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The distribution of life cycle stages of two deep-water pleuronectids, Dover sole (*Microstomus pacificus*) and rex sole (*Glyptocephalus zachirus*), at the northern extent of their range in the Gulf of Alaska

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Abstract

Dover sole (*Microstomus pacificus*) and rex sole (*Glyptocephalus zachirus*) are both commercially valuable, long-lived pleuronectids that are distributed widely throughout the North Pacific. While their ecology and life cycle have been described for southern stocks, few investigations have focused on these species at higher latitudes. We synthesized historical research survey data among critical developmental stages to determine the distribution of life cycle stages for both species in the northern Gulf of Alaska (GOA). Bottom trawl survey data from 1953 to 2004 (25 519 trawls) were used to characterize adult distribution during the non-spawning and spawning seasons, ichthyoplankton data from 1972 to 2003 (10 776 tows) were used to determine the spatial and vertical distribution of eggs and larvae, and small-meshed shrimp trawl survey data from 1972 to 2004 (6536 trawls) were used to characterize areas utilized by immature stages. During the non-spawning season, adult Dover sole and rex sole were widely distributed from the inner shelf to outer slope. While both species concentrated on the continental slope to spawn, Dover sole spawning areas were more geographically specific than rex sole. Although spawned in deep water, eggs of both species were found in surface waters near spawning areas. Dover sole larvae did not appear to have an organized migration from offshore spawning grounds toward coastal nursery areas, and our data indicated facultative settling to their juvenile habitat in winter. Rex sole larvae progressively moved cross-shelf toward shore as they grew from April to September, and larvae presumably settled in coastal nursery areas in the autumn. In contrast with studies in the southern end of their range, we found no evidence in the GOA that Dover or rex sole have pelagic larval stages longer than nine months; however, more sampling for large larvae is needed in winter offshore of the continental shelf as well as sampling for newly settled larvae over the shelf to verify an abbreviated pelagic larval stage for both species at the northern end of their range.

Keywords: Life cycle; Larval transport; Spawning; Pleuronectids; *Microstomus pacificus*; *Glyptocephalus zachirus*; Gulf of Alaska

1. Introduction

Transport of egg and larval stages is a critical aspect of the early life history of flatfishes because juvenile nurseries are almost always inshore of spawning areas

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(Minami and Tanaka, 1992). Flatfishes require specific nursery qualities defined by substrate, depth, temperature, salinity and predator/prey characteristics (Gibson, 1994) and nurseries must be adaptable to ontogenetic changes required by flatfishes as they develop (Able et al., 2005). Different species and even different regional stocks within species may utilize a variety of mechanisms for dispersal and/or target-oriented transport to suitable nurseries (Bailey et al., 2005).

Nursery areas for pleuronectids in coastal waters of Alaska have been identified along the Alaska Peninsula (Norcross et al., 1999), in the bays of Kodiak Island (Norcross et al., 1995), and in lower Cook Inlet (Abookire and Norcross, 1998). Flatfishes that spawn outside of their coastal nursery areas rely on larval transport from the spawning grounds for successful recruitment (Van der Veer and Witte, 1999; Bailey and Picquelle, 2002). For certain pleuronectids, such as rock soles (Stark and Somerton, 2002; *Lepidopsetta bilineata* and *L. polyxystra*), flathead sole (Porter, 2005; *Hippoglossoides elassodon*), and Alaska plaice (Bailey et al., 2003; *Pleuronectes quadrituberculatus*), spawning occurs on the continental shelf and larvae must be retained by eddies and coastal currents near suitable nursery habitats. Alternatively, Pacific halibut (*Hippoglossus stenolepis*) and arrowtooth flounder (*Atheresthes stomias*) spawn offshore and their larvae depend on cross-shelf transport presumably through sea valleys and troughs (Bailey and Picquelle, 2002).

