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Ocean transport paths for the early life history stages of offshore-spawning flatfishes: a case study in the Gulf of Alaska

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Abstract

Offshore- and deepwater-spawning flatfish species face the problem of transport of their planktonic stages to shallow juvenile nursery grounds that are often far shoreward in bays or estuaries. We compare life history attributes of four offshore-spawning flatfish species in the Gulf of Alaska: Pacific halibut (*Hippoglossus stenolepis*), arrowtooth flounder (*Atheresthes stomias*), rex sole (*Glyptocephalus zachirus*) and Dover sole (*Microstomus pacificus*) to examine how their larvae get from a spawning location at the edge or beyond the continental shelf to specific inshore nursery zones. We utilize historical records of survey catches of different life stages to characterize the stage-specific changes in distribution of spawning, planktonic stages and juvenile nursery areas. We infer transport mechanisms based on the shifts in distribution of the life stages and in comparison with local physical oceanography. This comparison provides insight into the different mechanisms marine species may use to solve the common 'problem' of planktonic drift and juvenile settlement.

Keywords Fish larvae, juvenile nursery, larval distribution, larval transport, ocean currents, spawning strategy

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Introduction

Organisms with planktonic stages release their offspring into an environment where they not only face the immediate issue of survival, but they must also 'anticipate' survival at later stages, which often have different and sometimes highly specific requirements. If the release area of eggs is within suitable habitat territory for juveniles, then it is advantageous to be retained there, and if distant from suitable habitat, then eggs and larvae need to be delivered there. This problem is acute for marine fishes, where planktonic stages have high mortality rates (commonly measured at 5–40% per day) and whose larval stages may metamorphose into quite different juvenile forms. Flatfishes share the same planktonic problems with many other species, but they represent an extreme in the process of metamorphosis between larvae and juveniles. Juvenile flatfishes exhibit markedly different morphological forms and behaviours and have different environmental requirements than their pelagic precursors.

Most flatfish species have their juvenile nurseries inshore of the spawning grounds (Minami and Tanaka 1992), and often these nurseries have specific qualities characterized by depth, temperature, salinity, sediment and predator/prey considerations, which define it as suitable habitat (Gibson 1994). For species that spawn offshore in deep water, finding suitable nursery habitat poses a particularly difficult and interesting problem for larvae: how to hit a target whose direction is often orthogonal to prevailing currents? Is hitching a planktonic ride on the right mass of water a random process in which only a few lucky passengers arrive at their destination? Or can discriminating behaviour among adults or larvae influence the outcome of the transport process? Success in this process of arriving at suitable inshore nurseries could play a role in recruitment variability. The concept that transport plays an important role in population regulation is supported by numerous correlative studies that associate planktonic transport to variability in year-class strength (Parker 1989; Wilderbuer *et al.* 2002). Detailed field research (Van der Veer and Witte 1999), modelling studies (Van der Veer *et al.* 1998) and comparative approaches (Van der Veer *et al.* 1990; Rijnsdorp *et al.* 1992) also support the importance of larval flatfish transport in the recruitment process.

Some flatfish species are known to utilize behavioural adaptations to modify their transport as plankton, or passively drifting particles. Among the best known and most sophisticated of these behaviours is selective tidal stream transport (STST), by which larvae alter their position in the water column to take advantage of vertically stratified tidal currents (Creutzberg *et al.* 1978; Rijnsdorp *et al.* 1985; Tanaka *et al.* 1989; Jager 1999; Forward and Tankersley 2001). Using STST, larvae that are spawned near to suitable nursery habitat can maintain themselves there by vertically migrating into counter-currents, and larvae that need directed transport can migrate into tidal currents flowing in the preferred direction. This behaviour is sophisticated in the sense that larvae need to have an innate sense of which direction to move in after receiving specific cues that reveal the orientation of water movement. The complex processes by which a larva recognizes the cues and clues which control its vertical migratory and settlement behaviour are not well understood (Metcalfe *et al.* 2006).

Besides STST, there are other ways flatfishes have developed their strategies to maximize delivery to nearshore nursery areas (Bailey *et al.* 2005). Like many other animals with planktonic stages, they locate their offspring where and when food abundance is high and predator abundance is low. They may broadcast their offspring where the probability of their transport in an advantageous direction is optimized (Gibson 1999; Rooper *et al.* 2006). Thus, there may be local adaptation to regional currents, or adaptations to take advantage of predictable seasonal events (Boehlert and Mundy 1987). For example, some flatfish species have extremely long planktonic periods of up to 2 years to ride seasonal downwelling currents to their inshore juvenile nurseries (Pearcy *et al.* 1977; Markle *et al.* 1992). In such circumstances, larvae may settle facultatively when suitable habitat is encountered (Tanaka *et al.* 1989; Abookire and Bailey 2007). However, when larvae are spawned near or within suitable juvenile habitat or there are specific transport mechanisms to deliver them there, planktonic life may be as short as 10 days (Minami and Tanaka 1992). Even within a species, there may be local adaptations reflecting quite different strategies. For example, plaice (*Pleuronectes platessa*, Pleuronectidae) larvae in the North Sea utilize bottom currents for transport to near-nursery areas and then use

STST to enter nurseries (Van der Veer *et al.* 1998); in the Kattegat/Belt Sea, spawning occurs offshore and larvae ride wind-driven currents inshore (Nielsen *et al.* 1998); and in the Irish Sea, plaice spawn nearshore and larvae utilize retention features to maintain themselves there (Nash and Geffen 1999).

In this paper, we compare life history attributes of four offshore-spawning flatfish species in the Gulf of Alaska (GOA): Pacific halibut (*Hippoglossus stenolepis*, Pleuronectidae), arrowtooth flounder (*Atheresthes stomias*, Pleuronectidae), rex sole (*Glyptocephalus zachirus*, Pleuronectidae) and Dover sole (*Microstomus pacificus*, Pleuronectidae), to examine how they solve a common ontogenetic problem of getting from a spawning location at the edge or beyond the continental shelf to specific inshore nursery zones. We utilize time series of survey catches of different life stages to characterize the horizontal distribution of spawning adults, planktonic egg and larval stages, and settled juveniles. Historical data are also used to characterize vertical distributions of eggs and larvae. We then infer species-specific transport mechanisms based on the shift in spatial distribution between successive life stages. These inferences are discussed in relation to cross-shelf circulation. New detailed information on circulation is presented from movement of satellite-tracked drifters. These comparisons provide insight into the different mechanisms marine species use to solve the problem of planktonic drift and juvenile settlement.

Data

Adult fish distribution data were extracted from the groundfish survey database (RACEBASE) of bottom trawl surveys conducted in the GOA and Aleutian Islands from 1976 to 2006 by the National Marine Fisheries Service (NMFS) and Alaska Fisheries Science Center (AFSC). These surveys represent extensive coverage of the GOA shelf and included 12 233 trawls. The gear used from 1980 onwards was a modified Poly Nor'eastern trawl net with roller gear and a 32-mm mesh codend liner; prior to 1980, a variety of bottom trawls were employed. Catches were standardized (catch per unit effort, CPUE) as kg km^{-2} such that total species weight (kg) was divided by the distance towed (km) multiplied by the width of the trawl (km). To isolate mature adult flatfishes, the CPUE was adjusted according to the percentage of mature-size fish that were measured for length in each haul and then assigned a spawning season according to parameters obtained from other studies (Table 1). Length data were not collected in several pre-1980 cruises; therefore, in these hauls, the total CPUE was assumed to equal adult CPUE if the average weight of a species was greater than or equal to the reported weight of a mature adult (Table 1).

Table 1 Total length (cm) and weight values used to estimate mature flatfishes and the range of their spawning season. Based on these parameters, adult flatfish data were isolated from the NMFS Bottom Trawl Survey database (1976–2006).

Species	Sex	Total length (cm)	Weight (kg)	Spawning season
Pacific halibut	Males and females	≥125[(1)]	19.5[(2)]	Dec–Mar[(3)]
Arrowtooth flounder	Females	≥53[(4)]	1.4[(5)]	Jan–Mar[(6)]
Rex sole	Females	>34[(7)]	0.37[(7)]	Oct–May[(7)]
Dover sole	Females	>43[(8)]	0.61[(8)]	Feb–May[(8)]

(1)Clark *et al.* (1999).
(2)Clark (1992).
(3)St. Pierre (1984).
(4)Zimmermann (1997).
(5)Turnock *et al.* (2005).
(6)Blood *et al.* (2007).
(7)Abookire (2006).
(8)Abookire and Macewicz (2003).

Juvenile fish distribution data were available from NMFS and the Alaska Department of Fish and Game (ADF&G) small-mesh trawl surveys for shrimp conducted from 1972 to 2005. The net used was a high-opening shrimp trawl with 31 mm stretched-mesh throughout and a 17-m tickler-chain attached to an 18.6-m foot-rope. The database contained total species count and total species weight information collected per trawl for 6411 hauls. Catches were standardized (CPUE) as kg km^{-2}, as described above. Because size information was not taken on individuals, in order to identify stations with juvenile flatfishes, the average individual weight at a station was calculated for each species and stations were retained if average weight was within the parameters listed in Table 2. This approach provided a conservative measure of juvenile fish distribution, as the criterion of average weight excluded catches where juvenile fish co-exist

Table 2 Parameters used to estimate catches of age-0 and age-1 flatfish from the ADFG–NMFS Shrimp Trawl Survey (1972–2005).

Species	Age-0 length	Age-1 length	LW equation
Pacific halibut	≤ 104 TL(1)	≤ 226 TL(1)	$\mathrm{ww} = 12.4341 - 0.3757 \times (\mathrm{TL}) + 0.0036 \times (\mathrm{TL}^2)$(2)
Arrowtooth flounder	≤ 104 TL(1)	≤ 170 TL(1)	$\mathrm{ww} = 0.000004 \times \mathrm{TL}^{3.1124}$(3)
Rex sole	≤ 90 SL(4)	≤ 140 TL(1)	$\mathrm{ww} = 0.000762 \times \mathrm{TL}_{\mathrm{cm}}{}^{3.6127}$(5)
Dover sole	≤ 65 SL(4)	≤ 236 TL(1,6)	$\mathrm{ww} = 0.0029 \times \mathrm{TL}_{\mathrm{cm}}{}^{3.3365}$ (6)

(1Norcross *et al.* (1998).

(2)Thomas Hurst, NMFS Fisheries Behaviour and Ecology Program, personal communication.

(3)Bouwens *et al.* (1999).

(4)Pearcy *et al.* (1977).

(5)Abookire (2006).

