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Early life ecology of Alaska plaice (*Pleuronectes quadrituberculatus*) in the eastern Bering Sea: Seasonality, distribution, and dispersal

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ABSTRACT

We examined the patterns of abundance and distribution of Alaska plaice, *Pleuronectes quadrituberculatus*, eggs, larvae and pelagic juveniles over the southeastern Bering Sea shelf to better understand factors controlling transport and recruitment of flatfish in the Bering Sea. Ichthyoplankton data were derived from plankton surveys conducted in 1997, 1999, 2002, 2003, and 2005. Temperature, salinity, depth, and abundance of micro-zooplankton were measured concurrently. Eggs and larvae were primarily collected from depths <200 m, with the majority occurring over bottom depths ranging 50–100 m. Eggs were present throughout the water column, though densities of preflexion stage larvae were concentrated at depths 10–20 m. There was no evidence of vertical migration for pre-flexion stages. Spawning in Alaska plaice occurs primarily east of Port Moller in April and May, and eggs and larvae appear to drift to the north and northeast, an observation based on satellite-tracked drifter information, model output, and collections of older, later-stage postlarvae. Connectivity between spawning areas and nursery habitats is likely influenced by wind forcing, so climate-mediated changes to dispersal trajectory or timing is expected to have significant impacts on recruitment in this species, though entrainment in consistent, directional currents may modify these effects.

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1. Introduction

Directed movement of eggs and larvae through dispersal routes that are spatially and temporally consistent is critical for benthic organisms with free-floating planktonic stages. Ichthyoplankton must either be advected toward appropriate habitat, or retained if spawning occurs in areas that also provide suitable juvenile nursery habitat (Bailey et al., 2005). The pelagic environment is dynamic and changing, and natural variations can influence the dispersal process, either by affecting the rate, timing, location, or extent of distribution (Able and Grothules, 2007). Factors that mitigate exacerbating effects increase the likelihood of successful recruitment and, potentially, population stability. Adaptations across all life history stages modulate the effects of natural variations, and include behavioral actions by adults (selective spawning in areas with significant likelihood of transport success; Bailey et al., 2008), physiological properties of eggs (buoyancy; Kendall and Kim, 1989; Kendall et al., 1994), and behavioral capabilities of larvae (selective vertical migration; Gibson, 2003), and juveniles (discriminating swimming behavior; reviewed by Leis, 2006; active habitat selection; Sponaugle and Cowen, 1996). Poorly developed, weakly swimming larvae risk deportation by unfavorable currents, but many possess the ability to affect macro-scale changes in their horizontal distribution by managing micro-scale changes to their vertical distribution (Leis, 2006).

Previous work has shown that decadal-scale variability in wind-forcing events in the eastern Bering Sea (BS) affects flatfish production by influencing dispersal routes of settling larvae (Wilderbuer et al., 2002), presumably by transporting larvae toward or away from suitable juvenile habitat. The water column along the coastal shelf (<50 m) is mixed by tidal and wind energies, but there is evidence of weak stratification and differential depth-specific current trajectories over the middle and inner shelves (Lanksbury et al., 2007). The middle shelf supports a two-layer system that is thermally stratified in spring and summer, with a wind-mixed upper layer and a tidally mixed bottom layer. Flow is strongly tidal (~20 cm s^{-1}), and there is an organized low-frequency flow that varies annually, with weak (~1 cm s^{-1}) northward flow in the winter and weak (<1 cm s^{-1}) southward flow in the summer (Stabeno et al., 2007). There is also a northward flow along the 50 m isobath (~2 cm s^{-1}) and a stronger northward flow along the 100 m isobath (5–7 cm s^{-1}). There is a vertical shear to flow over shelf, with the upper 10–15 m influenced by wind. Near-bottom flows tend to be weaker and less influenced by storms. Distribution of larvae below layers that are significantly wind-influenced can moderate the impacts of stochastic, dispersive wind events and increase the potential for directed recruitment to suitable nursery habitat.

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Table 1
Cruises, dates, and number of stations sampled.

Cruise	Dates	Neuston	Bongo	MOCNESS
4WE97	June 30–July 14	0	64	0
1GP99	July 12–July 26	0	60	0
3MF02	May 12–May 21	81	81	0
4MF03	May 17–May 24	62	62	1 (diel)
5MF05	May 9–May 20	94	74	21

Alaska plaice (*Pleuronectes quadrituberculatus*) is a shallow-water flatfish (Pleuronectidae) that occurs over the Bering Sea continental shelf (Pertseva-Ostromouva, 1961; Zhang et al., 1998) and sustains a marginal population in the Gulf of Alaska (Bailey et al., 2003). It is not known whether these represent a single stock, but the biomass of the Gulf of Alaska population seems much more variable than that in Bering Sea, perhaps due to extent of suitable nursery habitat (Iles and Beverton, 2000). Alaska plaice spawn over the middle shelf in spring, and pelagic eggs and larvae drift toward nursery areas located inshore of spawning grounds (Bailey et al., 2003). Juvenile nursery habitat has been characterized as areas of shallow (<50 m) sand and mud substratum, and juveniles recruit to the benthos through the summer and early autumn. Because Alaska plaice early life stages are pelagic, the species may be highly vulnerable to episodic environmental variations such as wind events, storms, and climate-induced changes in hydrography, particularly if stages are constrained to the upper, wind-influenced water column. Goals of the present study were to: 1) seasonally characterize the horizontal and vertical distribution of Alaska plaice eggs, larvae, and post larvae over the eastern BS shelf (spring, summer), 2) determine the timing and horizontal extent of dispersal of early life stages of this species, and 3) determine which biotic and abiotic variables influence egg and larval distributions.

2. Methods

2.1. Field data collection

Data on Alaska plaice eggs and larvae were obtained from five fisheries research cruises conducted in the eastern BS (Table 1). Cruises were selected for examination on the basis of either high incidence of egg and/or larval catch, or seasonality of occurrence. Cruises occurred from: June 30–July 14, 1997, July 12–July 26, 1999, May 12–May 21, 2002, May 17–May 24, 2003, and May 9–May 20, 2005 (Fig. 1). During the May cruises, the sampling grid was extended progressively eastward each year to maximize the likelihood of collecting Alaska plaice larvae. For all cruises, quantitative oblique (depth-integrated) samples were collected using 60 cm bongo nets (either 333 or 505 µm mesh), towed obliquely from 10 m off-bottom to the surface (300 m maximum depth). Previous work determined that Alaska plaice larval abundance and sizes collected were not significantly different between the two mesh sizes (personal observation). Data from these tows were used to examine geographic distribution, as well as seasonal and interannual variabilities in abundance. The speed of the ship (1.5–2.0 kts) was monitored and adjusted throughout the tow to maintain a wire angle of 45°. A Sea-Bird SBE 19[1] profiler was attached in-line between the wire terminus and the bongo array to collect real-time salinity, temperature, and pressure information from the towed net path. Sampling occurred 24-hours a day.

Surface (neuston) and depth-discrete sampling for ichthyoplankton also occurred on the three May cruises (2002, 2003, 2005). Data from these tows were used to evaluate patterns in vertical abundance and size structure. Neuston tows were conducted at virtually all stations where bongo sampling was conducted, using a Sameoto neuston array with 505 µm mesh (Sameoto and Jaroszynski, 1969; Jump et al., 2008). Depth-discrete sampling used a 1 m^2 multiple opening and closing net and environmental sampling system (MOCNESS; Wiebe et al., 1976) with 505 µm mesh nets at selected locations (Fig. 1). Depth intervals were: 0–10 m, 10–20 m, 20–30 m, 30–40 m, 40–50 m, and >60 m.

All biological material was fixed in 5% formalin. Ichthyoplankton samples were sorted, identified to the lowest possible taxon, measured (mm SL), and enumerated at the Plankton Sorting and Identification Center in Szczecin, Poland. Larval fish identifications were verified at the Alaska Fisheries Science Center in Seattle, WA.

2.2. Physical environment

Sea-Bird SBE 19 profiles (data not available for 1997) from oblique bongo tow activities were generated, and depth-integrated temperature and salinity contours were created to describe water column conditions. Data were mapped using ArcGIS software and interpolated using an Inverse-Distance-Weighted approach to visualize and identify water signatures.

