude. Cells in this area, depending on the month, could have more than 100 stations within them. To examine larval drift, the center and ellipse (centroid) of egg and larval abundance for early and late May 1994 and 1996 (two years with different flow regimes in Shelikof Strait) were calculated according to the methods described in Kendall and Picquelle (1989).

The vertical distribution of eggs and larvae was examined from samples from four 1-m² MOCNESS (multiple-

opening-closing-net and environmental sensing system) tows. For each tow, 6 to 8 depth intervals were sampled from near the sea floor to near the surface. The samples were collected during peak spawning in 1991 (one tow during day light), 1993 (one tow during day light), and 1996 (two tows: 1996A conducted during the night, and 1996B during day light). Eggs collected in each depth interval were categorized as early (stages 1–12), middle (stages 13–15), and late stage (stages 16–21) according to walleye pollock egg stages adapted from Blood et al. (1994). The late stage was divided into two categories: late A (stages 16–19) and late stage B (stages 20–21), to indicate which eggs were closest to time of hatching. Taking into account shrinkage in standard length due to collection and preservation (Theilacker and Porter, 1995), larvae were divided into three size categories based on development. Larvae <5 mm were classified as recently hatched, larvae 5–6 mm as prefeeding or first feeding, and larvae >6 mm as feeding, based not only on size but also on the amount of yolk present, and whether prey were visible in their gut. These categories were based on observations of flathead sole larvae

Table 2

The number of stations used each year to assess monthly flathead sole (*Hippoglossoides elassodon*) larval distribution in the western Gulf of Alaska.

Cruise year	Apr 1–15	Apr 16–30	May 1–15	May 16–31	Jun 1–15	Jun 16–30	Jul	Aug	Sep	Oct	Nov
1972	— ¹	27	40	—	—	—	—	—	—	—	—
1977	—	—	—	—	—	—	—	—	—	11	48
1978	60	2	—	—	—	69	20	—	57	67	118
1979	—	—	—	58	—	—	—	—	18	—	—
1981	61	123	16	136	—	—	—	—	—	—	—
1982	55	28	—	62	—	—	—	—	—	—	—
1983	—	—	1	63	—	—	—	—	—	—	—
1984	63	66	28	—	—	—	—	—	—	—	—
1985	87	28	62	135	54	—	—	—	—	—	—
1986	185	34	89	19	—	—	—	—	—	—	—
1987	177	83	—	58	—	15	4	—	—	—	—
1988	227	64	13	2	1	—	—	—	—	—	—
1989	128	69	132	34	1	—	—	—	—	—	—
1990	107	—	90	70	78	—	—	—	6	—	—
1991	90	150	119	97	—	—	—	—	—	—	—
1992	94	—	158	136	—	—	—	—	—	—	—
1993	96	—	141	90	24	—	—	—	—	—	—
1994	4	—	89	133	6	—	—	—	—	—	—
1995	—	—	—	98	—	—	—	—	—	—	—
1996	—	59	273	130	—	—	—	—	—	—	—
1997	—	—	—	100	—	—	—	—	—	—	—
1998	—	—	72	128	—	26	—	—	—	—	—
1999	—	—	6	233	83	—	—	—	—	—	—
Total	1434	733	1329	1782	247	110	24	0	81	78	166

¹ No stations.

reared in the laboratory (S. Porter, unpubl. data). In the laboratory, flathead sole larvae hatch with pigmented eyes, three tail pigment bands, and an open mouth (S. Porter, unpubl. data). Flathead sole larvae that were collected from MOCNESS tows and that did not have these features were classified as embryos (it was suspected that handling during collection may have caused some of the late stage eggs to prematurely hatch), and their lengths were not included in the weighted mean depth. For eggs and larvae, a weighted mean depth was calculated for each stage or size category, and depths were compared by using ANOVA and the Tukey HSD multiple comparison test.