(6)Abookire and Macewicz (2003).

ww, weight weight (g); TL, total length (mm); $\mathrm{TL}_{\mathrm{cm}}$, total length (cm); SL, standard length (mm).

with adults. The distribution of juveniles was also examined from the AFSC bottom trawl surveys.

In addition, nearly 400 obliquely-towed pelagic anchovy trawls with a 3-mm mesh codend liner that sampled the continental shelf (night and day) in September (2001, 2003, 2005; Wilson *et al.* 2006) were examined for age-0 flatfishes (data provided by M.T. Wilson, AFSC, 7600 Sand Point Way NE, Seattle, WA 98115, USA).

Data on flatfish eggs and larvae were extracted from the Ichthyoplankton Database (ICHBASE), a database encompassing a 30-year time series of ichthyoplankton data (10 776 tows) from cruises during 1972–2004 conducted by AFSC and partner institutions in the GOA (methods detailed in Matarese *et al.* 2003). To examine the distribution of ichthyoplankton, eggs were collected with 60 cm bongo tows with 333 or 505 **μ**m mesh netting and 1 m Tucker tows with 333 or 505 **μ**m mesh netting. Larvae were collected with bongo tows, Tucker tows, 6-ft frame Methot tows with 3 mm mesh netting and a 505-**μ**m mesh codend, and 6-ft Isaacs-Kidd Midwater Trawl (IKMT) tows with a 505-**μ**m mesh codend. All tows were quantitative and oblique, conducted in a standardized manner using flowmeters. In general, tows were made to 10 m off-bottom, but not deeper than 200 m. Catches were preserved in 5% formalin and returned to the laboratory. They were sorted, species identified and individuals measured at the Plankton Sorting and Identification Center, Szczecin, Poland. Species identifications were verified by the Recruitment Processes Taxonomic Project at AFSC.

To determine vertical distribution of eggs and larvae, data were examined from 151 series of 1 m^2 vertical Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) tows with 153–505 μm mesh nets collected from 1991 through 2003. In general, five to nine nets were fished obliquely over 10 m depth intervals in the upper 100 m of the water column. At greater depths, the sample depth intervals ranged from 10 to 40 m. Catches in nets were reported for only those tows with non-zero catches and by the mid-sample depth interval sampled by each net.

The Gulf of Alaska setting

Shelf features

The relatively narrow (approximately 200 km) continental shelf of the northern GOA basin is bordered by the Alaska coastline to the north and the continental slope margin to the south (Fig. 1). The shelf is characterized by historical glacial scouring, so the present-day bottom topography is rugged and irregular. Ridges, banks, sea valleys and troughs punctuate and traverse the coastal domain (Mueter 2004; Stabeno *et al.* 2004). This mosaic of distinctive underwater features contributes to variations in large-scale geostrophic flow (Warren and Owens 1988; Stabeno *et al.* 2004), variations in tidal amplification and steering, and local patterns of upwelling and downwelling. Likewise, the bathymetric heterogeneity contributes to mesoscale circulation variability such as eddy formation, trajectory, and transport, and

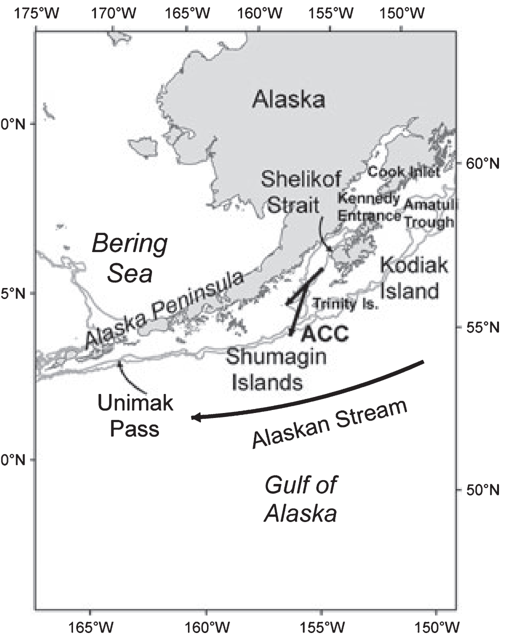

Figure 1 The western Gulf of Alaska showing major currents and geographical features.

cross-shelf flux between the offshore basin and the shelf.

The shelf region is largely a landscape of mud and sand sediment fragmented by areas of rock, stone and gravel or mixtures (Fig. 2). Rocky zones are more prevalent in nearshore depths <50 m compared to intermediate depths. In some areas, there is expansive coverage of shell detritus. There can be extensive eelgrass beds in sheltered nearshore waters and in bays.

Circulation

Pertinent features of circulation with respect to advection of planktonic stages of flatfishes are summarized here. The cyclonic subarctic gyre is the predominant circulation feature in the North Pacific Ocean basin (Weingartner 2007). Driven by the West Wind Drift, the gyre bifurcates at the continental margin of North America into the Alaska Current, which flows northwards, and California Current, which flows southwards. The slow-moving Alaska Current accelerates at the head of the GOA to form the narrow (approximately 100 km) Alaskan Stream (Fig. 1), a vigorous (50–100 cm s^{-1}) offshore current that flows along the continental slope approximately 150 km from the coastline (Reed 1984; Reed and Schumacher 1986; Musgrave *et al.* 1992). The Alaskan Stream follows the Alaska Peninsula and the Aleutian Islands chain, with a portion flowing through the deep Aleutian passes (Ladd *et al.* 2005), to eventually turn northwest around the Aleutian Arc (Reed and

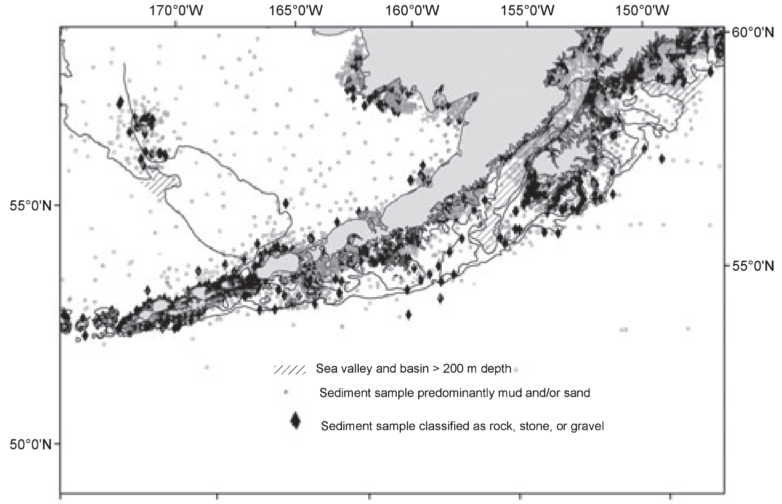

Figure 2 Sediment characteristics of the western Gulf of Alaska (from NIMA, National Imagery and Mapping Agency; Springfield, Virginia). In addition shown are the 100- and 200-m isobaths. Deep-sea valleys penetrating the continental shelf are shaded. The preferred habitats of flatfish juveniles are believed to be in shallow coastal waters in mud and sand sediments (small circles). Rock, stone and gravel sediment samples that may represent poor habitats are emphasized with large black diamonds.

Stabeno 1989). Large (approximately 200 km diameter), slow-moving (1–4 km per day; Okkonen *et al.* 2003) basin eddies form as meanders from the Alaskan Stream and propagate along the shelf edge. These basin-formed eddies can persist at the shelf break for months, contacting and influencing shelf circulation. It has been hypothesized that these basin-formed eddies are a source of exchange between the basin and the shelf (Musgrave *et al.* 1992; Thompson and Gower 1998; Stabeno *et al.* 2004; Ladd *et al.* 2005).

Flow on the GOA continental shelf is dominated by the narrow (<30 km) Alaska Coastal Current (ACC), a wind- and buoyancy-driven coastal current that is mediated by downwelling-favourable winds and freshwater input from streams along the coastline (Reed and Schumacher 1986). Wind stress and freshwater input to the ACC are seasonally variable (Weingartner *et al.* 2005), with strong, persistent, downwelling-favourable winds in the winter and relaxed or weakly upwelling-favourable wind fields in summer (Stabeno *et al.* 2004). Freshwater input to the ACC is minimal in winter when precipitation occurs in the form of snow, moderate in spring and summer in the form of ice-melt runoff, and greatest in the autumn when precipitation is at a maximum (Royer 2005; Weingartner *et al.* 2005; Weingartner 2007). Interannual variability in the ACC is related to variations in the Aleutian Low Pressure System, a large-scale atmospheric circulation in the North Pacific that varies in intensity and position from year-to-year. Differences in wind strength and temperature contribute to variations in ACC transport, while differences in precipitation contribute to variations in baroclinicity (Hermann and Stabeno 1996). Baroclinic instabilities in the ACC serve to generate mesoscale eddies on the shelf that may act to retain nutrients, zooplankton and ichthyoplankton (Schumacher *et al.* 1993). Unlike the slower-moving basin-formed eddies described above, mesoscale shelf-formed eddies are smaller (approximately 20 km diameter), and propagate quickly (Schumacher *et al.* 1993).

The heterogeneous bottom topography and complex bathymetry in the GOA give rise to complicated circulation patterns, particularly in large, submarine canyons. Amplification and resonance of tides in canyons is not well-characterized, although canyon-related changes in tidal vectors likely play an important role in the delivery of propagules between the slope and the shelf. Seasonal variations in the direction and magnitude of geostrophic currents are also critical to slope–shelf exchange (Favorite and Ingraham 1977). Autumn, winter and spring circulation tends to favour downwelling conditions, although relaxation of downwelling in summer contributes to deep water ingress to the shelf (Weingartner 2007). Deep water currents tend to flow up troughs (Lagerloef 1983), generally up the east side and out the western side (Ladd *et al.* 2005). In the Shelikof sea valley, there is estuarine-type circulation with inward deepwater flow and outward flow at the surface (Reed *et al.* 1987). Narrow tidal currents associated with steep slopes of the sea valley and concentrated at the pycnocline (Reed and Schumacher 1989) may be an important feature of transport that is not well understood. Finally, tidally-generated internal waves, the presence of shelf–slope eddies, or anomalous current meanders may also create interfaces between oceanic and shelf water in submarine canyons.

Life history attributes of offshore-spawning flatfishes

Spawning

From 12 233 bottom trawl hauls taken over 30 years, 1997 adult Pacific halibut were captured in 1127 hauls; 289 097 adult female arrowtooth flounder were captured in 4774 hauls; 106 580 adult female rex sole were captured in 3154 hauls, and 31 915 adult female Dover sole were captured in 2107 hauls. Adults of all four species were widely distributed from the inner shelf to the outer slope in the non-spawning season (Figs 3a, 4a, 5a & 6a).