Sensors on the MOCNESS frame collected temperature and salinity information over the vertical towed path. In addition, prior to each MOCNESS tow, salinity and temperature profiles were collected at the same depth strata as above using a conductivity, temperature and depth (CTD) profiler. In 2003, Niskin bottles were attached to the CTD rosette to collect associated microzooplankton to evaluate the potential prey field for Alaska plaice larvae at each discrete depth. Temperature and salinity profiles taken from either MOCNESS sensors or from corresponding CTD casts were examined and compared with larval abundance and length data from MOCNESS sampling using a mixed model ANOVA (Sokal and Rohlf, 1995) with time or station as random factors. When differences were found, a Tukey pairwise multiple comparison test was used to test which depth bins were different.

Temperature data from two year-long, taut-wire moorings deployed along the Alaska Peninsula were also examined. The first mooring was located at (56.50 °N, 161.00 °W) at a water depth of 23 m, and the second was located at (56.42 °N, 160.22 °W) at a water depth of 62 m (Fig. 2). Temperature was sampled hourly. The two moorings straddled the 50 m isobath, and provided information on seasonal differences in temperature between inshore and offshore. Temperature data were low-pass filtered with a cosine-squared, tapered Lanczos filter (half amplitude 35 h, half power 42 h) to remove high frequency currents, particularly the tidal currents. The time series was then re-sampled at 6-h increments. Current meters were not deployed on the moorings.

Dispersal of larvae from hypothesized spawning areas to potential settlement habitat was evaluated by examining trajectories from "holey-sock" satellite-tracked drifters. Drifters were drogued at either 40 m (below the mixed layer) or at 16 m (within the mixed layer). Mixed layer depth over the shelf was approximately 20 m in all years. Sixteen trajectories were deemed appropriate for examination, based upon the previously established criteria that they: 1) were released in a geographic area of interest, 2) were released in the appropriate season, and 3) did not prematurely run aground. Thirteen of these drifters were drogued at 40 m and three were drogued at 16 m. There were approximately 15 position fixes per day.

2.3. Eggs and larvae distributions

2.3.1. Horizontal

Depth-integrated patterns of distribution and abundance of Alaska plaice eggs and larvae collected were mapped using ESRI ArcMap 9.2. Geographic coverage of the sampling grids was spatio-temporally varied (see Fig. 1), so it was inappropriate to statistically compare interannual abundances. However, the three May cruises (2002, 2003, 2005) were conducted at virtually the same time of year, and much of

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[1] Use of trade names does not imply endorsement by the National Marine Fisheries Service/NOAA.

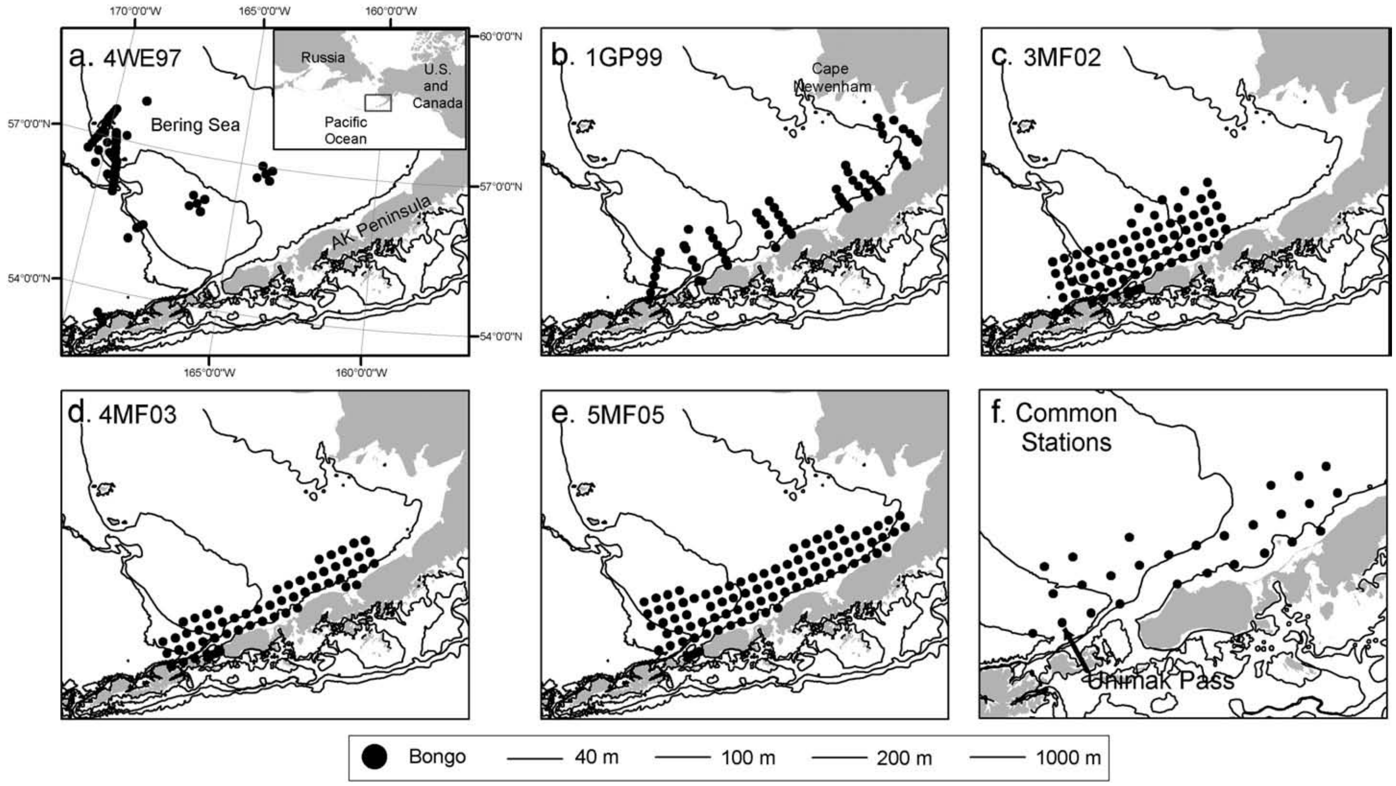

Fig. 1. Bongo sample collection by year (a–e). Stations common to all cruises (f).

the grids were overlapping, so an examination of interannual variations in larval abundance in these years was possible. A subset of 27 stations occupied in all 3 years were examined, and variations in abundance was evaluated (Fig. 1). Nonparametric approaches were used due to the high incidence of zero counts. A Wilcoxon signed ranks test was used to determine whether there were differences in abundance within the core grid of stations.

To look at relationships with temperature, salinity, and bottom depth, Spearman rank correlations were calculated on larval catch per unit effort, catch-weighted mean length, temperature, salinity, and bottom depth. Spring cruises were the only ones deemed to have sufficient sampling to warrant statistical examination. Variations in abundance on other cruises were examined qualitatively. Also, to determine whether there were differences in Alaska plaice larval abundance along the Alaska Peninsula, we pooled all data from the series of spring cruises and regressed the 4th root transformed larval CPUE onto longitude. Data were slightly non-normal, so a Spearman rank correlation coefficient between larval catch and longitude was also computed.

2.3.2. Vertical

Differences in vertical distribution of eggs and larvae were examined using three approaches. First, catches between neuston (surface) and bongo (oblique) tows were compared to determine whether catches were relatively higher in the surface waters or in the water column. Differences in standardized larval catch (4th root transformed) between neuston and bongo tows were examined at stations where both tows were conducted. Then, because catches were highly skewed due to the presence of many zero counts, data were converted to presence/absence for statistical analyses. Multiple approaches were used to compare the data between the two gears including Wilcoxon signed ranks test, Pearson chi-square, likelihood ratio chi square, Yates corrected cChi-square, and Fisher exact test.

Second, vertical patterns in egg and larval abundance, as well as larval length (mean weighted by CPUE), were evaluated using data collected from diel, depth-discrete MOCNESS tows. A fourth root transform was used to help normalize the CPUE data for larvae and eggs from two cruises. The normalized catch-weighted mean larval lengths were normally distributed and did not need to be transformed. A mixed model nested ANOVA was used to test for diel/depth interaction effects. Measurements of physical variables at each depth, including temperature, salinity, and microzooplankton (for larvae), were added to the model one at a time as covariates to determine their importance. Spearman correlation coefficients were computed on CPUE, depth, and all covariates. In addition, catch data were classified as above or below the thermocline and depth nested within thermocline was also tested. This same analysis was also performed using normalized catch-weighted mean larval length.