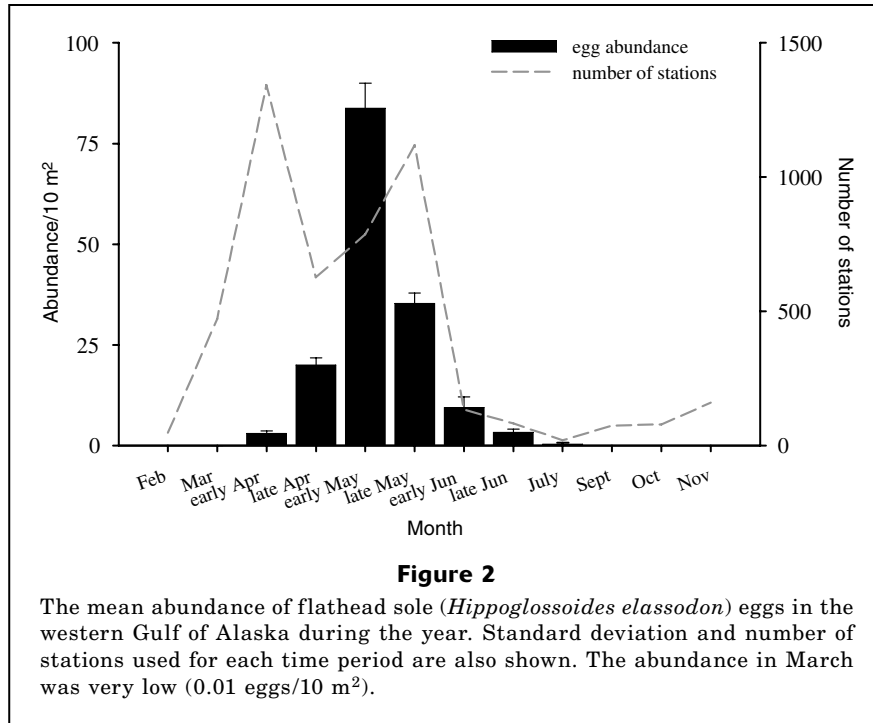
Results

Eggs

Geographic distribution and abundance Eggs were collected as early as March but in small numbers (Figs. 2 and 3A). Most spawning began from early to mid-April

(Fig. 3B) near the Kenai Peninsula and then progressed with time southwest into Shelikof Strait and along the Alaska Peninsula. There are two main areas where peak spawning (from early to mid-May) occurred: Shelikof Strait and between the Shumagin Islands and Unimak Island (Fig. 3C). In June, spawning generally declined in these areas and was most intense around Kodiak Island (3D). Eggs were collected as late as July (one station in 1978, on the eastern side of Kodiak Island).

Vertical distribution There were similar trends in the vertical distribution of eggs among tows (Fig. 4). Abundance peaked at about 20 to 35 m below the surface, decreased at greater depth, and then slightly increased below 125 m. Because the trend of the catches of the tows were similar, we were able to increase sample size in the depth intervals by pooling data from similar depth intervals for further analyses. Eggs were pelagic and most abundant near the surface (mean depth 43 ± 10 m) and at the deep sampling depths (mean depth 149 ± 6 m); abundance was low in mid-water (Fig. 4). Late-stage eggs (stages 16–21) dominated the depths of



high abundance. Early stage eggs were most abundant in mid-water; they accounted for 79% of the total number of eggs collected between 50 and 159 m depth. Sixty-six percent of all eggs collected above 66 m depth were middle- and late-stage A eggs. The largest numbers of late-stage B eggs were found below 124 m depth, where they accounted for 83% of all eggs collected. Mean egg stage depth showed that as the eggs developed from the early stages to the middle stages they rose toward the surface (mean depth of the eggs changed from 54 to 28 m); then in the later stages of development the eggs sank and hatched at depth. Late-stage B eggs were collected significantly deeper (mean depth 90 ± 37 m) than late-stage A eggs (mean depth 35 ± 7 m; ANOVA, $P=0.007$; Tukey HSD multiple comparison test, $P=0.006$).

Larvae

Geographic distribution and abundance Larvae were found from early April to October, but they were most abundant from mid-May to mid-June (Fig. 5). From mid- to late April, larvae were most abundant near the Kenai Peninsula (Fig. 6A), and as spring progressed their abundance increased southwest along the Alaska Peninsula (Fig. 6B). Peak abundance occurred during the first two weeks of June in the southern portion of Shelikof Strait (Fig. 6C). From mid- to late June larvae were most abundant on the east side of Kodiak Island (Fig. 6D). Although most of the surveys were conducted in this area, it is possible that larvae may have been abundant elsewhere in the study area during this time. From July through October, only the area east of Kodiak Island was surveyed, and larval abundance there was low.

Larval drift Satellite-tracked drifters released in May 1994 and drogued at 40 m indicated that the Alaska Coastal Current flow was strong and moving to the southwest—typical surface current flow for this area (Bailey⁴). In May 1996, drifters showed that flow was weak, disorganized and moving somewhat to the northeast (Bailey et al., 1999). In early May 1994, very few flathead sole larvae were collected; therefore the center point of the flathead sole egg distribution was used to infer the starting location of larval drift. Size-at-age data have shown that the growth rate for flathead sole larvae is 0.3 mm/day in Auke Bay, Alaska (Haldorson et al., 1989). Using this growth rate, we determined that larvae hatched in early May could have grown as much as 6 mm in the 21 days between surveys. The size class of larvae greater than 9 mm was assumed to include larvae that had hatched from the eggs present in early May. The location of the centers of distribution of the early May eggs and late May larvae indicated that the larvae had drifted southward over the continental shelf (Fig. 7). In 1996 all the larvae collected in early May were 7.1 mm and smaller (range 4.2 to 7.1 mm). The area was surveyed 26 days later, and growth of about 8 mm could have occurred between surveys. For larvae collected at the end of May, the size group longer than 12 mm was assumed to include the early May larval group. The location of the centers of distribution of the early May and late May larvae showed that the larvae were retained at nearly the same location (Fig. 8).