Pacific halibut has a relatively condensed reproductive season and primarily spawns along the continental slope east of Kodiak Island. During the spawning season for halibut (December to March; St. Pierre 1984), mature-size Pacific halibut concentrated along the continental slope east of Kodiak and in the deep gullies northeast of Kodiak between depths of 130–366 m (Fig. 3b). No sampling occurred in December. In March, some mature-size Pacific halibut remained along the slope northeast of Kodiak, but most individuals had migrated to the west side of Kodiak Island in Shelikof Strait. These data suggest that Pacific halibut undergo rapid migration away from the slope once spawning is complete in late February or early March.

Egg and larval abundance estimates also indicate a condensed period of spawning, with most eggs captured in February and high numbers of small

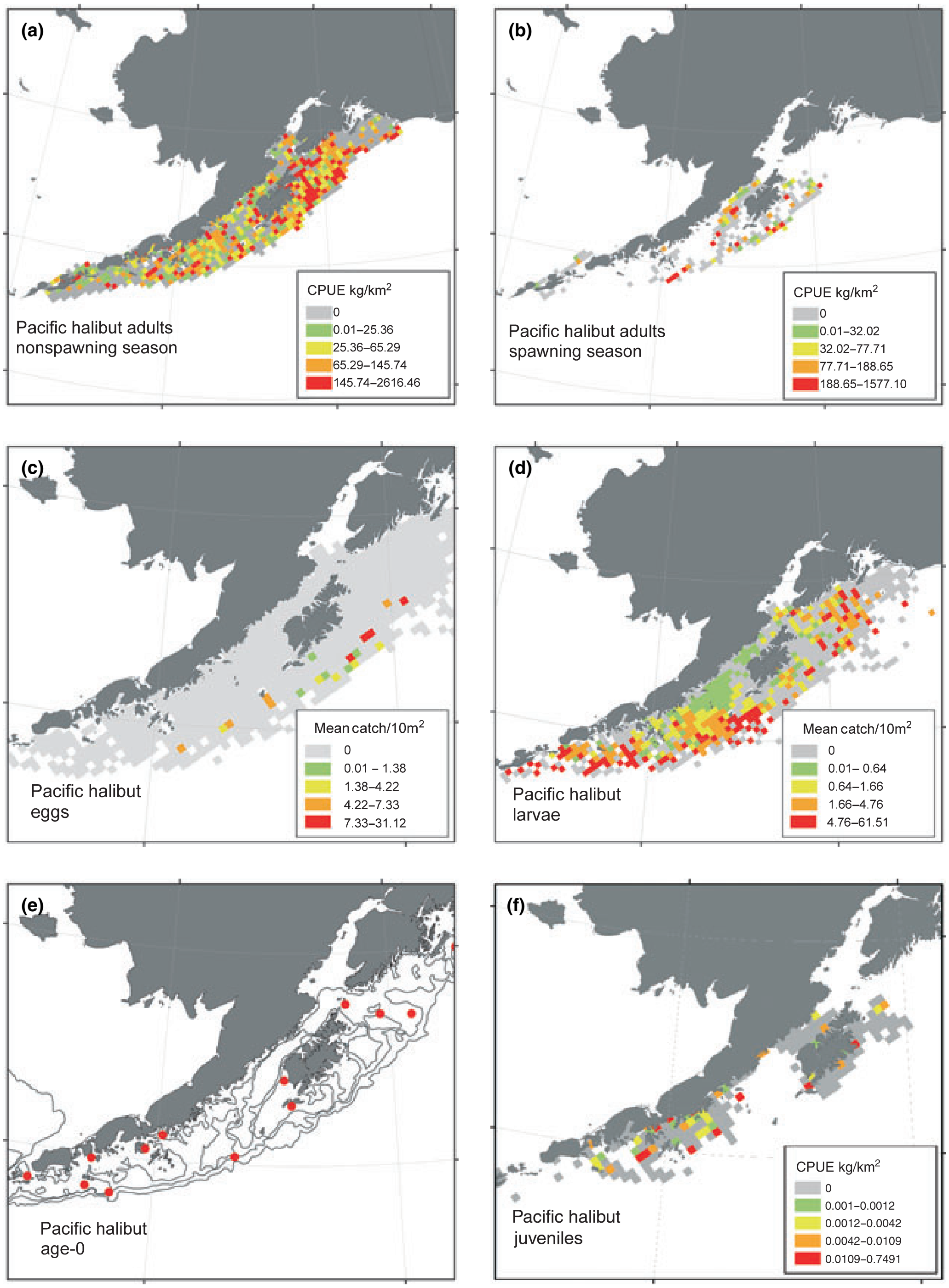

Figure 3 Distribution of Pacific halibut life stages: (a) adults during the non-spawning season from AFSC bottom trawl surveys; (b) adults during the spawning season from AFSC bottom trawl surveys; (c) eggs from AFSC ichthyoplankton surveys; (d) larvae from AFSC ichthyoplankton surveys; (e) age-0 juveniles from AFSC bottom trawl surveys (only occurrence is shown because of gear mesh size and escapement); and (f) age-0 and age-1 juveniles from ADF&G shrimp trawl surveys. Colour gradients represent average densities per sampling unit of all samples within the areas represented by 20 km × 20 km squares.

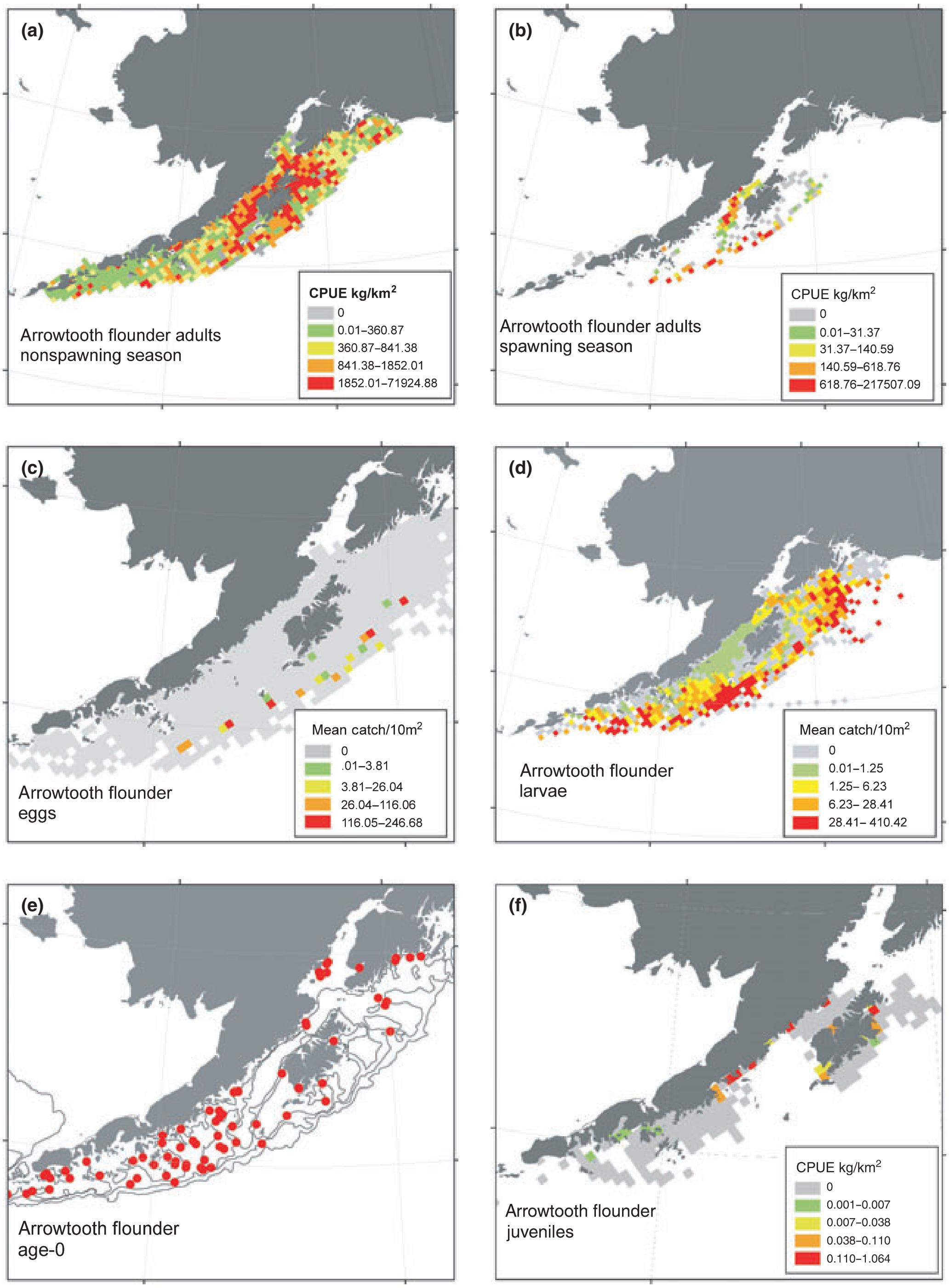

Figure 4 Distribution of arrowtooth flounder life stages: (a) adults during the non-spawning season from AFSC bottom trawl surveys; (b) adults during the spawning season from AFSC bottom trawl surveys; (c) eggs from AFSC ichthyoplankton surveys; (d) larvae from AFSC ichthyoplankton surveys; (e) age-0 juveniles from AFSC bottom trawl surveys (only occurrence is shown because of gear mesh size and escapement); and (f) age-0 and age-1 juveniles from ADF&G shrimp trawl surveys. Colour gradients represent average densities per sampling unit of all samples within the areas represented by 20 km × 20 km squares.