Dover sole (*Microstomus pacificus*) and rex sole (*Glyptocephalus zachirus*) are long-lived, deep-water pleuronectids that are distinctive because their larvae can grow to exceptionally large sizes and experience an extended pelagic phase. Collections off the coast of Oregon have included pelagic Dover sole larvae measuring 65 mm standard length (SL) and rex sole larvae of 89 mm SL (Pearcy et al., 1977). The vast majority of pleuronectid species metamorphose in six months or less (Castillo, 1995); however, Dover sole larvae have a very prolonged pelagic stage that reportedly lasts between 9 months and 2 years off the U.S. West coast (Pearcy et al., 1977; Markle et al., 1992; Butler et al., 1996), and rex sole larvae are pelagic for about 12 months (Pearcy et al., 1977). Due to the extended duration of their pelagic larval stage, they are vulnerable to dispersal and drift for many months. Given the prolonged time spent in the plankton, environmental factors that impact pelagic survival may actually affect two year-classes and thereby compound recruitment variability for these two unique species.

Dover sole range from southern Baja California to the Gulf of Alaska (GOA), and rex sole have a slightly broader range from central Baja California to the western Bering Sea (Mecklenburg et al., 2002). In addition to their vast geographic ranges, both species inhabit wide depth ranges from shallow nearshore waters up to 1244 m for Dover sole and 850 m for rex sole (Mecklenburg et al., 2002). Historically these species supported an important commercial fishery off the U.S. West coast (Hosie and Horton, 1977; Brodziak and Mikus, 2000), but since the early 1990s the largest commercial harvests of Dover and rex sole have occurred in the central GOA on the continental shelf and slope east of Kodiak Island (Turnock et al., 2002). Until recently, the reproductive biology and spawning season of these species was only described for southern stocks off the U.S. West coast and reproductive adaptations employed at higher latitudes were unknown. Similarly, the ecology and life cycles for these species are unknown at higher latitudes and may be unique. Hence, the main objective of this study was to determine the spawning grounds, egg and larval distribution, and nursery areas of Dover and rex sole in the northern GOA (Fig. 1) through synthesis of historical research survey data among critical developmental stages.

2. Methods

2.1. Collections of adults

Adult fish distribution data were extracted from the groundfish survey database (RACEBASE), available from the bottom trawl surveys conducted in the GOA and Aleutian Islands from 1953 to 2004 by the National Marine Fisheries Service (NMFS) Alaska Fisheries Science Center (AFSC). These surveys represent extensive coverage of the GOA shelf and included 25 519 trawls. The gear used was a modified poly Nor'eastern trawl net with roller gear and a 32 mm mesh codend liner. Only female Dover sole with total length (TL) >43 cm (Abookire and Macewicz, 2003) and female rex sole >34 cm TL (Abookire, 2006) were considered mature adults and included in the analysis. Spawning seasons were defined from previous histological examinations of ovarian tissue as February–May for Dover sole (Abookire and Macewicz, 2003) and October–May for rex sole (Abookire, 2006).

2.2. Collections of eggs and larvae

Data on flatfish eggs and larvae were extracted from the Ichthyoplankton Cruise Database (IchBase), a database encompassing a 30-year time series of ichthyoplankton data (10 776 tows; Table 1) from cruises during 1972–2003 conducted by AFSC and partner institutions in the Gulf of Alaska (methods detailed in Matarese