⁴ Bailey, K. M. 2002. Personal commun. NOAA, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

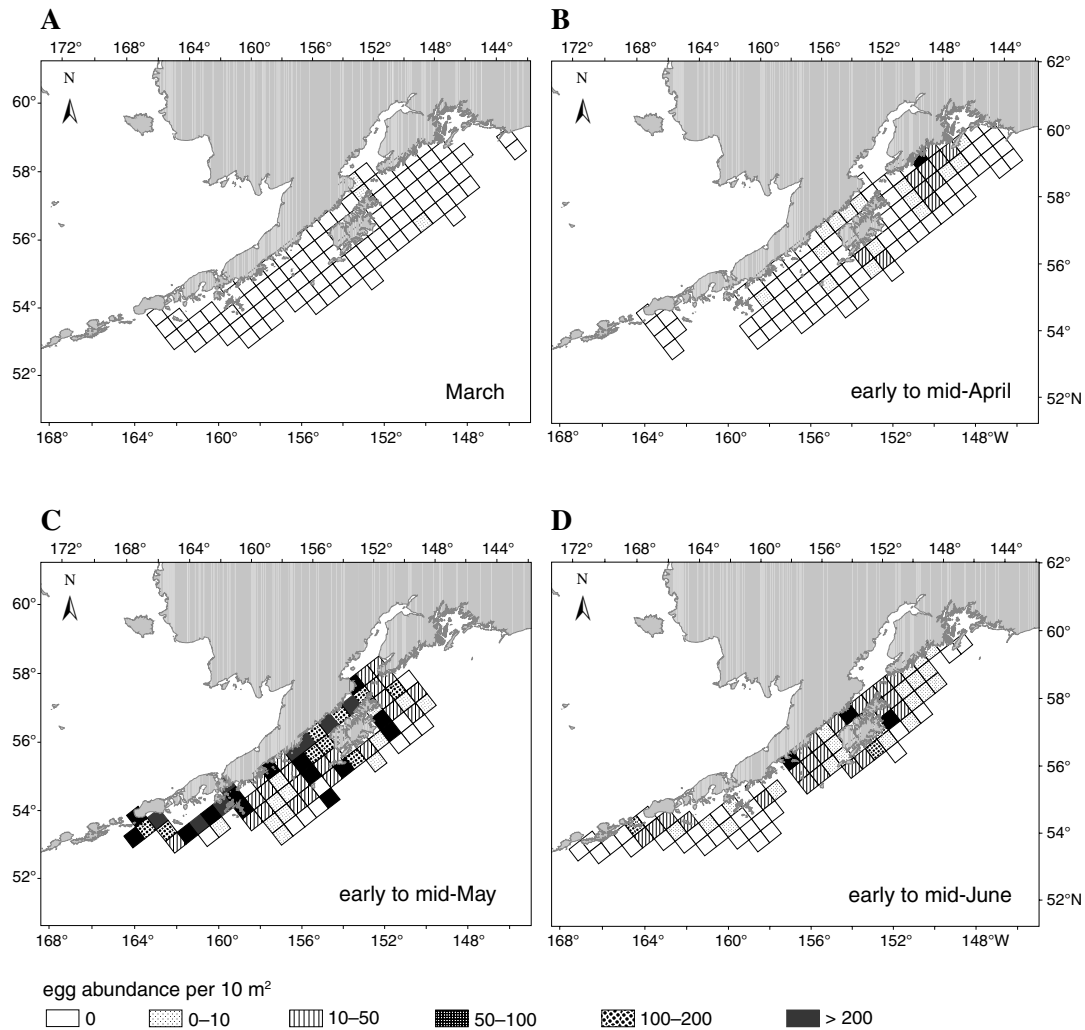


Figure 3

The geographic distribution of flathead sole (*H. elassodon*) eggs in the western Gulf of Alaska during the spawning season; (A) March, (B) early to mid-April, (C) early to mid-May, (D) early to mid-June.