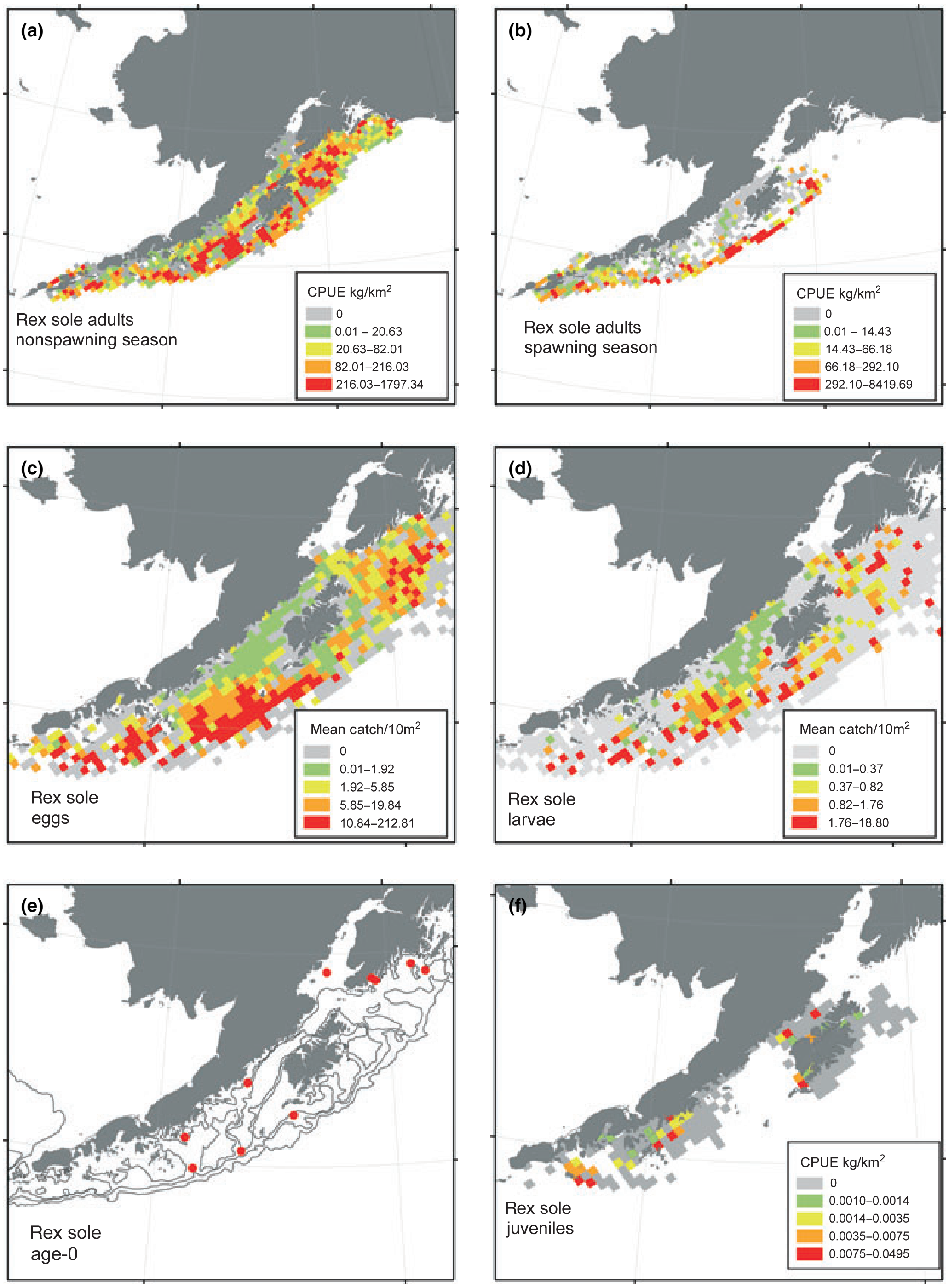

Figure 5 Distribution of rex sole life stages: (a) adults during the non-spawning season from AFSC bottom trawl surveys; (b) adults during the spawning season from AFSC bottom trawl surveys; (c) eggs from AFSC ichthyoplankton surveys; (d) larvae from AFSC ichthyoplankton surveys; (e) age-0 juveniles from AFSC bottom trawl surveys (only occurrence is shown because of gear mesh size and escapement); and (f) age-0 and age-1 juveniles from ADF&G shrimp trawl surveys. Colour gradients represent average densities per sampling unit of all samples within the areas represented by 20 km × 20 km squares.

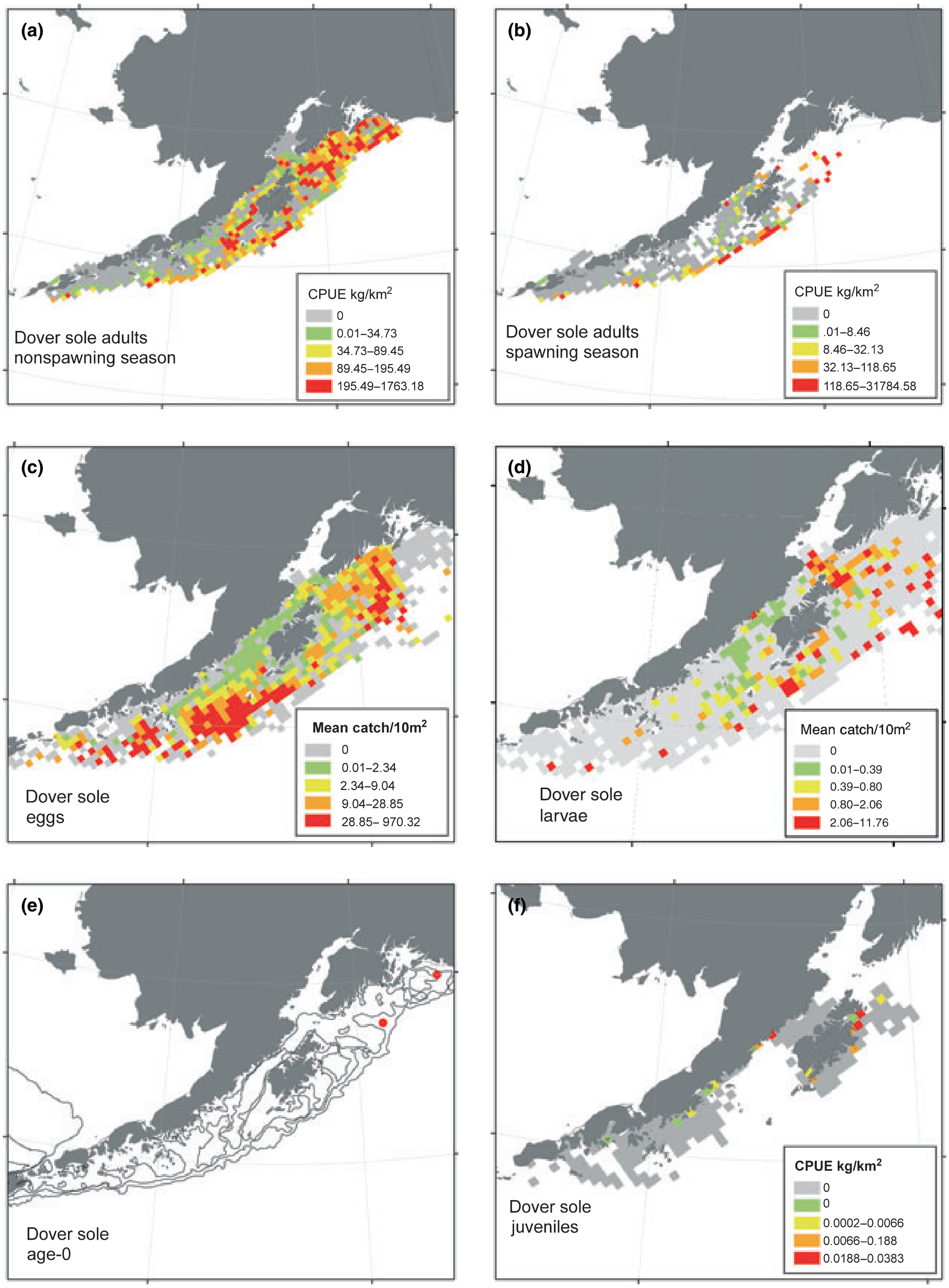

Figure 6 Distribution of Dover sole life stages: (a) adults during the non-spawning season from AFSC bottom trawl surveys; (b) adults during the spawning season from AFSC bottom trawl surveys; (c) eggs from AFSC ichthyoplankton surveys (d) larvae from AFSC ichthyoplankton surveys; (e) age-0 juveniles from AFSC bottom trawl surveys (only occurrence is shown because of gear mesh size and escapement); and (f) age-0 and age-1 juveniles from ADF&G shrimp trawl surveys. Colour gradients represent average densities per sampling unit of all samples within the areas represented by 20 km × 20 km squares.

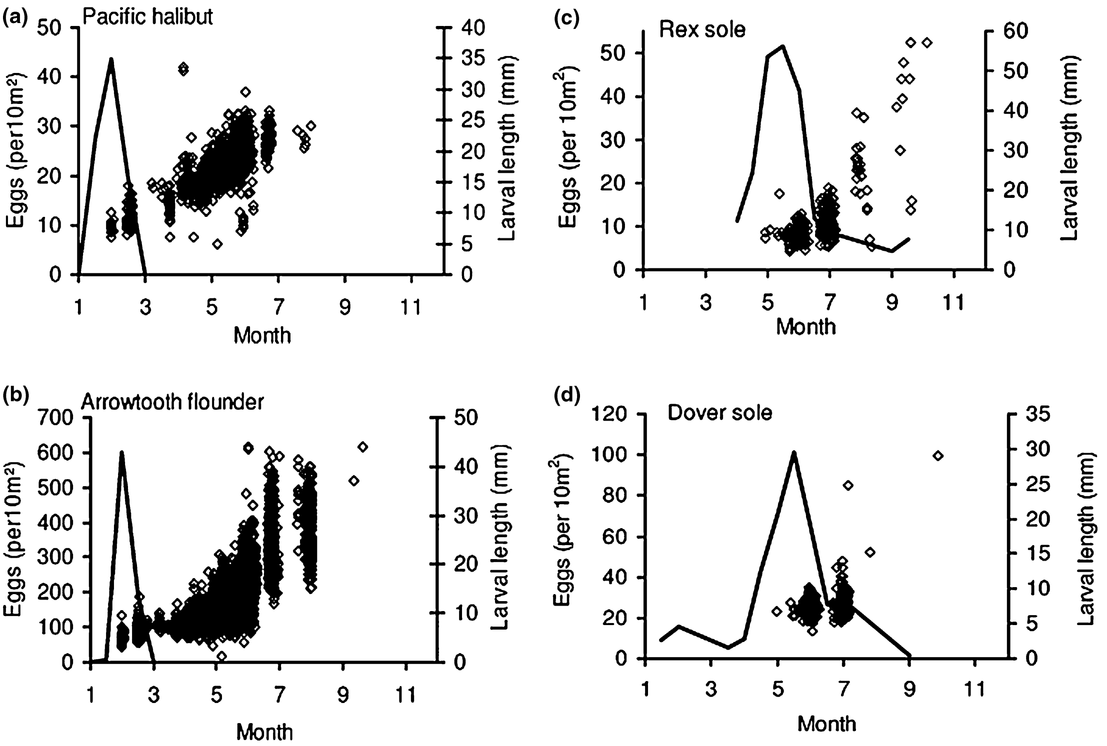

Figure 7 Monthly mean abundance of eggs (line, left ordinate) and sizes of larvae (diamonds, right ordinate) from AFSC ichthyoplankton survey data: (a) Pacific halibut; (b) arrowtooth flounder; (c) rex sole; and (d) Dover sole.

recently hatched larvae caught from February–April (Fig. 7a). Almost all eggs are caught along the continental shelf; however, it should be noted that very few surveys have sampled the offshore regions for Pacific halibut eggs. On the contrary, larvae are more dispersed and near the surface. (These same caveats pertain to the other species discussed below). Given that the larvae are probably about a month old since being spawned, the peak spawning date probably extends through March.