Finally, to determine whether there were unique depth-discrete patterns of vertical distribution in differing water masses, vertical egg and larval distribution data were examined and compared among 3 geographic strata that had been assigned *a priori*. Strata A was comprised of tows along the 100 m isobath, Strata B comprised tows between the 100 m and 50 m isobaths, and Strata C comprised tows along the 50 m isobath (Fig. 2). These *a priori* designations were based on bathymetric features that support flows with unique water mass signatures (Stabeno et al., 2002; Kachel et al., 2002).

2.4. Larval size

Length frequency histograms were created to evaluate larval size distributions within each cruise. Geographic differences in larval size were also examined. Confounding effects of growth during the sampling period were controlled by standardizing larval sizes to a predicted size on a single date during each cruise using a growth rate of 0.15 mm d^{-1} based on published information for European plaice (Ryland, 1966; Ehrlich et al., 1976; Hovenkamp, 1992; Kennedy et al., 2007). For the May series of cruises, sizes were standardized to 17 May, a date common to all three spring cruises. Other cruises were standardized to predicted larval size on 19 July.

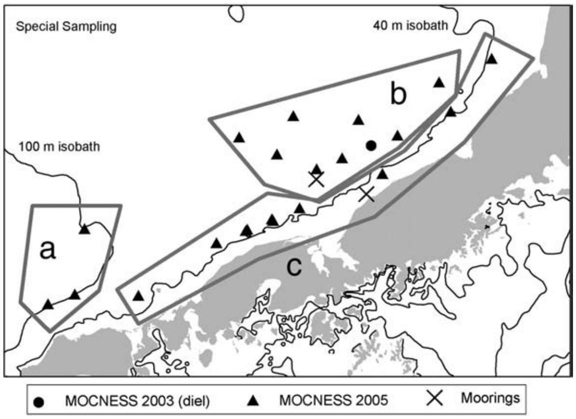

Fig. 2. Special sampling: areas where MOCNESS sampling was conducted (2004, 2005) and locations of 2 subsurface moorings deployed by the NOAA/Pacific Marine Environmental Laboratory (PMEL) to collect seasonal temperature and salinity information. Binned geographic areas of MOCNESS sampling in 2005.

2.5. Seasonal analyses

Historical collections of Alaska plaice eggs and larvae made by the Eco FOCI program in the Bering Sea were examined (1988–2005) to elucidate seasonal patterns in abundance. Historical distributional data were not evaluated since they are available elsewhere (Bailey et al., 2003). Quantitative collections were made with bongo net gear (333 or 505 µm mesh), towed obliquely from bottom to surface. Abundances of eggs and larvae were binned into 2-week intervals to visualize seasonal presence in the water column. Estimates of time of spawning, and duration of the egg and larval stages were made.

2.6. Surface model

An ocean current simulation model (OSCURS) was used to evaluate the potential for egg and larval drift with wind-influenced surface currents in each year of study (Ingraham and Miyahara, 1988). The OSCURS model computes ocean surface drift from daily sea level pressure fields over the Bering Sea, and total flow is calculated as the vector sum of baroclinic and geostrophic flow, and surface wind drift. This model has been used previously to model the dispersal of flatfish early life history stages in the eastern BS (Wilderbuer et al., 2002). Particles were initialized at a single point, 56.3° N 161° W on April 1, which corresponds with the observed center of distribution of Alaska plaice eggs in spring. Simulated drifts were run until August 1, a time interval that spanned the seasonal appearance and disappearance of eggs and larvae from the water column.

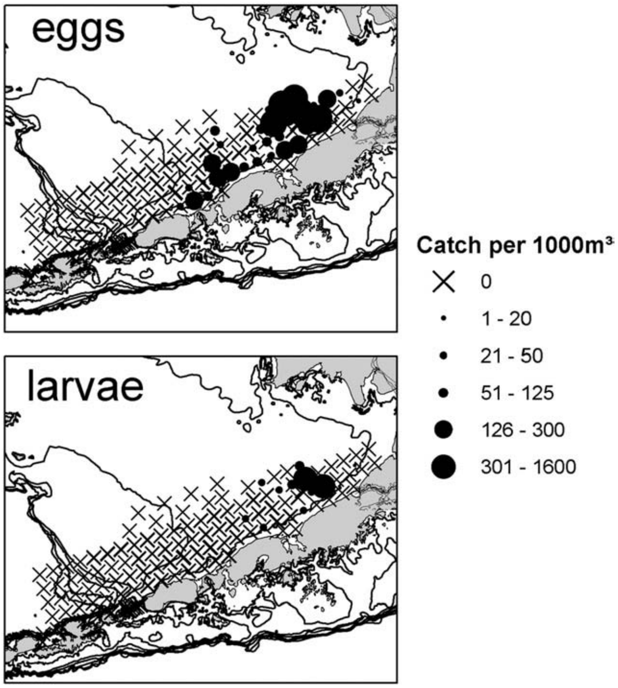

Fig. 3. Catches of Alaska plaice eggs (top) and larvae (bottom) in surface neuston tows in the Eastern Bering Sea.

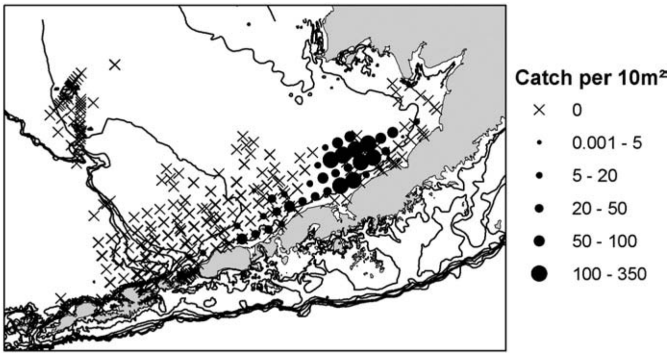

Fig. 4. Catches of Alaska plaice eggs in oblique bongo tows in the Eastern Bering Sea.

3. Results

3.1. Egg and larval distributions

3.1.1. Horizontal

In May, Alaska plaice eggs were collected from both bongo and neuston tows (Figs. 3, 4), with comparatively higher catches ($p = 0.047$) occurring in 2005 than in other years (2002, 2003). Bongo nets consistently collected more larvae (Fig. 5) than neuston nets ($p < 0.001$). Catches of eggs were not significantly different between bongo and neuston nets in 2002 or 2005, but significant differences were detected in 2003 ($p < 0.05$), with greater catches in the oblique bongo gear than in the surface neuston gear. Eggs were not collected in summer sampling indicating that spawning is complete by late spring.

Spring catches of Alaska plaice larvae were significantly lower in the neuston compared to bongo tows in 2003 ($p < 0.001$) and 2005 ($p < 0.001$). Interannual differences in larval abundance in May (2002, 2003, 2005) evaluated at core stations showed that larval abundance was significantly greater in 2005 than in 2003, but caution should be used when interpreting this result due to the high incidence of zero catch within the grid stations. The regression on longitude indicated a significant relationship ($p < 0.001$) between longitude and larval

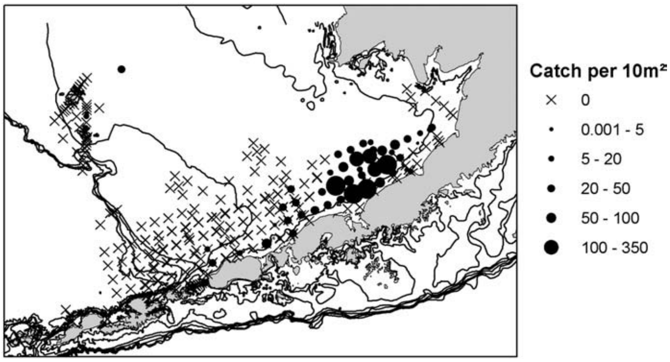

Fig. 5. Catches of Alaska plaice larvae in oblique bongo tows in the Eastern Bering Sea.

Table 2
Mean (±standard error) vertical distribution of Alaska plaice eggs collected from MOCNESS tows in 2003 and 2005.