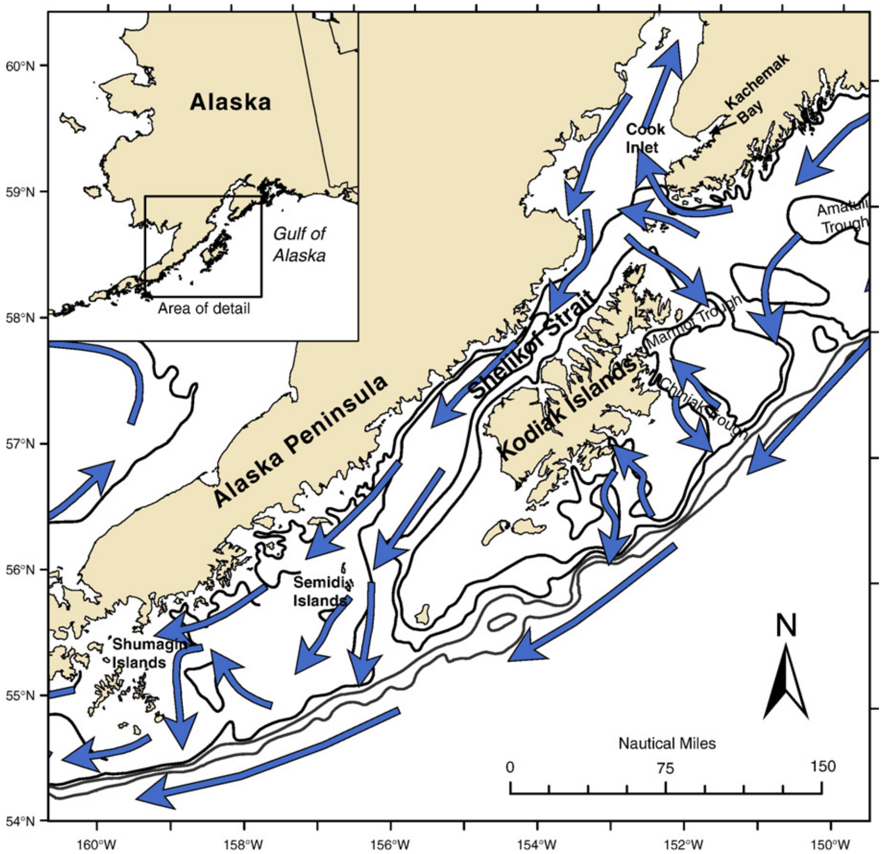

Fig. 1. Area of investigation in the Gulf of Alaska. Directions of surface currents are denoted with arrows, and bathymetric contours are drawn at depths of 200, 400, and 1000 m. Izhut Bay (Iz) is abbreviated. Note that because the projection is not square, longitude and latitude vary on both sides of the graph.

et al., 2003). To examine the distribution of ichthyoplankton, eggs were collected with 60-cm bongo tows with 333–505 μm mesh netting and 1-m Tucker tows with 333–505 μm mesh netting, and larvae were collected with bongo tows, Tucker tows, 6-ft frame Methot tows with 3-mm mesh netting and 505 μm mesh codend, and 6-ft Isaacs–Kidd Midwater Trawl (IKMT) tows with a 505 μm mesh codend. All tows were quantitative and oblique, conducted in a standardized manner using flowmeters. In general, tows were made to the deeper of either 200 m or 10 m off bottom. Catches were preserved in 5% formalin and returned to the laboratory. They were sorted, identified to species and measured at the Plankton Sorting and Identification Center, Szczecin, Poland. Ichthyoplankton identifications were verified by the taxonomic team at AFSC.

To determine vertical distribution of eggs and larvae, data were examined from 151 series of 1-m Mocness tows with 153–505 μm mesh netting collected from 1991 to 2003. In general, 5–9 nets were fished obliquely over 10 m depth intervals in the upper 100 m of the water column. At deeper depths the sampling interval was 10–40 m. Catches in nets were reported for only those tows with positive incidences and by the average depth interval sampled by each net. Bimonthly egg abundance was also examined to estimate the peak adult spawning period.