Vertical distribution There were similar trends in the vertical distribution of larvae among tows (Fig. 9). Abundance peaked at about 15 to 30 m below the surface, then decreased, and larvae were collected from the deepest sampling depth interval from one tow (1996A; Fig. 9). Because the tows were alike, to increase sample size in the depth intervals, we pooled data from similar depth intervals but from different tows for further analyses. Larval abundance was highest near the surface and at the deepest depths sampled (Fig. 9). In Auke Bay, Alaska, flathead sole larvae migrated vertically at night no more than 15 m, ending at 20 m depth, and they were less aggregated (Haldorson et al., 1993). This depth was much shallower than the depth at which larvae and late-stage eggs were collected in tow 1996A (sampling depth interval was 174–236 m). Therefore the deep concentration of larvae in 1996 was probably due to eggs hatching rather than to vertical

migration. The deepest sample comprised embryos and larvae (the larvae, however, were too damaged to determine whether they were prefeeding or feeding larvae), and samples collected above 100 m were a mixture of embryos and prefeeding larvae (29%), and feeding larvae (71%). The smallest larvae (<5 mm) were found in deepest water (mean depth 166 ± 32 m), and larger larvae (≥ 5 mm) were found in shallower water (above about 60 m depth; ANOVA, $P < 0.001$; Tukey HSD multiple comparison test, $P < 0.001$). The size distribution of the larvae indicated that soon after hatching they rise to the surface to feed.

Discussion

Flathead sole inhabit the continental shelf of the North Pacific Ocean, and the area used for the present study

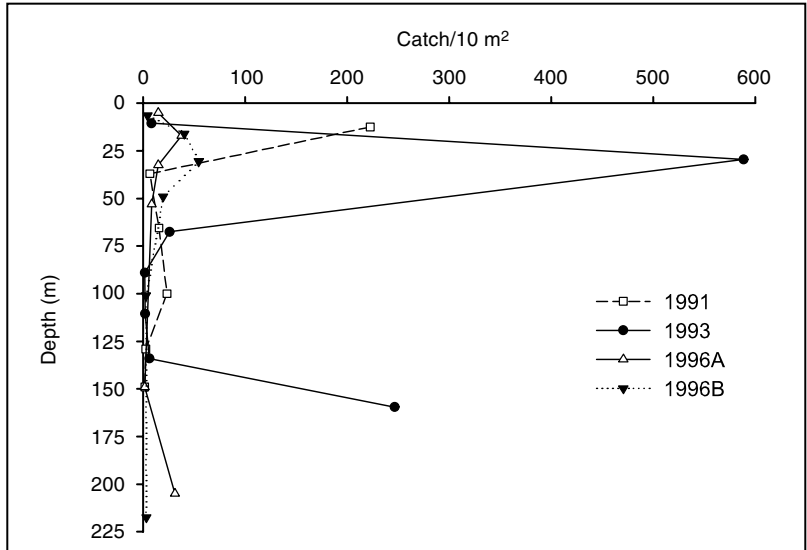


Figure 4

The vertical distribution of flathead sole (*H. elassodon*) eggs collected from four MOCNESS tows conducted in 1991, 1993, 1996 during peak spawning. Symbols indicate the mean of the depth interval that the samples were collected in.

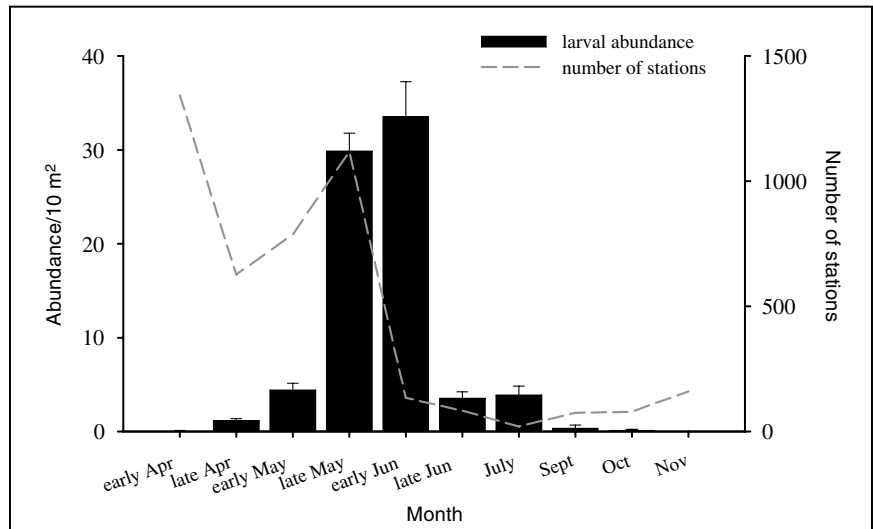


Figure 5

The mean abundance of flathead sole (*H. elassodon*) larvae in the western Gulf of Alaska during the year. Standard deviation and number of stations used for each time period are also shown. Abundance in early April and October was very low, 0.06 and 0.11 larvae/10 m², respectively.

contains the highest relative abundance of adult flathead sole off the west coast of North America (Wolotira et al.¹). Generally, outside the study area the abundance of adult flathead sole is low (Wolotira et al.¹); therefore these areas most likely had very little effect on the abundance of eggs and larvae collected from within the study area.