Cruise	Depth interval	Catch 10 m^{-2} (±standard deviation)
4MF03	0–10 m	3.24 (3.83)
	10–20 m	5.67 (9.56)
	20–30 m	17.61 (6.73)
	30–40 m	10.64 (4.84)
	40–50 m	13.29 (6.48)
	50–60 m	NA
	Below 60 m	NA
5MF05	0–10 m	32.31 (14.73)
	10–20 m	17.32 (6.21)
	20–30 m	8.75 (3.39)
	30–40 m	7.87 (3.41)
	40–50 m	3.54 (1.26)
	50–60 m	1.58 (0.48)
	Below 60 m	0

catch, with more larvae occurring to the east. Catches of larvae from summer cruises (July) were along the eastern peninsula and in the immediate vicinity of the Pribilof Islands (Fig. 5).

3.1.2. Vertical

Vertical distributions of Alaska plaice eggs were dissimilar between 2003 and 2005, though results were not significant (Table 2). In 2005, abundances of eggs collected 0–10 m and 10–20 m were statistically similar to one another, and significantly higher than abundances collected from below 20 m depth. Most of the variability in the data for eggs was explained by depth, and there was no significant relationship with temperature or salinity, though it should be noted that temperature, salinity and depth are all correlated, and the relationship with depth may mask effects of temperature and salinity.

Distributions of larvae showed consistent significant depth-specific patterns (Fig. 6). In 2003 and 2005, larvae occurred between 0–20 m depth, with few larvae deeper than 30 m ($p<0.001$). The relationship of larvae with the thermocline was significant ($p<0.001$), and larvae occurred within the thermally mixed layer. Larval distribution was not related to microzooplankton availability, and larvae did not appear to exhibit diel patterns of vertical movement. Geographic distribution of larvae (2005) appeared to be related to water mass, with few larvae collected along the 100 m isobath, and greater numbers collected along the 50 m isobath. However, in all water masses, larvae appeared concentrated 0–20 m depth. Variations in vertical larval abundance were significantly related to temperature but not to diel periodicity, bottom depth, salinity, or availability of microzooplankton.

Table 3
Mean size of Alaska plaice larvae by cruise.

Cruise	Mean size (mm SL)	Standard deviation
4WE97	8.73	0.73
1GP99	8.10	0.81
3MF02	4.99	0.25
4MF03	6.14	1.1
5MF05	6.1	0.49

3.2. Larval size data

Sizes of larvae ranged from 2.5–9.8 mm SL. In spring collections, mean larval size was 5.5 mm SL, and there were no significant differences in size among the 3 spring cruises (Table 3, Fig. 7). There appeared to be distinct size structure within certain geographic areas. In May, larger larvae were collected in Unimak Pass and around Unimak Island compared along the Alaska Peninsula (Fig. 8). Unfortunately, due to a preponderance of zero counts, the data were not sufficiently robust to permit statistical examination of size breaks. However, there is a visual trend toward larger larvae in the Unimak vicinity in spring. Summer-collected larvae were the largest (7–10 mm SL) and were found to the east in the Bristol Bay area and to the north in the Pribilof Islands area, indicating dispersal to those two regions.

Variability in larval size distribution with depth was better explained by thermocline ($p=0.002$) than by depth, with smaller larvae collected below the thermocline.

3.3. Physical environment

Temperature and salinity data from concurrent bongo tows were plotted and mapped (Figs. 9, 10). Cooler, high-salinity water intruded from the slope basin up onto the continental shelf, and catches of larval Alaska plaice in this water mass were low. Warmer, fresher water was observed along the Alaska Peninsula, coincident with higher catches of plaice eggs and larvae. The presence of a distinct water mass along the 50 m isobath extending from approximately Unimak Island toward Bristol Bay was determined during all May cruises. Also, a distinct thermocline was observed in all years, at approximately 20–25 m depth (not shown). Mooring data (Fig. 11) indicated seasonal patterns of warming and cooling of the bottom water at both mooring sites. Higher rates of change and more extreme temperatures were observed at the shallow mooring (23 m). At the deeper site (62 m), there was a two-layer structure during the summer months. As expected, the warmest temperatures were observed in 2005 (average temperature in May, 4.7 °C, 23 m mooring; 3.5 °C 62 m mooring, respectively) and coolest were observed in 1999

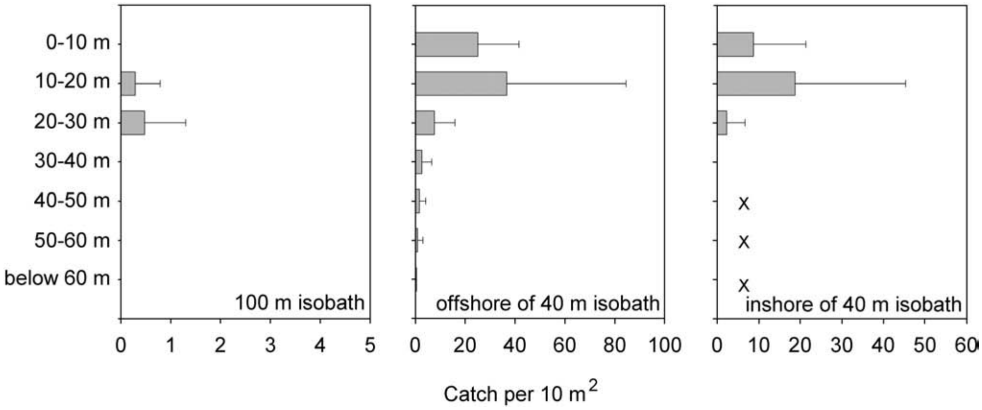

Fig. 6. Vertical distribution of Alaska plaice larvae collected from MOCNESS tows in 2005 binned by geographic area (see Fig. 2). Xs indicate that no tow was conducted at that depth. Note differing scale on the abscissa.

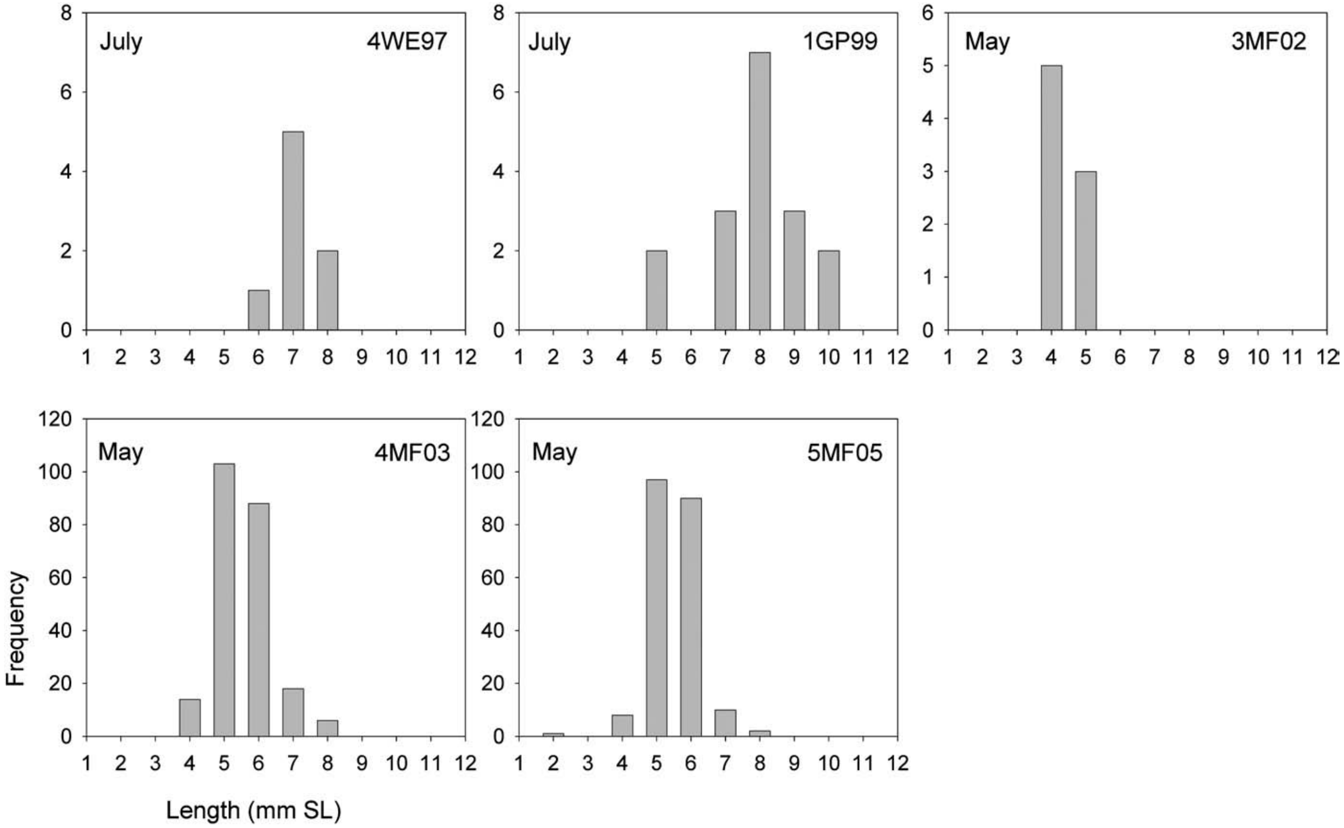

Fig. 7. Length-frequency histograms of larval size (mm SL) by cruise.