2.3. Collections of immature fish

Immature fish distribution data were available from the small-mesh trawl surveys for shrimp conducted by

Table 1
Sample size of collections extracted from IchBase during 1972–2003 (n = 10 776)

	January – March	April – June	July – September
Bongo and Tucker tows	729	7482	1716
Methot tows	0	402	348
Isaacs–Kidd Midwater Trawl tows	0	99	0

There were no collections from October to December.

the NMFS and Alaska Department of Fish and Game (ADF and G) in the GOA from 1972 to 2004. 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 footrope. The database contains total species count and total species weight information collected per trawl for 6536 trawls. Individual length data were only collected from 2002 to 2004. Therefore, to isolate immature fish, length-weight regression models from Abookire and Macewicz (2003) and Abookire (2006) were solved for the minimum length at maturity for Dover and rex sole, respectively. The distribution of immature fish was examined from catches where the average species weight in a haul was <0.31 kg for Dover sole and <0.15 kg for rex sole. This is a conservative measure of immature fish distribution, as these criteria of average weight exclude catches where immature fish coexist with adults. Because our classification of immature fish spans several year-classes and due to the low occurrence of trawls with average species weight indicative of newly settled or age-1 fish, we use the term immature rather than juvenile.

3. Results

3.1. Adult fish

From 25 519 bottom trawl hauls taken over 51 years, 18 058 adult female Dover sole were captured in 2032 hauls and 62 910 adult female rex sole were captured in 3647 hauls. Adults of both species were widely distributed from the inner shelf to the outer slope in the non-spawning season. During the spawning season, adult Dover sole aggregated almost exclusively along the slope (Fig. 2a–b) in a few specific locations and adult rex sole concentrated along the slope but also appeared on the outer shelf (Fig. 3a–b).

3.2. Eggs and larvae

Geographical distributions. Dover sole eggs were mostly found between the 200 and 1000 m isobaths over the continental outer shelf and slope region and extending into the outer Shelikof Strait and Amatuli Trough (Fig. 2c). This was consistent with the distribution of