In the western Gulf of Alaska flathead sole spawn in three main areas during the spring: near the Kenai Peninsula, in Shelikof Strait, and in the area between the Shumagin Islands and Unimak Island. Spawning progresses in a southwesterly direction along the Alaska Peninsula. Flathead sole in spawning condition are abundant from March through May (Hirschberger and

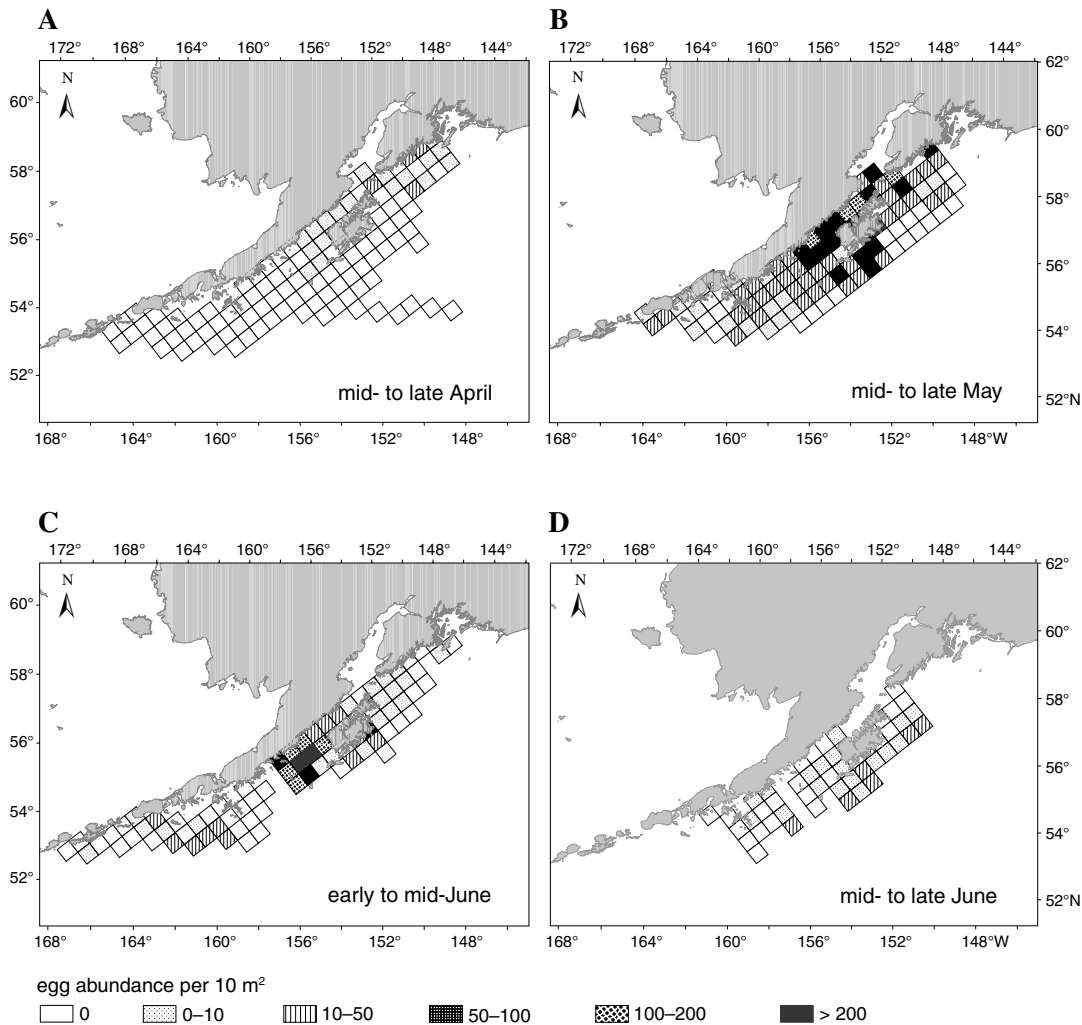


Figure 6

The geographic distribution of flathead sole (*H. elassodon*) larvae in the western Gulf of Alaska during months of the spawning season. (A) mid- to late April, (B) mid- to late May, (C) early to mid-June, (D) mid- to late June.

Smith²), which correlates with the period when eggs were collected in the present study. Peak spawning occurred from early to mid-May, and by the end of June spawning was nearing completion. Larval abundance peaked from early to mid-June in the southern portion of Shelikof Strait. In late July, late-stage flathead sole larvae were the most abundant of larval fish collected in the Gulf of Alaska between the Semidi Islands and Unimak Island (Brodeur et al., 1995). Flathead sole larvae have also been found on the east side of Kodiak Island during the summer (Kendall and Dunn, 1985).