(average temperature in May, 1.6 °C, 23 m mooring; −0.3 °C, 62 m mooring, respectively).

Satellite-tracked drifters (Fig. 12) confirm previous observations (Lanksbury et al., 2007) of water movement in two principal directions: along the Alaska Peninsula (50 m isobath) and northward in the direction of the Pribilof Islands. Drifters drogued at 40 m and 16 m demonstrated this pattern of bifurcation, suggesting that these two pathways may be important dispersal routes.

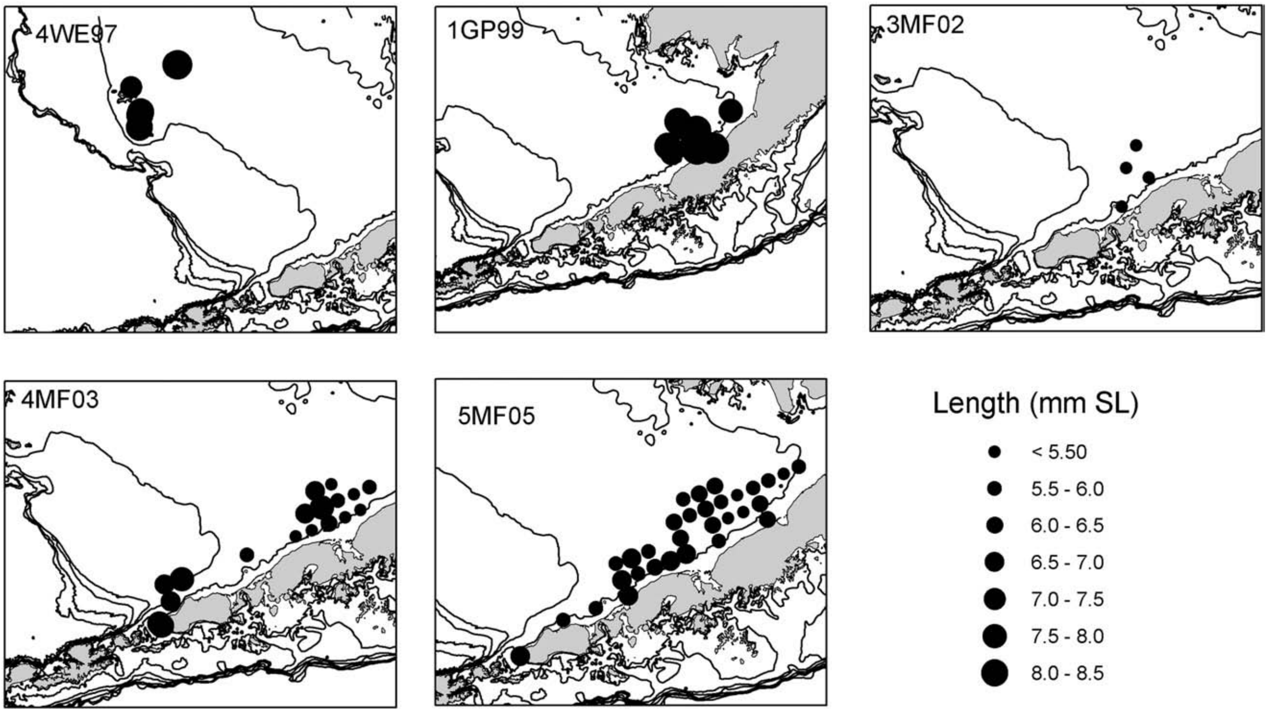

Fig. 8. Mean lengths of Alaska plaice larvae collected in oblique bongo tows.

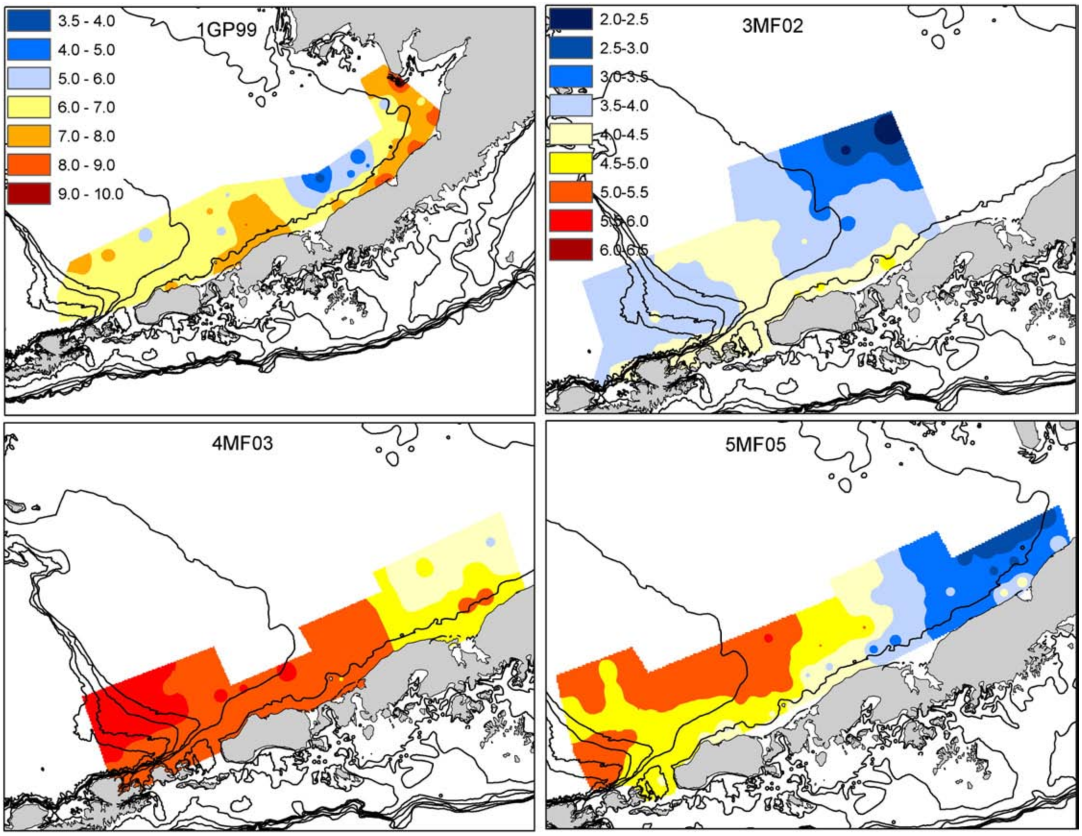

Fig. 9. Interpolated temperature fields by cruise. Data were not available for 1997. Note the two different temperature legends for July (1GP99) and May (3MF02, 4MF03 and 5MF05) cruises.