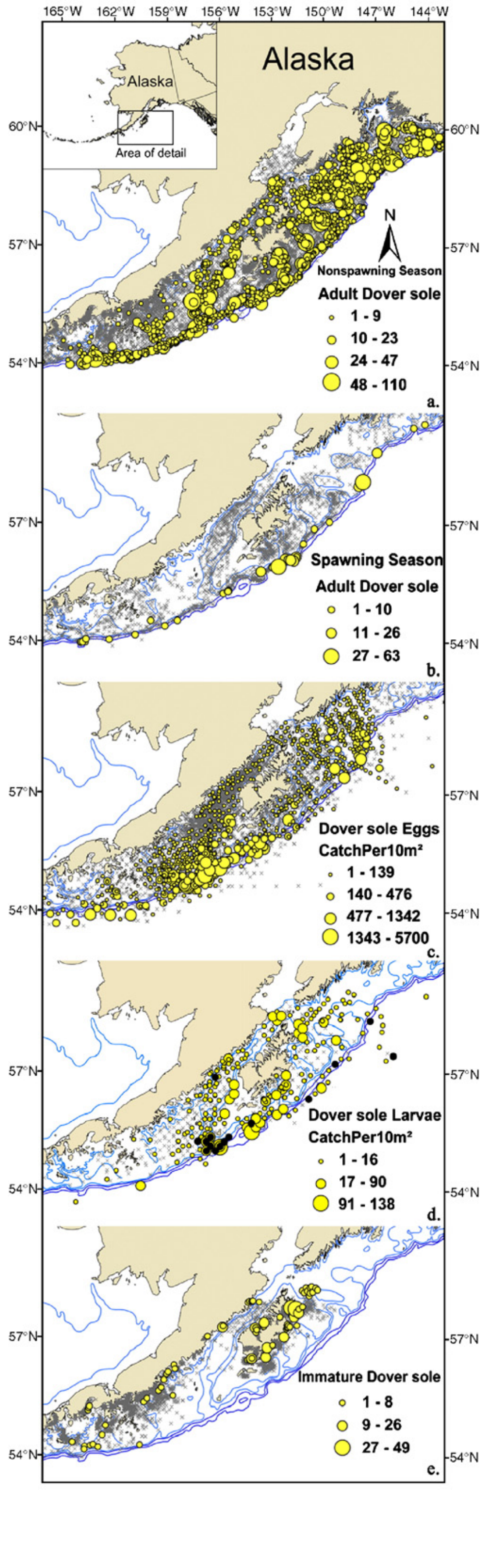

Fig. 2. Distribution of Dover sole at critical developmental stages. Maps are in the following order from top to bottom: (a) adult Dover sole during non-spawning season, (b) adult Dover sole during the spawning season (February–May), (c) Dover sole eggs, (d) Dover sole larvae with black dots denoting locations where the largest larvae (15–29 mm) were captured, and (e) immature Dover sole. Stations with zero catch are denoted with a grey cross. Size of circles is scaled for abundance according to map legends. Depth contours are drawn at 200, 400, and 1000 m.

spawners. Dover sole larvae were present across the continental shelf but concentrated in the inner entrance region of Shelikof Strait (through Amatuli Trough) and

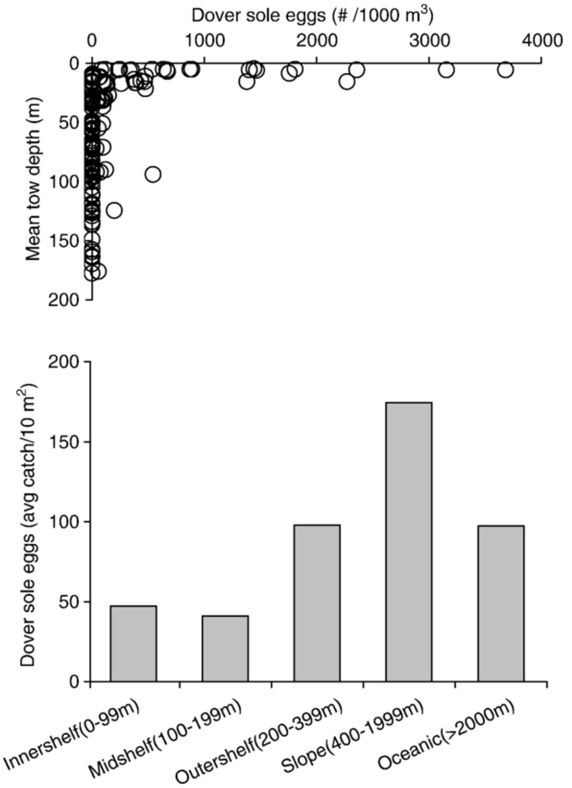

Fig. 4. Vertical distribution of Dover sole eggs in the water column (upper graph) and their spatial distribution in relation to bottom depth from the average catches of positive tows (lower graph).

at the outer exit region of the Strait, largely on the Kodiak side of the Strait (Figs. 1 and 2d).

The distribution of Dover sole eggs and larvae by size category was examined in relation to bottom depth from the average catches of positive tows. As noted above eggs were mostly located over the outer continental shelf and slope (Fig. 4). All size categories of larvae were distributed evenly across the shelf and into oceanic water. No Dover sole larvae > 10 mm were caught in the shallowest depth (inner shelf) zone (Fig. 5); furthermore, the largest larvae (15–29 mm) were mostly caught offshore along the slope (Fig. 2d).

Rex sole eggs were more widely distributed than Dover sole eggs, an observation that was consistent with