Similar to Pacific halibut, arrowtooth flounder has a relatively short spawning season and primarily spawns along the continental slope east of Kodiak Island. Spawning begins in late January and ends in approximately March (Blood *et al.* 2007). During peak spawning in January and February (n = 64 stations), mature-size females are concentrated along the continental slope southwest, south and east of Kodiak Island at depths of 190–340 m and as deep as 485 m (Fig. 4b). In early March and in April, some adult arrowtooth remained along the slope south of Kodiak, but most individuals had migrated towards Shelikof Strait. As with Pacific halibut, the monthly distribution of mature-size female arrowtooth flounder indicates a prompt migration away from the slope once spawning is complete. Egg and larval abundances also indicate that most spawning occurs in February, but small recently hatched larvae have been caught in May, indicating that some spawning can occur through April (Fig. 7b). By comparison, the spawning of arrowtooth flounder off the Washington coast is reported to occur from September through March (Rickey 1995) and in the Bering Sea, spawning is reported from December through March (Pertzeva-Ostroumova 1961).

Unlike Pacific halibut and arrowtooth flounder, both rex sole and Dover sole have protracted spawning seasons. Between October and May, mature-size female rex sole (n = 36 524 in 596 hauls) concentrated along the outer shelf and slope at depths of 100–350 m (Fig. 5b). During the Dover sole spawning season, mature females (n = 12 124 in 246 hauls) aggregated almost exclusively along the slope at depths of 310–500 m (Fig. 6b). Neither rex nor Dover sole changed their monthly distribution pattern either during or at the very end of their spawning season.

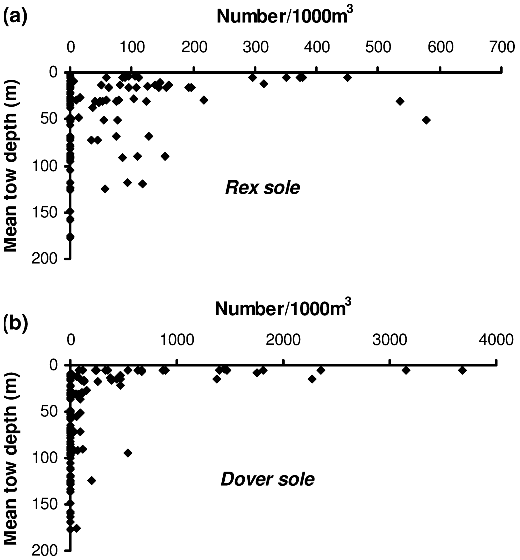

Figure 8 Vertical distribution of eggs determined from mean tow depth and egg density from MOCNESS tows: (a) rex sole; and (b) Dover sole.

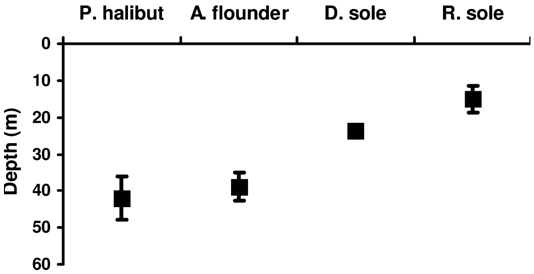

Figure 9 Mean vertical distribution from MOCNESS tows of larvae: Pacific halibut; arrowtooth flounder; Dover sole; and rex sole. Vertical bars represent ±1 SD.

Egg and larval data indicate that rex sole eggs are abundant in the water in late April to mid-June, and small recently hatched larvae are abundant through early July (Fig. 7c). By comparison, off the Oregon coast, rex sole spawn from January to June (Hosie 1975) and small larvae are most abundant in March–June (Pearcy *et al.* 1977).

Dover sole eggs are most abundant in the GOA in May and June, and small recently hatched larvae are abundant through early July (Fig. 7d). By comparison, off the Oregon coast, spawning occurs from February through July with a peak in April (Markle *et al.* 1992), and small Dover sole larvae are found in the water from March to June (Pearcy *et al.* 1977).

Patterns in egg and larval distributions

Arrowtooth flounder and Pacific halibut eggs are deeper in the water column and farther offshore than the historical vertically stratified net tows in ICHBASE. However, Blood *et al.* (2007) report catches from a set of horizontally towed bongo nets over the slope, and indicate that arrowtooth flounder eggs were caught at around 400 m depth. About 90% of all eggs were caught over the slope and most of the eggs caught over the shelf were late-stage eggs. Thompson and Van Cleve (1936) reported Pacific halibut eggs below 200 m and as deep as 700 m. By contrast, Dover and rex sole eggs are found in near-surface waters (Fig. 8a & b). As spawning of all species occurs near bottom, the differences in vertical distribution of eggs likely arise from species-specific buoyancy differences.

Vertical distribution of larvae also shows that mean distributions of Dover and rex sole larvae are shallower than larvae of Pacific halibut and arrowtooth flounder (Fig. 9). The mean depth of rex sole is located in shallow depths at around 15 m and Dover sole mean depth is at 25 m. Mean depth of arrowtooth and Pacific halibut is around 30 m. Previous studies indicate that the smallest arrowtooth and Pacific halibut larvae are considerably deeper than larger larvae. For example, the mean distribution of arrowtooth larvae <7 mm in length is between 100 and 150 m, while that of small Pacific halibut <13 mm is between 200 and 300 m (Bailey and Picquelle 2002). These results indicate an ontogenetic movement of larvae towards the surface.

Comparison of egg and larval distributions in Figs 3–7 suggests that larvae of arrowtooth flounder and Pacific halibut are located inshore of eggs. However, this pattern is not so clear for Dover sole and rex sole. Fig. 10a–d shows the distribution of catches of the largest 10% of the size distribution of larvae and juveniles caught in plankton trawls (bongo, Tucker and Methot trawls) compared to high concentrations of eggs; this reinforces the demonstration of onshore movement of arrowtooth flounder and Pacific halibut larvae. However, the distribution of large Dover and rex sole larvae is not markedly different from that of eggs, suggesting a comparative lack of directed, onshore movement with development.

Examining the geographical distribution of the mean lengths of larvae in plankton tows reveals interesting patterns that reflect advection trajectories.

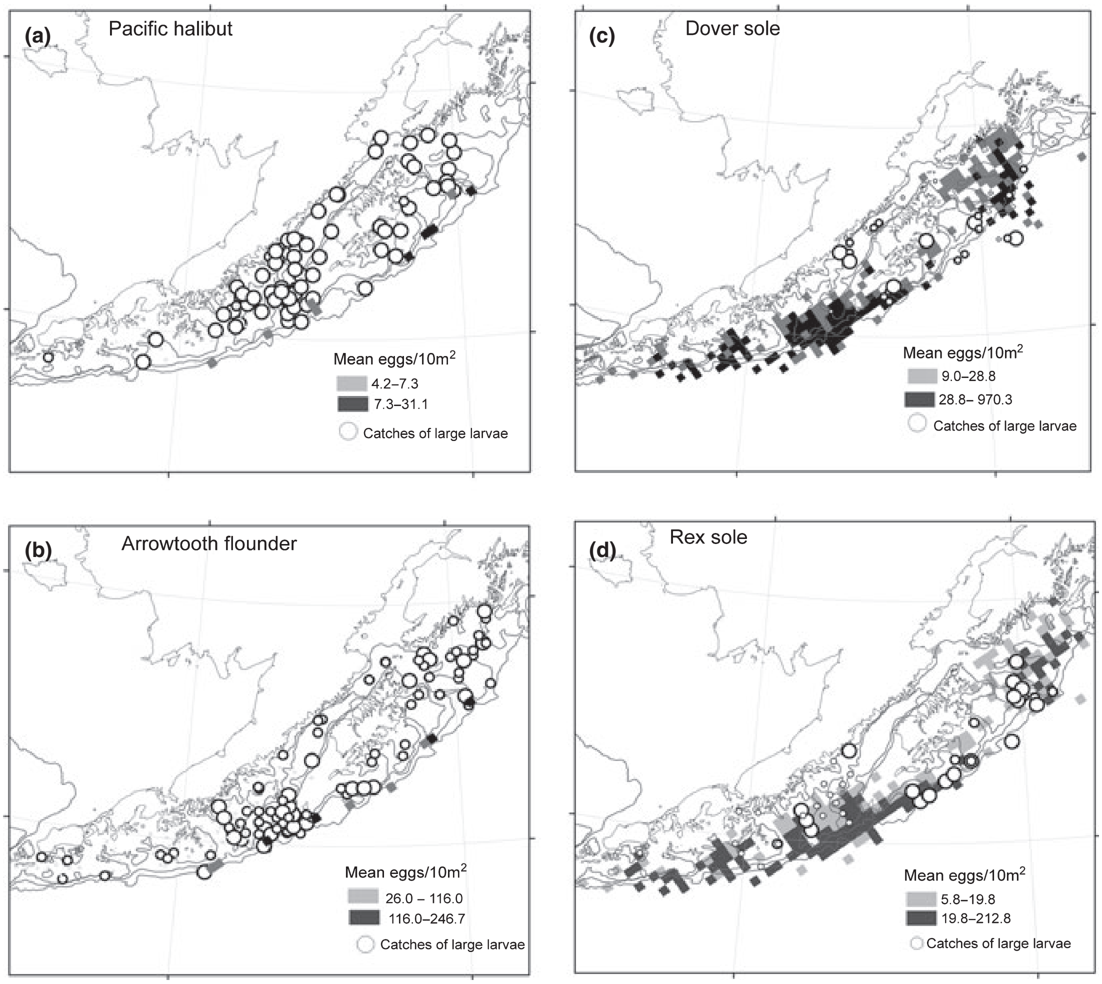

Figure 10 Mean egg density (shaded squares showing only the highest mean egg density categories) and distribution of advanced-stage larvae (in the top 10% of the size range) from AFSC ichthyoplankton surveys: (a) Pacific halibut; (b) arrowtooth flounder; (c) rex sole; and (d) Dover sole. For Pacfic halibut and arrowtooth flounder, large larvae are inshore of eggs.