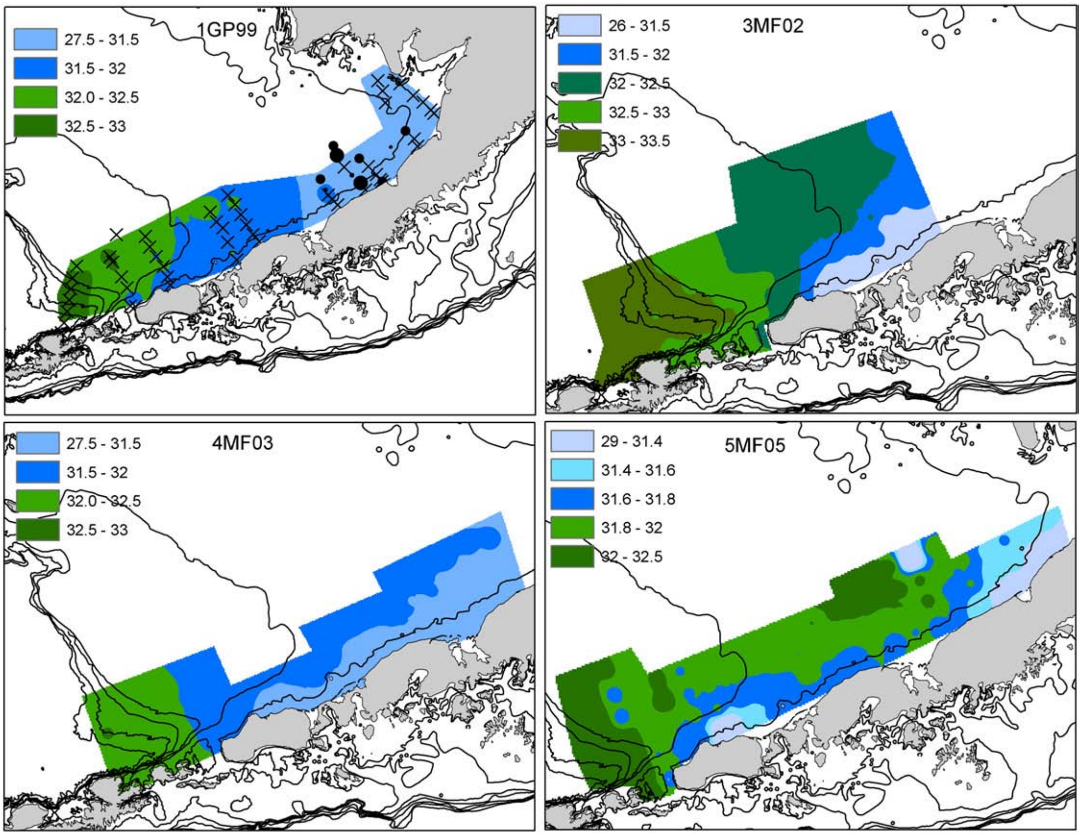

Fig. 10. Interpolated salinity fields by cruise. Data were not available for 1997. Note different scales among figures.

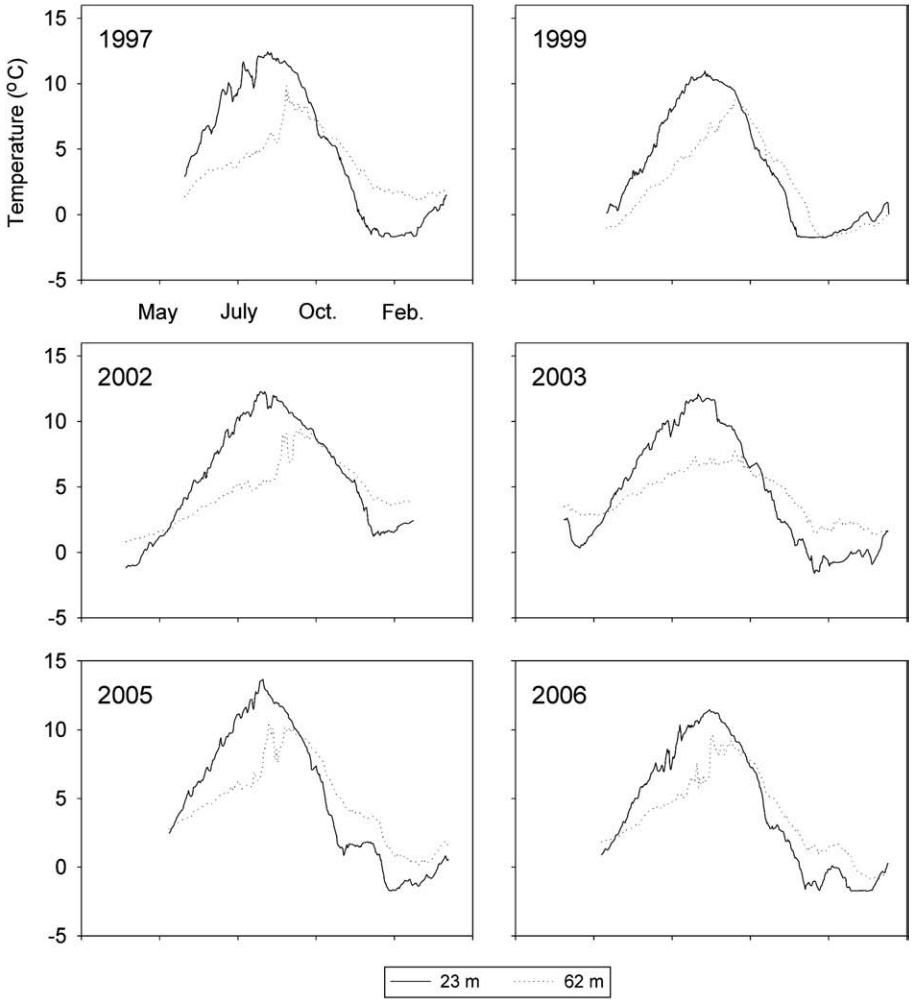

Fig. 11. Seasonal bottom temperatures measured at two moorings deployed in the geographic region of interest from February–October in each year. One mooring was deployed at 23 m depth (solid line) and one at 62 m depth (dashed line).

3.4. Seasonal analyses

Retrospective examination of historical catches indicates a peak in egg abundance in the eastern BS in early April, with a significant drop in egg abundance in late April and May (Fig. 13). Eggs are present in the water column through the month of May, and potentially through June, though reduced effort in summer months precludes direct observation. Alaska plaice larvae were not collected from the water column in April, though high catches of larvae were made throughout the month of May. Interestingly, catches of larvae were also high in July, though this may be an indirect consequence of comparatively greater sampling effort in that month relative to other summer months (June, August).

3.5. Surface model

Results from the OSCURS model indicated significant potential for wind-induced dispersal of near-surface entrained egg and larval stages. Larvae tended to be dispersed either eastward and inshore, or northwards and to the west. In certain years wind forcing was initially from the north, so particles immediately became trapped in inshore waters (1999, 2003, 2006). Such a scenario would quickly position larvae over suitable nursery areas, which might support improved settlement in this species. It was apparent that near-surface larvae were highly vulnerable to the effects of wind forcing, as simulations in other years (1999, 2003, 2006) demonstrated that larvae could be transported far out over the middle and outer shelves (Fig. 14). We hypothesize that such circumstances would be less than ideal, with larvae ultimately situated far from shallow water.

4. Discussion

Goals of the study were to: 1) seasonally characterize the horizontal and vertical distribution of Alaska plaice eggs, larvae, and post larvae over the eastern BS shelf (spring, summer), 2) determine the timing and extent of early life dispersal in this species, and 3) determine the biotic and abiotic variables that influence egg and larval distributions.

4.1. Seasonal characterization

Alaska plaice eggs were collected primarily between the 50 m and 100 m isobaths in April and May, observations that are in accordance with previously-published reports of spawning (Zhang et al., 1998) and egg occurrence (Bailey et al., 2003) for this species. Eggs are present in near-surface waters, and the duration of the egg phase is likely 2–4 weeks (temperature-dependent), as approximated from the first observances of larvae in the plankton. This duration is a significant portion of the planktonic stage, so an improved understanding of drift pathways of eggs is important to fully understanding dispersal and distribution of pelagic phases. Primarily pre-flexion larval stages are present in the water column in May. Larger, post-flexion sizes are present in summer near the Pribilof Islands and in the