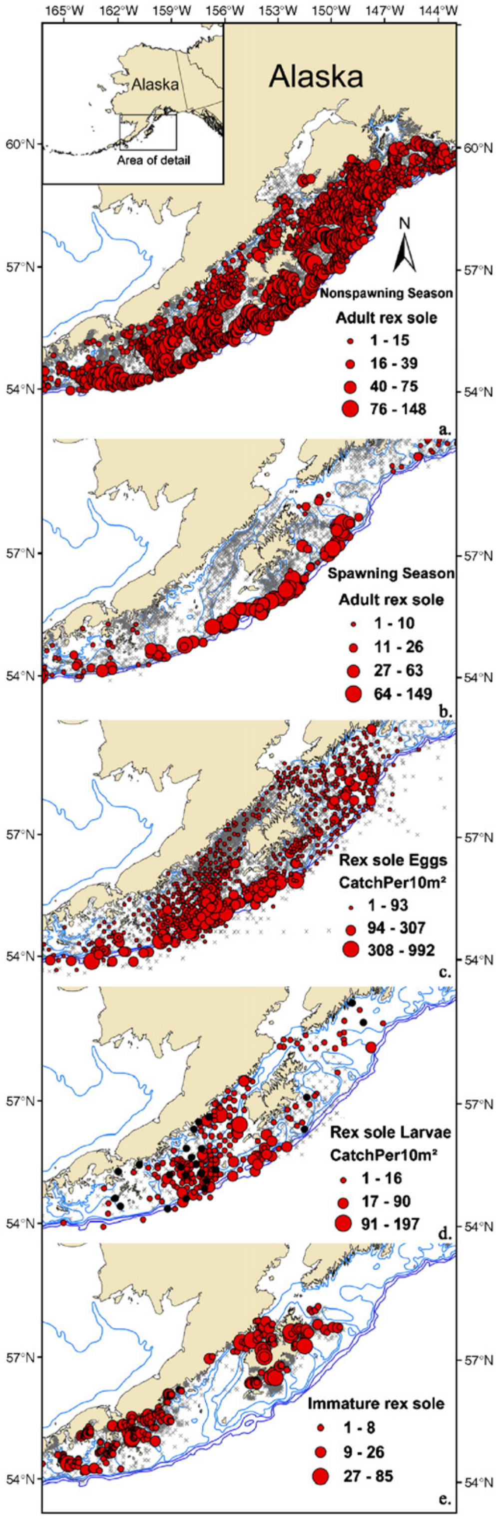

Fig. 3. Distribution of rex sole at critical developmental stages. Maps are in the following order from top to bottom: (a) adult rex sole during non-spawning season, (b) adult rex sole during the spawning season (October – May), (c) rex sole eggs, (d) rex sole larvae with black dots denoting locations where the largest larvae (20–59 mm) were captured, and (e) immature rex sole. Stations with zero catch are denoted with a grey cross. Size of circles is scaled for abundance according to map legends. Depth contours are drawn at 200, 400, and 1000 m.

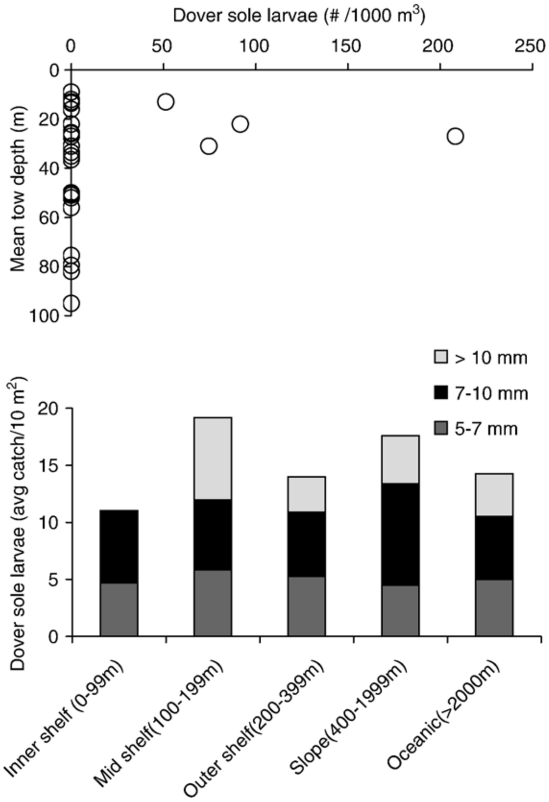

Fig. 5. Vertical distribution of Dover sole larvae in the water column (upper graph) and their spatial distribution by size category in relation to bottom depth from the average catches of positive tows (lower graph). No Dover sole larvae >10 mm were caught in the shallowest depth (inner shelf) zone.