In the case of Pacific halibut and arrowtooth flounder, there is an offshore–onshore gradient of increasing mean length that supports the observation of onshore movement of larvae (Fig. 11a–d). In the case of arrowtooth flounder there also may be a downstream gradient over the shelf of increasing size, with the smallest larvae around Kodiak Island and the largest mean lengths between the Shumagin Islands and Unimak Pass. By contrast, there is no similar pattern of an onshore or downstream gradient in mean length distribution for either Dover or rex sole, both of whose largest larvae are distributed evenly across the width and length of the shelf.

Juvenile nurseries

From 6411 shrimp trawl hauls taken over 34 years, two age-0 Pacific halibut were captured at two stations and 1420 age-1 Pacific halibut were captured at 65 stations. Age-0 arrowtooth flounder (n = 2909) were captured at two stations, and 11 323 age-1 arrowtooth flounder were captured at 50 stations. No age-0 rex sole were captured, but 631 age-1 rex sole were captured at 54 stations. Five age-0 Dover sole (45–50 mm TL) were captured in two widely separated areas in October; three individuals were caught at 35 fathoms in Wide Bay and two individuals were caught at 95 fathoms near Izhut

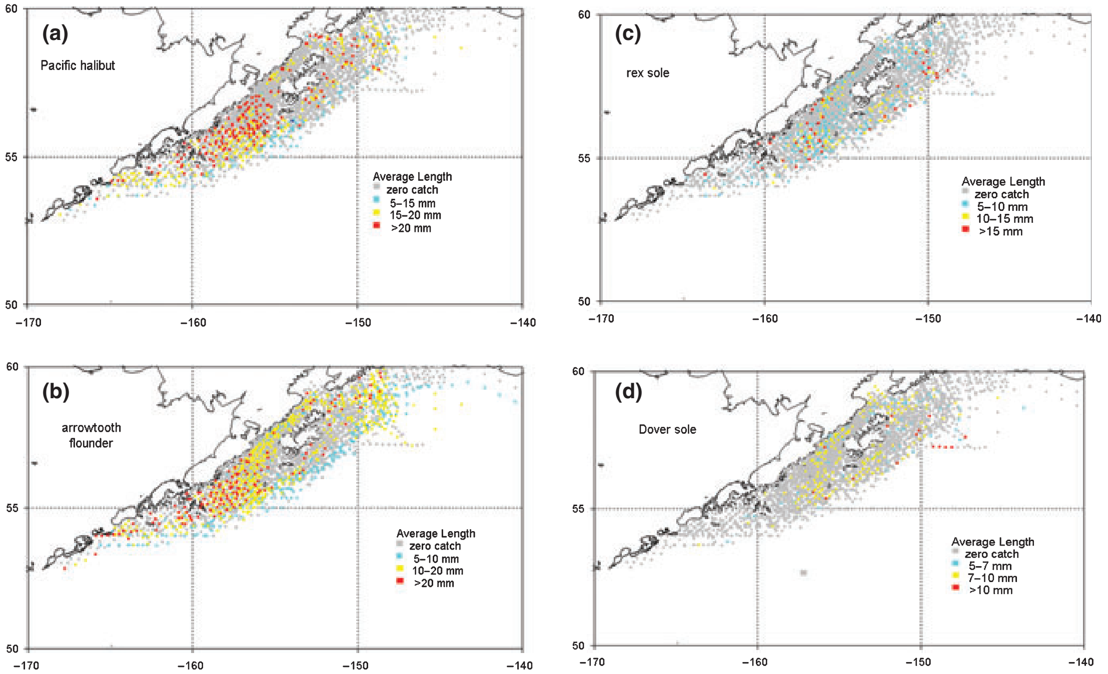

Figure 11 Mean lengths of larvae in samples from AFSC ichthyoplankton surveys: (a) Pacific halibut; (b) arrowtooth flounder; (c) rex sole; and (d) Dover sole. For Pacific halibut and arrowtooth flounder, the distribution of catches with larger mean lengths is inshore of those with smaller mean lengths, whereas there does not appear to be a trend for Dover and rex sole.

Bay. Age-1 Dover sole ($n = 284$) were captured at 20 stations, all nearshore in bays.

Age-0 Pacific halibut have been caught in beam trawl surveys near or outside the mouths of bays <40 m (average 26 m) depth on mixed sand substrata (Norcross *et al.* 1999). In shrimp trawl surveys, several catches of age-0 halibut were made in bays or nearshore, and age-1 halibut were similarly most abundant in bays around Kodiak Island or nearshore, with a few over the shelf (Fig. 3e).

Arrowtooth flounder age-0 juveniles, like halibut, are found in beam trawls nearshore, but in somewhat deeper water (average 55 m) in mixed sand sediment with a high mud content (Norcross *et al.* 1999). In shrimp trawl surveys, age-0 arrowtooth flounder were caught nearshore or in bays, and age-1 catches were similarly located (Fig. 4e). In the GOA, no rex sole <60 mm were captured in beam trawls nearshore (Norcross *et al.* 1998), although age-1 rex sole (69 mm) were captured in August in Kachemak Bay (Abookire *et al.* 2001). No age-0 rex sole were caught in shrimp trawls surveys, but age-1 rex sole were found both in bays near Kodiak Island and in deeper water over the continental shelf (Fig. 5e). By comparison, off Oregon, age-0 rex sole from 40 to 60 mm SL are found in bottom trawls at 150–200 m (Pearcy *et al.* 1977).

Ancillary studies of juvenile flatfishes using beam trawls have collected age-1 Dover sole nearshore in bays in August (Norcross *et al.* 1998; Abookire *et al.* 2001). Our analysis of historical shrimp trawl data found five age-0 Dover sole juveniles (<50 mm) in bays near Kodiak Island and age-1 juveniles were most abundant in bays around Kodiak (Fig. 6e). Scattered individuals were found nearshore over the shelf region. By comparison, off the Oregon coast young Dover sole juveniles are largely found at 130–183 m (Demory 1975, footnoted in Percy *et al.* 1977), but stage-3 larvae may have a ‘landing zone’ over depths of 55–300 m, where they occupy the bottom in daytime and become pelagic at night (Markle *et al.* 1992). Dover sole larvae (40–50 mm SL) can be found in bottom trawl samples. Juveniles progressively move inshore over several months and the age-1 distribution peaks at about 100 m, although the depth of maximum abundance may shift seasonally (Pearcy *et al.* 1977).

The distribution of juvenile flatfishes was also examined from AFSC bottom trawl catches. These nets have a mesh size that is too large to quantitatively sample small juvenile flatfishes, but the relative catch distributions largely support the above findings (Table 3). Dover and rex sole juveniles are distributed in deeper water than arrowtooth flounder and Pacific halibut. Age-1 Dover sole and Pacific halibut juveniles in particular are found in shallower water than age-0s of these species. However, these data also show that age-0 juveniles are not restricted to coastal shallow zones and bays, as individuals of all species can be found offshore.

Discussion of transport mechanisms

Successful movement from offshore and deepwater spawning grounds to shallower, inshore nurseries is a complex, multi-step process involving different biological and physical mechanisms and strategies (Boehlert and Mundy 1987). First, animals need to get from the mesopelagic realm over the slope to the epipelagic zone over the outer shelf, then from the outer shelf–slope onto the mid-shelf, and finally from the mid-shelf to specific nursery habitats. Moreover, the mechanisms exploited to successfully complete each step of the sequence are species-specific. Finally, it is likely that local- and meso-scale singularities in hydrography, bathymetry or landscape structure contribute to regional differences in transport processes as well.

In the GOA, there are several main physical mechanisms for cross-shelf transport of water: (i) episodes of downwelling relaxation that result in transport of offshore water onto the shelf at depth; (ii) bathymetric steering into canyons with strong tidal mixing; (iii) eddies along the shelf break, which can mix water onto the shelf, but largely result in offshore flux (Ladd *et al.* 2005); and (iv) seasonal or episodic periods of downwelling favourable conditions that may transport larvae with surface waters inshore. Offshore-spawning flatfishes may variously take advantage of all these mechanisms for successful colonization of onshore nurseries.

Table 3 Mean depth and standard deviations of offshore-spawning flatfish age-0 and age-1 juveniles caught in AFSC triennial summer bottom trawl surveys, 1984–2005.

	Age-0			Age-1		
Species	Mean depth (m)	Standard deviation (m)	*n*	Mean depth (m)	Standard deviation (m)	*n*
Pacific halibut	101.8	54.1	24	36.7	18.9	1567
Arrowtooth flounder	106.4	43.0	236	110.3	42.5	5150
Dover sole	204.0	132.9	2	104.2	66.5	575
Rex sole	172.0	80.0	27	158.7	76.1	256

n is number caught and measured for length.

Spawning location and season

Spawning location is a critical initial condition in the transport process, as site-specific variability in temperature, hydrography and circulation patterns can profoundly affect horizontal transport and dispersal. In the case of offshore-spawning flatfishes, a spawning orientation that takes advantage of landscape features and organized currents connecting the slope with the shelf seems most suited to on-shelf delivery of eggs. However, maps of the distribution of mature-size adult Pacific halibut and arrowtooth flounder show these species both located in inner Shelikof Strait (as well as some other nearshore areas) and over the continental slope. This observation of spawner distribution is in contrast with egg and larval distributions, which clearly indicate highest densities over the slope. It should be noted that the terms 'mature-size' and 'spawning-condition' are not equivalent, and maturity data on adult Pacific halibut and arrowtooth flounder captured in Shelikof Strait were not collected. Pacific halibut and arrowtooth flounder eggs have not been caught in Shelikof Strait in 25 years of sampling. Furthermore, very few larval halibut or arrowtooth flounder have been captured in Shelikof Strait or the upper sea valley. Therefore, it appears that neither species is actually spawning in Shelikof Strait. The concentrations of arrowtooth and Pacific halibut eggs and small-sized larvae over the continental slope provide more convincing evidence that spawning in these species actually occurs there. The presence of mature-size females in the Shelikof Strait region during the end of their spawning season may be indicative of very quick, rapid migration away from the slope after spawning. However, our data do not suggest rapid migrations between the slope and continental shelf immediately after spawning for adult female rex or Dover sole. In these species, the spawning and egg concentrations tend to co-occur, indicating that the adults maintain a protracted occupation of the slope margin.