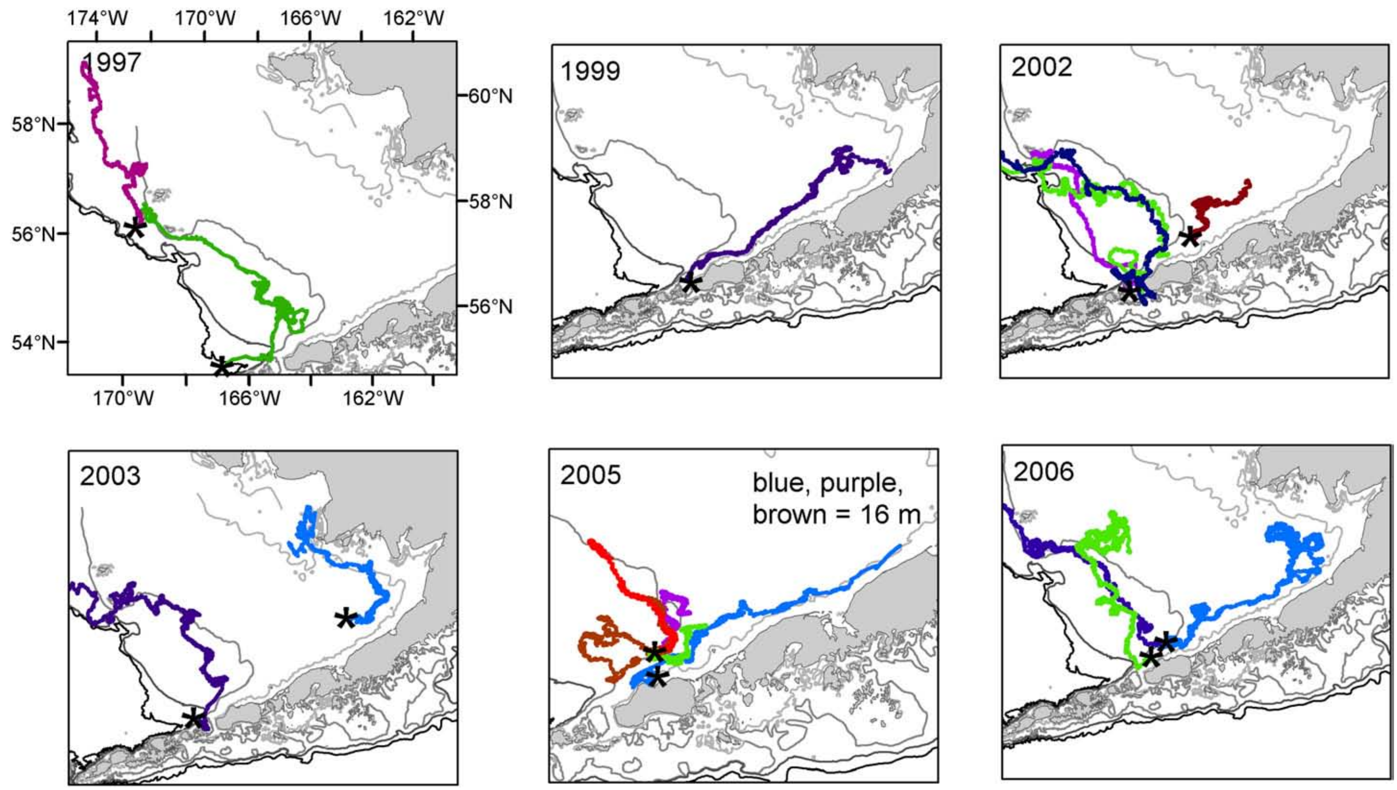

Fig. 12. Drifters deployed in the geographic region of interest by year. Drifters in 1997, 1999, 2002, and 2003 were drogued at 40 m depth. Drifters released in 2005 were drogued at one of two depths: blue, purple, brown indicate a 16-m drogue, red, green indicate a 40 m drogue. Asterisks indicate initial release point.

Bristol Bay vicinity, and previous work has collected settled age-0 Alaska plaice from the inner shelf as far north as Nunivak Island (Norcross and Holladay, 2005). Nearshore beam trawl surveys in autumn (2006, 2008) extending from Unimak Island to Bristol Bay over bottom depths ranging from 40 m–200 m collected no age-0 Alaska plaice in nearly 50 tows (Duffy-Anderson, unpublished), and this lack of capture is preliminary evidence for nursery areas located inshore of the 50 m isobath, in very shallow water (<40 m).

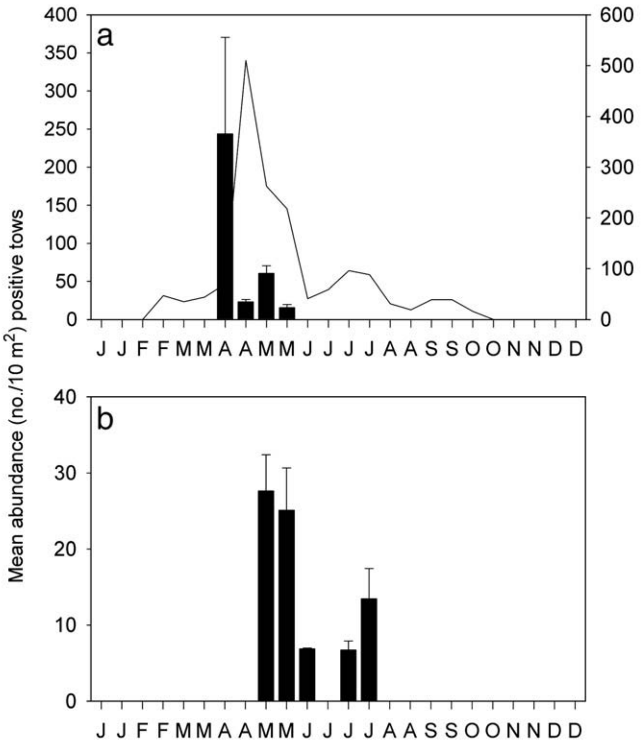

Fig. 13. Patterns of abundance of Alaska plaice eggs (a) and larvae (b) plotted by half-month as determined from all bongo sampling conducted by the Eco FOCI Program in the Bering Sea (1979–2005).

4.1.1. *Timing and extent of dispersal*

The Alaska Peninsula is an important spawning area for Alaska plaice, and since vertical distributions of eggs and pre-flexion larvae center 0–20 m depth, wind-influenced currents undoubtedly affect their distribution. Results from the OSCURS surface model showed that potential drift of particles entrained in near-surface currents could be as far northwest as the Pribilof Islands, or could be as close as Bristol Bay. Few settled, age-0 Alaska plaice have been collected over the Bering Sea shelf, though data from the Gulf of Alaska and Bering Sea (Norcross and Holladay. 2005; personal observation) suggest juvenile nurseries are located in very shallow water.

We were not able to resolve whether older, post-flexion stage larvae demonstrate vertical migrations, though directed changes in vertical position with ontogeny have been well-documented among members of the family Pleuronectidae (Haldorson et al., 1993; Rijnsdorp et al., 1985; Grioche et al., 2000). It is interesting to note that the timing of spawning in Alaska plaice, at least along the Alaska Peninsula, is roughly concomitant with the establishment of the Bering Coastal Current (BCC; Schumacher and Stabeno, 1998; Stabeno et al., 2005), a persistent, directional current that flows along the 50 m isobath. Selected vertical excursions away from near-surface layers could enhance retention in the directed BCC, mitigating unfavorable drift. Mean flow in the BCC in winter is sluggish (<1 cm s^{-1}), but the currents organize and strengthen (2−3 cm s^{-1}) in approximately mid- to late May and remains more vigorous through September (Stabeno et al., 2002). The BCC is the baroclinic flow along a portion of the southeast Bering Sea inner front, a well-described frontal feature over the Bering Sea shelf that separates the well-mixed coastal waters

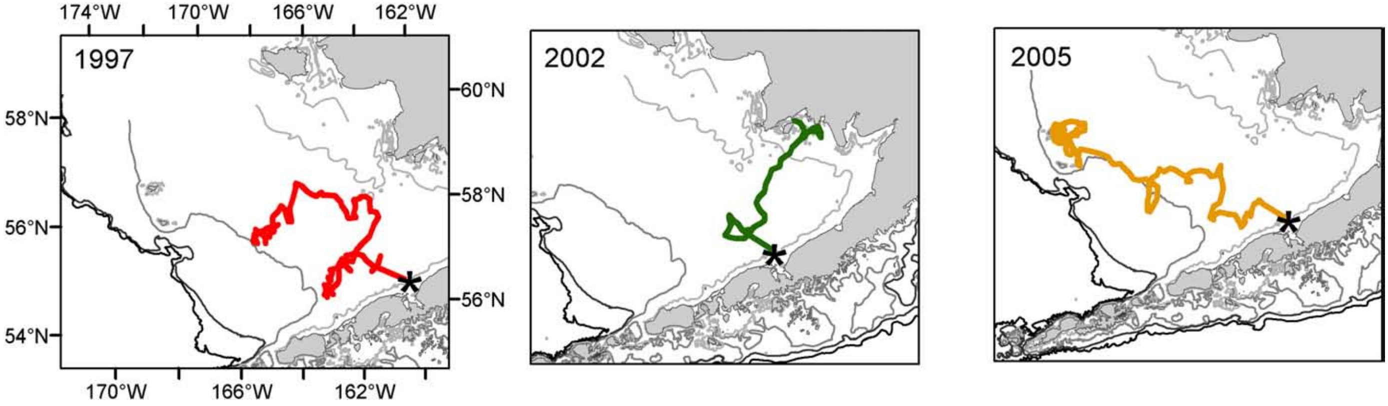

Fig. 14. Results of OSCURS model indicting potential wind-induced surface drift trajectories. Asterisks indicate initial release point.