Laboratory observations of the changes in density of flathead sole eggs during development are inconsistent. Results of one study showed that egg density decreased throughout development to hatching (Alderdice and Forrester, 1974). Another study found that up to 24 hours before hatching the eggs floated at the surface of

a container and then sank to the bottom and hatched (Miller, 1969), indicating that density had increased late in development. A field study of the vertical distribution of Atlantic halibut (*Hippoglossus hippoglossus*) eggs in Norwegian fjords showed that later stage eggs had a higher density (and were found deeper) than earlier egg stages (Haug et al., 1986). Results from the present study support the findings of Miller (1969), in that the density of flathead sole eggs in the present study appeared to increase near the time of hatching. For the larvae of both the arrowtooth flounder (*Atheresthes stomas*) and Pacific halibut (*Hippoglossus stenolepis*), small larvae were found deep and larger sizes migrated towards the surface (Bailey and Picquelle, 2002). In the present study, flathead sole larvae had a similar vertical distribution pattern indicating that after hatching in deep water they rise to near the surface to feed.

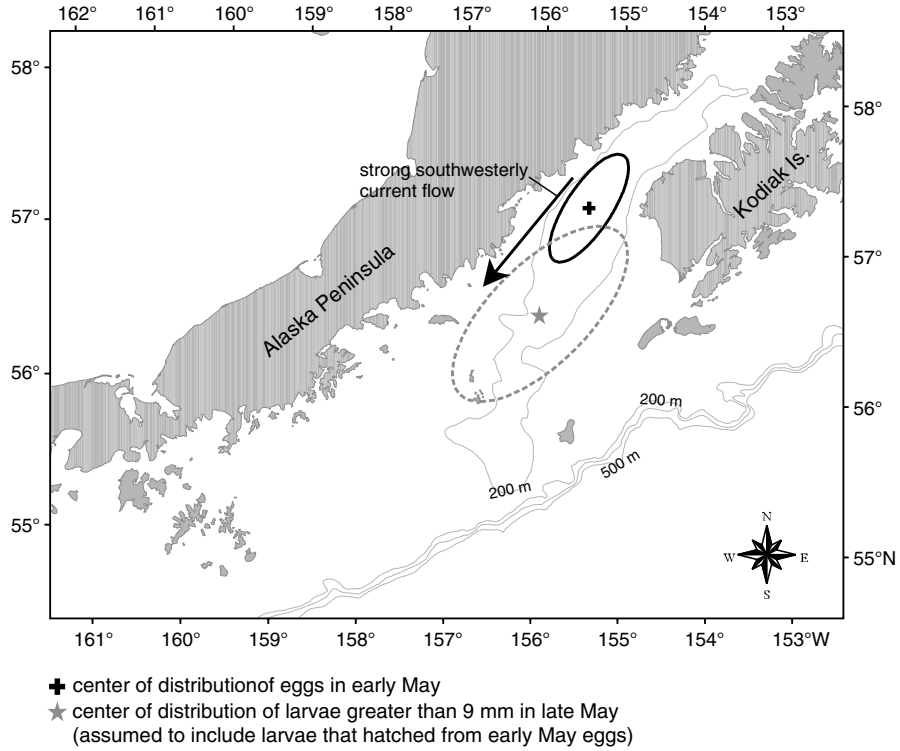


Figure 7

The drift of flathead sole (*H. elassodon*) larvae in Shelikof Strait during May 1994. Surface current flow was strong and southwesterly.