Based on the distribution of eggs and early larval stages, specific spawning grounds for Pacific halibut, arrowtooth flounder and Dover sole include the southwestern exit region of Shelikof Strait, Amatuli Trough, and to a lesser extent the sea valley south of the Trinity Islands. On the contrary, rex sole appear to have a more general, less site-specific pattern of spawning distribution, and in turn, their juvenile nursery areas are broader and less specific than those of the other species.

Spawning time and duration of the planktonic stage would be key factors in strategies to utilize seasonally changing hydrographic conditions for onshore transport. Blood *et al.* (2007) hypothesized that arrowtooth flounder commence spawning in late January and most adult females have spent ovaries by late February. While they do not provide an approximate end-date for the spawning season, the presence of small larvae (<5 mm) through early May suggests that some adults are spawning as late as early April (Blood *et al.* 2007). Our data coincide with their findings, as in March and April the vast majority of adult female arrowtooth flounder have moved away from the slope towards and into Shelikof Strait; however, a few hauls in early March and April did capture mature females on the slope. Peak spawning for arrowtooth flounder likely occurs in February, but individuals also appear to have some flexibility and arrowtooth flounder may spawn as late as April. Halibut may have an even shorter spawning season concentrated in the winter months December–March (St. Pierre 1984). Compared to halibut and arrowtooth flounder, both rex sole and Dover sole have protracted and possibly later spawning seasons that extend to June.

Transport onto the shelf

Spawning grounds located at the exit region of submarine canyons (Amatuli, Shelikof, Trinity, etc.) exploit deepwater circulation patterns that transport slope waters up troughs and into the shelf domain. Eggs and larvae at the edges of these features passively penetrate the continental shelf in deep currents that flow up the east sides of the troughs. However, mean flows exit the same canyons on the west side; so it seems likely that some modification of vertical position or passive mixing and entrapment prevents larvae from returning offshore. Ladd *et al.* (2005) postulated that the convoluted bathymetry in submarine canyons amplified tidal signals, generated vertical instabilities, and enhanced cross-isobath movement of water. They presented evidence that these processes resulted in up-mixing of deep nutrients into the euphotic zone, which along with active larval behaviour, seem feasible mechanisms for upward movement of larvae. Tidal transport is especially enhanced in lower Cook Inlet and tidal models also indicate enhanced shoreward tidal currents in Amatuli trough, Kennedy Entrance and the Shelikof sea valley (Foreman *et al.* 2000).

The position of the Alaskan Stream also affects the magnitude of flow up canyons (Stabeno *et al.* 2004). The Alaskan Stream should exert its greatest influence on up-canyon transport when the current is concentrated at the shelf break, and least influence when the flow is further from the shelf edge boundary (Stabeno, personal communication). Thompson *et al.* (1990) suggest that the near-shelf configuration is most common in winter, coincident with the timing of production Pacific halibut and arrowtooth flounder eggs and larvae. Representative paths of satellite-tracked drifters drogued at 40 m show the potential areas where larvae travelling in the coastal edge of the Alaskan Stream along the outer shelf may enter shelf waters (Fig. 12a). In particular, there is a noticeable commonality in drifter trajectories near the entrance to Shelikof Strait, with drifters entering the Strait on the eastern side of the sea valley (Fig. 12a, inset). Factors affecting circulation in Shelikof Strait are fundamentally different from factors affecting circulation in other nearby canyons (Amatuli, Barnabus, Chiniak). Whereas deepwater ingress in these lesser canyons is primarily driven by tidal amplification, Shelikof supports a two-layer, estuarine-like flow driven by the ACC and freshwater runoff in the top layers and ingress of saline water from the continental slope at the bottom (Reed *et al.* 1987).

The intermittent presence of large eddies can interrupt the flow of the Alaskan Stream, altering circulation and influencing slope–shelf exchange (Weingartner 2007). Anticyclonic eddies formed off the continental shelf can aggregate larvae living in near-surface waters and draw deep-living eggs and early-stage larvae towards the surface through upwelling. In particular, 'Yakutat' eddies formed in winter propagate along the shelf break, and often pause near Kodiak Island for several months (Ladd *et al.* 2005). Representative trajectories of satellite-tracked drifters influenced by Yakutat eddies (Fig. 12b) show the potential for different fates of

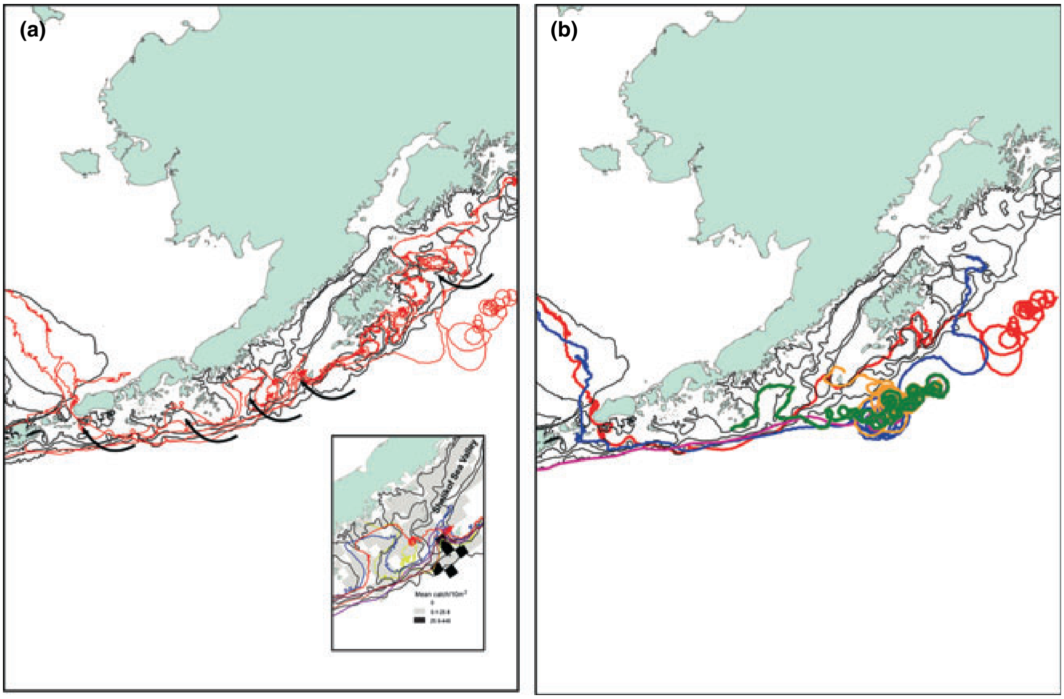

Figure 12 (a) Trajectories of satellite-tracked drifters in the coastal edge of the Alaskan Stream that show where larvae in the current may enter the shelf region. Drifters were drogued at 40 m. Most likely pathways marked with black arrows. (Inset)Trajectories of satellite-tracked drifters over 100–200 m southwest of Kodiak I. that show flow up the western side of the exit region of the Shelikof Sea Valley. Several drifters show a strong tidal signal and one shows a transgression across the shelf that is relatively common in this vicinity. Drifters were drogued at 40 m. In addition shown is the mean aggregate abundance of larvae of all four offshore-spawning flatfish species, showing movement of larvae up the eastern side of the sea valley. (b) Trajectories of satellite-tracked drifters released in offshore eddies showing potential pathways. Drifters were drogued at 40 m.

larvae. Two drifters stayed offshore, never reaching the shallow waters of the continental shelf, one of which entered the Bering Sea through Unimak Pass. The others showed tracks that could potentially bring larvae onto the shelf. One drifter traversed the shelf off Kodiak Island, following the complex topography, and travelling downstream, deflected into the entrance of Shelikof Strait before moving off-shelf into the Alaskan Stream. Another drifter entered the shelf through Shelikof Strait and grounded near Chirikof Island, and the final one entered the shelf zone near the Shumagin Islands.

Transport along the shelf

Once over the shelf domain, satellite-tracked drifter data (above) indicate that drifters meandered over the shelf or exited the sea valley back into the Alaskan Stream. From 1985 to 2005, 37 drifters travelled past Kodiak Island in the Alaskan Stream. Of those that were inside the 200 m isobath when passing by Chirikof Island, 18 of 23 (78%) showed a deflection into the Shelikof Sea Valley and 17 of those transgressed shallow water <100 m within 6 months. Most of those crossed the shelf just downstream of the sea valley. Among the drifters passing Chirikof Island outside of 1000 m, only 1 of 14 (7%) showed a deflection towards Shelikof Strait, but 11 eventually crossed the shelf in waters <100 m; however, most of those shelf entries occurred in Unimak Pass or in the Aleutian Islands. Drifters appear to be retained along distinct isobaths, closely following major topographic features in the GOA. For example, drifters often follow the arc of the 100-m isobath immediately west of the Shumagin Islands (Fig. 13a), showing the opportunity for larvae to be delivered nearshore either to the Peninsula or to the Shumagin Islands. These observations illustrate the importance of bathymetric steering in the GOA, and suggest that co-incident larval transport should occur along these bathymetric pathways.