from the middle shelf two-layered system (Kachel et al., 2002). While the integrated water column flow is persistent, the surface flow can be disrupted by winds. The inner front typically follows the 50 m isobath from Unimak Island along the Alaska Peninsula, turning north-eastward along the isobath in the vicinity of Bristol Bay, and then north toward Nunivak Island, all areas that potentially serve as favorable inshore nursery habitat for juvenile Alaska plaice (see above). We postulate that post spawning in the spring and early summer near the BCC promotes the entrainment of larvae in this consistent, directional current, which offers a retention mechanism for early life stages spawned near shore to recruit to habitat areas along the coast. Entrainment in the BCC would help moderate the effects of storms or other wind events that could adversely disperse larvae concentrated the upper water column to unsuitable habitat areas. Moreover, the inner front could be a source of enhanced production (Kachel et al., 2002) so entrainment within its boundaries may also increase feeding and growth potential of developing larvae.

4.2. Biotic and abiotic influences

In spite of the potential for entrainment in the BCC, simulations from the OSCURS model demonstrate that wind forcing has the potential to significantly affect distribution of eggs and larvae in the near-surface layers. Winds that result in surface movement inshore foster the retention of larvae in areas that are contiguous with presumed nursery habitat, while wind fields that direct currents over the middle and outer shelves have the potential to transport larvae to potentially unsuitable habitat areas. Satellite-tracked drifter trajectories drogued within the

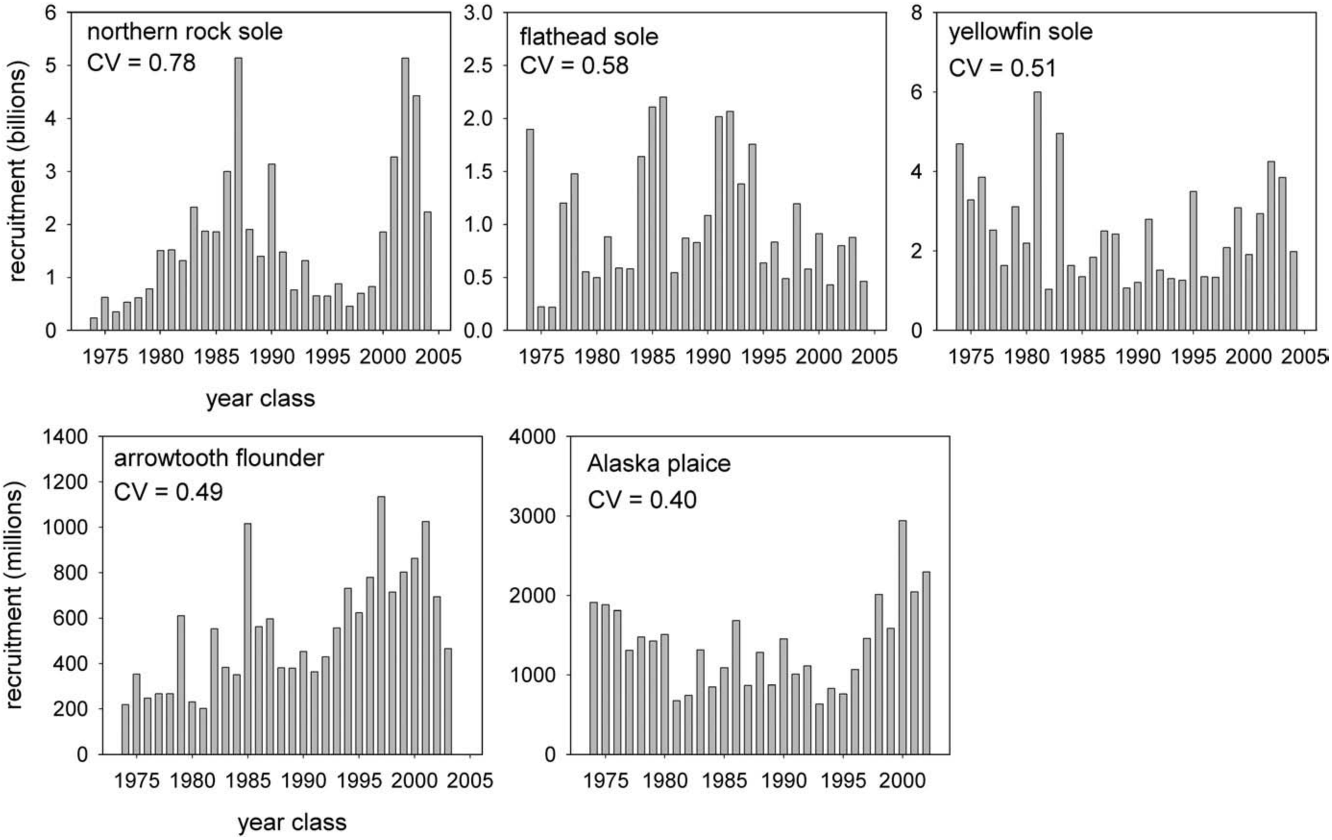

Fig. 15. Recruitment of the five major flatfish species in the eastern Bering Sea. CV = coefficient of variation.

mixed layer support model-derived observations. Trajectories also demonstrate that predominant subsurface flow along the Peninsula is to the east and north, and it is likely that these also influence Alaska plaice larvae as well.

Alaska plaice larvae are not only vulnerable to the effects of variations in hydrography they are affected by thermal conditions as well. During the late 1990s, sea ice covered most of the southeastern shelf into spring, resulting in an extensive cold pool over the southern shelf. Even in 1997, with its shallow wind-mixed layer and resulting warm surface temperatures, the bottom layer remained below 2 °C during the summer. In contrast, there was much less ice during 2001–2005, resulting over the southeastern shelf in warmer surface temperatures and no cold pool (Stabeno et al., 2007). Abundances of larvae in 2005 were high, most likely due to geographic variations in collection areas rather than differences in egg or larval production, although the very warm conditions in 2005 may have impacted production. Warmer temperatures can lead to improved feeding conditions and better survival, though temperature-associated impacts on growth in 2005 appeared to be negligible. Larval sizes collected in 2005 were comparable to sizes from spring collections in other years, making differences in adult spawning time or larval growth rate unlikely.

In summary, the complex, and nonlinear process of dispersal may be mitigated in Alaska plaice via adaptive strategies that act to dampen the effects of environmental heterogeneity. Alaska plaice spawn in a geographic area that supports seasonally-pulsed, directional currents. Since pre-flexion larvae appear to occur within the mixed layer so they are subject to wind-induced changes in current direction and speed. However, these effects may be modulated by entrainment in consistent currents that mitigate spatio-temporal heterogeneity. Interestingly, of the five major species of flatfish found on the EBS shelf (Alaska plaice, yellowfin sole, northern rock sole, arrowtooth flounder, and flathead sole), Alaska plaice are estimated to have the lowest variability in recruitment from the 1972–2002 year classes (Fig. 15) (Stockhausen et al., 2007; Wilderbuer and Nichol, 2007a,b; Wilderbuer et al., 2007a,b. Since the success of flatfish recruitment is believed to be a function of the location and timing of spawning in relation to the proximity of desirable nursery locations and ocean hydrodynamics, as well as adequate food supply and avoidance of predators, the early life ecology of Alaska plaice appears well-suited to mediate these variable climate events. However, given that eggs and pre-flexion stages do tend to occur within the wind mixed layer, climate-mediated variations in wind forcing events and associated changes in hydrography could still affect dispersal, and potentially recruitment, in this species.

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