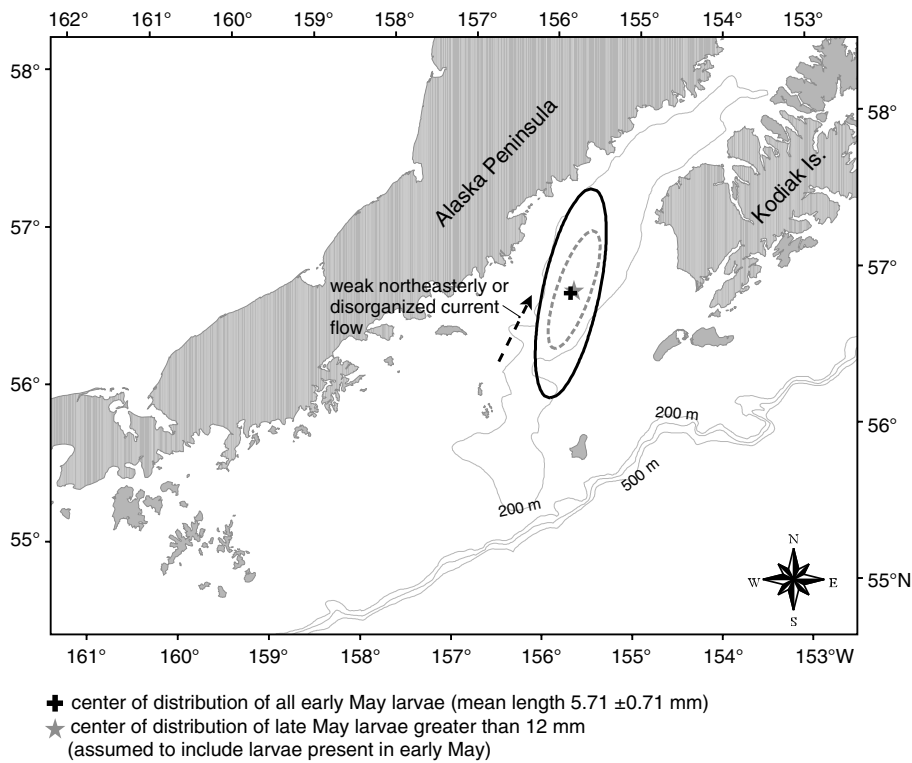
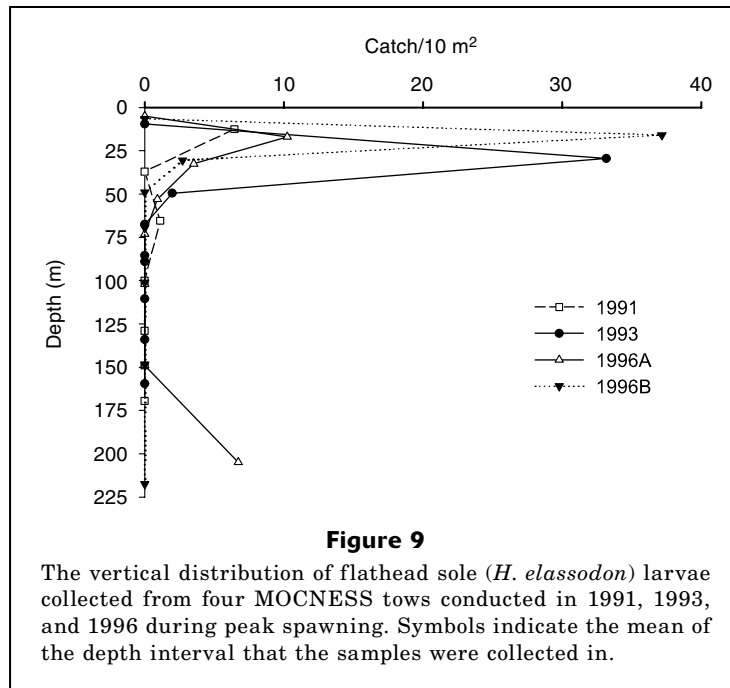


Figure 8

The drift of flathead sole (*H. elassodon*) larvae in Shelikof Strait during May 1996. Surface current flow was disorganized, or weak, and to the northeast.



Some species of flatfish spawn offshore (e.g., arrowtooth flounder and Pacific halibut, Bailey and Picquelle, 2002), but the present study has shown that flathead sole spawn on the continental shelf. Flathead sole nursery areas have been found to be in the bays of the Alaska Peninsula and Kodiak Island (Norcross et al., 1999), and it is crucial that the larvae remain on the shelf near their nursery areas. Changes in egg density may be a mechanism for retaining flathead sole larvae on the shelf. For arrowtooth flounder and Pacific halibut larvae in the western Gulf of Alaska, it has been suggested that deep water currents (100–400 m depth in sea valleys and in troughs in the continental shelf) transport these larvae from the offshore areas where they hatch to their nearshore nurseries (Bailey and Picquelle, 2002). By sinking when they are nearing hatching, flathead sole eggs that have drifted southwesterly (i.e. away from nursery areas) with the surface currents can be brought back (along with newly hatched larvae) toward inshore juvenile nursery areas. Alternatively, the act of sinking as they near hatching may be a way for newly hatched larvae to avoid predation by keeping them out of the surface waters where they are likely to encounter predators. The physical environmental conditions of Shelikof Strait may also serve to retain flathead sole larvae on the shelf. In May 1994 when the Alaska Coastal Current flow was strong and to the southwest, larvae drifted southward but remained on the continental shelf. In May 1996 when the flow was weak, disorganized, and moving somewhat to the northeast, the larvae remained at virtually the same location for the entire month because surface current flow in Shelikof Strait was weakened and reversed because of anomalous atmospheric con-

ditions. Under both flow regimes larvae remained on the continental shelf in southern Shelikof Strait. Eddies may also be an important retention mechanism for flathead sole larvae because entrainment in one of these could slow drift. Under typical conditions in Shelikof Strait (i.e., strong southwesterly current flow), eddies frequently occur and they drift slower than the water surrounding them (Kendall et al., 1996). They can also remain nearly stationary for two weeks (Schumacher et al., 1993). Both biological and environmental factors may work together to retain flathead sole larvae on the continental shelf and keep them near their nursery areas.