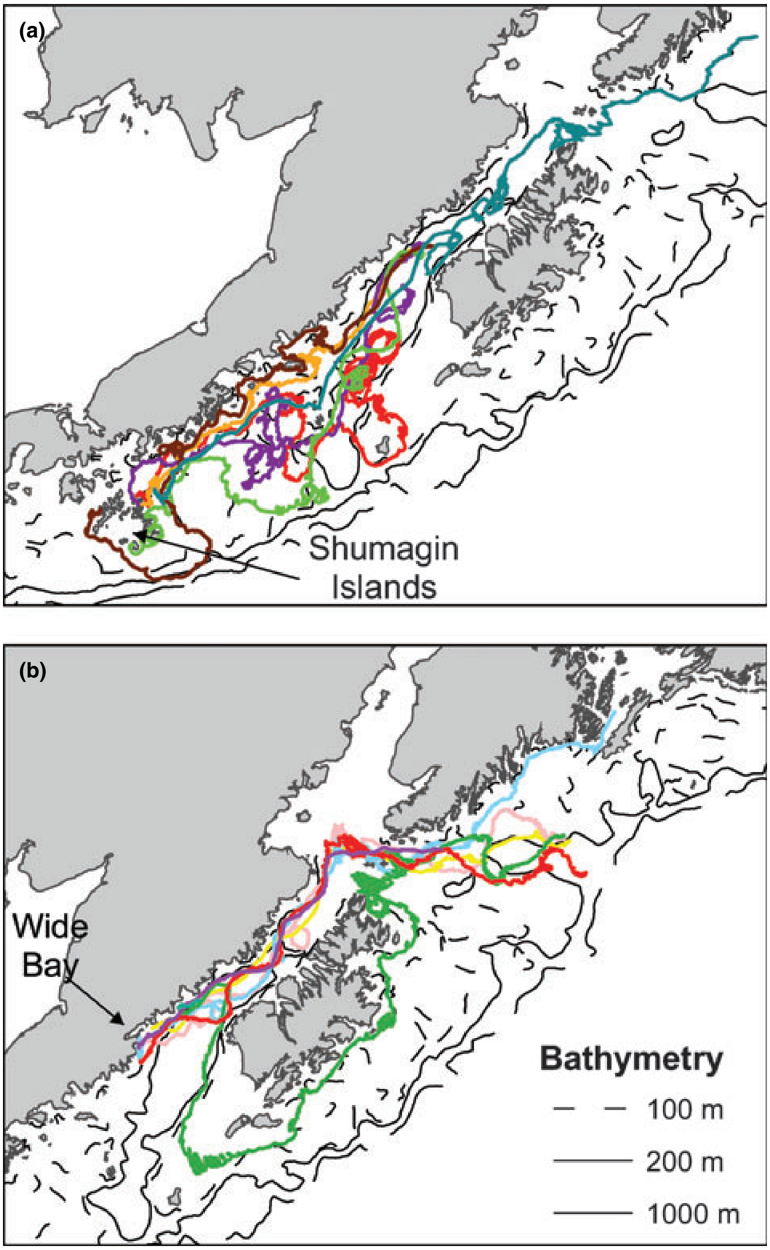

Figure 13 Trajectories of satellite-tracked drifters that ran aground: (a) in the Shumagin Islands; and (b) along the Alaska Peninsula near Wide Bay. Drifters were initially released at the eastern-most point of the trajectory, and grounded at the western-most point of the trajectory. Drifters were drogued at 40 m.

Further analysis of the satellite-tracked drifters for evidence of grounding may indicate regions where larvae may be brought close inshore near favourable nursery regions. Drifters in the Alaskan Stream that transgress onto the continental shelf, or those released in the ACC, often ground in the Shumagin Islands or near Wide Bay along the Alaska Peninsula or (Fig. 13a & b). These areas also support comparatively high abundances of immature arrowtooth and Pacific halibut, suggesting coincident movement of drifters and larvae.

Offshore-spawning flatfish species, and particularly Dover and rex sole that spawn later and settle from the plankton in autumn and winter, may be using seasonal changes in transport to move inshore towards nurseries. As noted earlier, rex and Dover sole larvae occur above the mixed layer (<40 m depth) and may benefit from increases in the intensity of downwelling favourable winds during autumn months to advect them inshore. The seasonal peak in wind-induced onshore transport also coincides with settlement of rex and Dover sole. Spawning time and the duration of the planktonic stage would be key factors in utilization of downwelling.

Larval behaviours

Different species of flatfish larvae within a geographic region may display different vertical migration behaviours that influence their advection patterns (Grioche *et al.* 2000). Larval behaviours that lead to differences in transport patterns need more specific study. However, it seems clear that the offshore-spawning flatfish species demonstrate different vertical distribution and ontogenetic migration patterns associated with favourable transport conditions and seasonally varying onshore circulation. For example, arrowtooth flounder and Pacific halibut eggs remain relatively deep in the water column and are retained in waters over the continental slope and outer shelf. Deep water column distribution is an adaptation for retention used by other species as well (Koutsikopoulos *et al.* 1991; Grioche *et al.* 2000). Early-stage larvae rise in the water column and appear to accumulate in sea valleys, and later-stage larvae begin to appear in nearshore regions and bays. For both of these species, there is a larval size gradient with larvae of increasing size found further inshore, indicating directed movement.

In the case of Dover and rex sole, eggs float quickly to the surface layer, where they get dispersed in wind-driven surface currents. The currents have a mean climatological orientation, but over the short duration of the egg stage, currents can be variable. Thus, Dover and rex sole eggs and early-stage larvae are widely dispersed over the continental shelf. There is no size gradient of larvae across the shelf that would indicate larvae of increasing size are accumulating closer to shore. These species have a long planktonic life, juveniles have a long and flexible settling period (Abookire and Bailey 2007) and the juvenile stages of these species, especially rex sole, are not dependent on bays and can settle in relatively deep waters over the shelf. For Dover sole, movement of post-larvae into shallower water may occur after settlement (Markle *et al.* 1992). All of these factors indicate an adaptable and facultative settling process.

Hare and Govoni (2005) found that the average vertical distribution patterns of larvae are related to the three-layer transport patterns of waters of the southeast U.S. continental shelf. Taxa that are retained on the shelf live in deep water, while those that are exported from the shelf inhabit intermediate water. Species that are transported into estuaries live in shallow water where wind-driven transport may carry them inshore. These results are broadly similar to the findings for flatfish larvae in the northeast Atlantic and other seas (for example: Koutsikopoulos *et al.* 1991; Amara *et al.* 1998; Grioche *et al.* 2000). In the California Current, vertical distribution of larval bivalves is a critical factor in their transport. Slow-swimming bivalve larvae above the thermocline are swept offshore during upwelling, but those below the thermocline were brought onshore. Some other taxa were not swept onshore or offshore by upwelling, but they seem to use behaviour to maintain themselves on the shelf (Shanks and Brink 2005).

Settlement and recruitment issues

While it is clear that Pacific halibut and arrowtooth flounder achieve a size appropriate for settlement by July–August and have moved inshore near settlement habitat, the fate of rex and Dover sole larvae is less obvious from our data. Off the Oregon coast, it is well-established that rex and Dover sole have long planktonic lives, up to 18 months (Pearcy *et al.* 1977; Markle *et al.* 1992; Butler *et al.* 1996). However, in the GOA, the distribution of Dover and rex sole post-larvae remains unresolved. Several alternative hypotheses are: (i) Dover and rex sole larvae settle facultatively and indiscriminately anywhere along the continental shelf and overwinter there, moving inshore by age-1 to appear in nearshore nursery areas around Kodiak Island and along the Alaska Peninsula; (ii) Larvae do not settle on the continental shelf, but rather post-larvae are advected offshore during periods of relaxed summer downwelling, and settlement occurs relatively offshore in deep water at comparatively small sizes; (iii) Larvae remain in the plankton offshore for over a year, settling at very large sizes. Post-settlement fish then move inshore after the first winter (age-1) when they have attained sufficient sizes to be less vulnerable to inshore piscivorous groundfishes.

Habitat specificity is critical to optimal growth and survival of the earliest settling sizes of flatfish larvae, as many young-of-the-year flatfishes have comparatively narrow home ranges with demonstrated site-fidelity and specialized requirements (Able and Fahay 1998; Burrows *et al.* 2004). Although the juveniles of the offshore species examined here appear to have relatively nearshore nurseries (Norcross *et al.* 1998, 1999), age-0 juveniles of all species can be found across the continental shelf in waters to 200 m depth (Figs 3e, 4e, 5e & 6e), and in some cases deeper (Dover and rex sole). In general, our current assertions of juvenile nursery habitat requirements is constrained by limited geographic sampling and gear-specificity issues.

Abundance of suitable prey is an important component in habitat quality (Gibson 1994). Diet similarities and differences exist among juvenile arrowtooth flounder and Pacific halibut, and juvenile Dover and rex sole that are reflected in juvenile nurseries. While the diets of age-0 arrowtooth flounder juveniles have not been specifically studied, juveniles <200 mm largely eat pandalid shrimp, euphausiids and capelin (Yang 1993), and adults are piscivorous. Adult Pacific halibut are also piscivorous, but on the nursery grounds, age-0 halibut eat mainly crustaceans, including crabs and crab larvae, copepods, pandalid shrimp, euphausiids and amphipods (St-Pierre and Trumble 2000). Holladay and Norcross (1995) found age-0 Pacific halibut to consume mysids, cumaceans and amphipods. Halibut <250 mm eat crabs, cephalopods, shrimp and small fish (Yang 1993). Juvenile Dover sole and rex sole appear to share commonalties as well, although knowledge of their diets is largely based on studies from Oregon (Pearcy and Hancock 1978). The diet of rex sole <100 mm SL diet is mostly crustaceans, mixed with a smaller proportion of annelids, and adult rex sole feed almost exclusively on benthic invertebrates. Dover sole <100 mm SL eat a diet of mostly annelids, comprised of a few species of polychaetes, in summer, and mixed annelids and crustaceans (mostly amphipods) in winter. Adult Dover sole also feed almost exclusively on benthic invertebrates. Whether these diet similarities and differences are a result of habitat selection or a cause of habitat selection is unknown.

The leverage of transport in the recruitment process of marine flatfishes depends on several key factors, including the proximity of spawning to the juvenile nursery, orientation to prevailing currents, and the size and continuity of the target nursery habitat (Gibson 1994). Transport to inshore nursery grounds must be relatively important for recruitment of the offshore-spawning species examined here; in a region like the northern GOA, the suitable juvenile flatfish nursery is relatively narrow and fragmented. By comparison, the inner shelf of the Bering Sea provides a continuous and vast extent of potentially suitable juvenile habitat (Bailey *et al.* 2003). For both the GOA and Bering Sea systems, if larvae are using passive transport mechanisms to arrive on the shelf, then variability in strength and direction of ocean currents plays a major role in successful recruitment to the shelf zone, but finding a suitable nursery area is an additional obstacle in the GOA. It seems likely that, given the specific habitat requirements of settling flatfish juveniles (depth, turbidity levels, substrata, prey availability, predation avoidance, etc.), as well as the discontinuous availability of suitable habitat in the GOA, late-stage larvae and juveniles probably exert some active control over the process of nursery localization and selection.

Future studies

The inferences we have made about species-specific differences in spawning and distribution of early ontogenetic stages are based on broad-scale and non-targeted surveys. Better data on spawning grounds, including how adults locate spawning grounds and whether they return to the same areas, contributes to knowing whether spawning ground selection is highly specific and locally adapted. Information on the swimming capabilities of larvae, their behaviour in currents and to shear in the water column, and the timing and extent of vertical movements in the water column, helps in understanding the interaction of larvae with currents and especially with tidal flows. Details of settlement behaviour and nursery requirements, facultative and obligate settling with ontogeny, and behaviour on suitable and unsuitable habitat can provide a better understanding of post-transport processes. In particular, optimal habitats for growth and survival of juveniles are not well known. A combination of directed studies including laboratory experiments, at-sea tagging, targeted surveys and vertical structured sampling with simultaneous information on water flow and benthic sampling in the GOA during fall and winter would be useful approaches to solving these problems. These future studies will be critical to understanding the effects of climate change, over-fishing and human-induced changes in nursery quality on flatfish productivity.

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