Acknowledgments

I would like to thank Debbie Blood and Angie Lind for determining developmental stages of flathead sole eggs, and Susan Picquelle for assistance with egg and larval distribution charts. Kevin Bailey and Jeff Napp provided helpful comments on an early draft of this manuscript. Two anonymous reviewers offered improvements. This research is contribution FOCI-0475 to NOAA's Fisheries-Oceanography Coordinated Investigations.

Literature cited

- Alderdice, D. F., and C. R. Forrester.
1974. Early development and distribution of the flathead sole (*Hippoglossoides elassodon*). *J. Fish. Res. Board Can.* 31:1899–1918.

- Bailey, K. M., N. A. Bond, and P. J. Stabeno.
1999. Anomalous transport of walleye pollock larvae linked to ocean and atmospheric patterns in May 1996. *Fish. Oceanogr.* 8:264–273.
- Bailey, K. M., and S. J. Picquelle.
2002. Larval distribution of offshore spawning flatfish in the Gulf of Alaska: potential transport pathways and enhanced onshore transport during ENSO events. *Mar. Ecol. Prog. Ser.* 236:205–217.
- Bailey, K. M., P. J. Stabeno, and D. A. Powers.
1997. The role of larval retention and transport features in mortality and potential gene flow of walleye pollock. *J. Fish Biol.* 51 (suppl. A):135–154.
- Blood, D. M., A. C. Matarese, and M. M. Yoklavich.
1994. Embryonic development of walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. *Fish. Bull.* 92:207–222.
- Brodeur, R. D., M. S. Busby, and M. T. Wilson.
1995. Summer distribution of early life stages of walleye pollock, *Theragra chalcogramma*, and associated species in the western Gulf of Alaska. *Fish. Bull.* 93:603–618.
- Haldorson, L., A. J. Paul, D. Serritt, and J. Watts.
1989. Annual and seasonal variation in growth of larval walleye pollock and flathead sole in a southeastern Alaska bay. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer* 191:220–225.
- Haldorson, L., M. Prichett, A. J. Paul, and D. Ziemann.
1993. Vertical distribution and migration of fish larvae in a northeastern Pacific bay. *Mar. Ecol. Prog. Ser.* 101:67–80.
- Haug, T., E. Kjørsvik, and P. Solemdal.
1986. Influence of some physical and biological factors on the density and vertical distribution of Atlantic halibut *Hippoglossus hippoglossus* eggs. *Mar. Ecol. Prog. Ser.* 33:207–216.
- Kendall, A. W., Jr., and J. R. Dunn.
1985. Ichthyoplankton of the continental shelf near Kodiak Island Alaska. NOAA Tech. Rep. NMFS 20, 89 p.
- Kendall, A. W., Jr., and S. J. Picquelle.
1989. Egg and larval distributions of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. *Fish. Bull.* 88:133–154.
- Kendall, A. W., Jr., J. D. Schumacher, and S. Kim.
1996. Walleye pollock recruitment in Shelikof Strait: applied fisheries oceanography. *Fish. Oceanogr.* 5 (suppl. 1):4–18.
- Matarese, A. C., A. W. Kendall Jr., D. M. Blood, and B. M. Vinter.
1989. Laboratory guide to early life history stages of northeast Pacific fishes. NOAA Tech. Rep. NMFS 80, 652 p.
- Miller, B. S.
1969. Life history observations on normal and tumor-bearing flathead sole in East Sound, Orcas Island (Washington). Ph.D. diss., 131 p. Univ. Washington, Seattle, WA.
- Norcross, B. L., A. Blanchard, and B. A. Holladay.
1999. Comparison of models for defining nearshore flatfish nursery areas in Alaskan waters. *Fish. Oceanogr.* 8:50–67.
- Rose, C. S.
1982. A study of the distribution and growth of flathead sole (*Hippoglossoides elassodon*). M.S. thesis, 59 p. Univ. Washington, Seattle, WA.
- Schumacher, J. D., P. J. Stabeno, and S. J. Bograd.
1993. Characteristics of an eddy over a continental shelf: Shelikof Strait, Alaska. *J. Geophys. Res.* 98: 8395–8404.
- Theilacker, G. H., and S. M. Porter.
1995. Condition of larval walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska assessed with histological and shrinkage indices. *Fish. Bull.* 93:333–344.
- Watts, J. D.
1988. Diet and growth of first-year flathead sole (*Hippoglossoides elassodon*) in Auke Bay, Alaska. M.S. thesis, 80 p. Univ. Alaska, Juneau, AK.