the distribution of adult rex sole during the spawning season. Like Dover sole, rex sole eggs were concentrated along the continental slope, in outer Shelikof Strait, and in Amatuli Trough, but rex sole eggs also extended inshore through Chiniak and Marmot Troughs and near the sea valley crossing the shelf east of the Shumagin Islands (Figs. 1 and 3c). Rex sole larvae were distributed across the shelf region, with concentrations extending up Shelikof Strait, and along the 100–200 m isobath along the sides of the Strait (Fig. 3d).

The distribution of rex sole eggs and larvae by size category was examined in relation to bottom depth from the average catches of positive tows. As noted above, eggs were mostly located over the continental shelf and slope (Fig. 6). All size categories of larvae were distributed evenly across the shelf and into oceanic water. The largest rex sole larvae were absent in the deepest depth (oceanic) zone (Fig. 7).

Vertical distribution of eggs and larvae. Dover sole eggs in 31 vertical Mocness series were mainly found in the upper 40 m of the water column with the highest concentrations in the upper 20 m (Fig. 4). Several deep catches of eggs between 80–120 m were examined and were found to be very early stage eggs. High catches of Dover sole eggs were also recorded in neuston tows, with catches to 279,178 eggs/1000 m^3. There were relatively few incidences (4 vertical series) of Dover sole larvae in the Mocness tows. All Dover sole larvae (size range 6.0–15.2 mm) were caught in the upper 30 m of the water column (Fig. 5).

Rex sole eggs in 34 vertical Mocness series were mainly found in the upper 40 m of the water column with highest concentrations in the upper 20 m (Fig. 6). There were numerous catches in deeper water from 80–130 m, but an examination of eggs from several of these tows showed them to be very early stages. Rex sole eggs were also common in neuston tows, with maximum catches of 878 eggs/1000 m^3. Rex sole larvae were caught in 6 Mocness tow series, and all larvae (size range 5.1–38.3 mm) were in the upper 40 m of the water column, with most in the upper 20 m (Fig. 7).

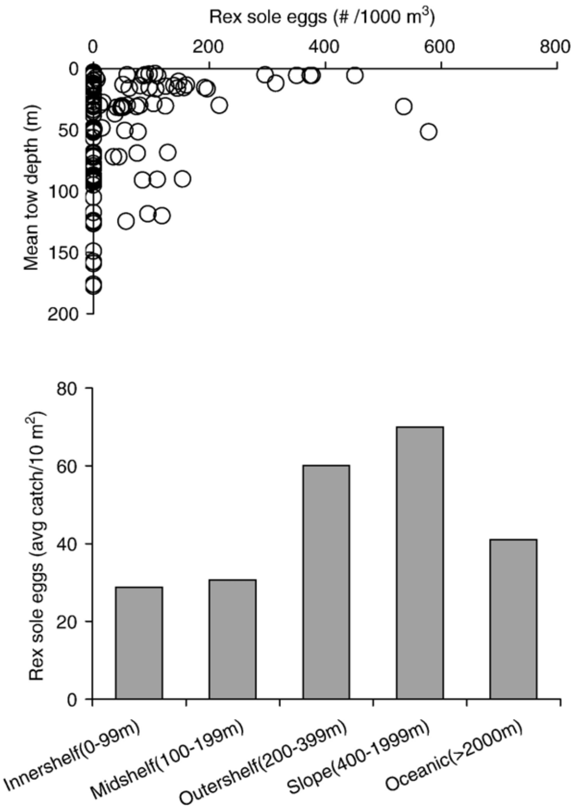

Fig. 6. Vertical distribution of rex sole eggs in the water column (upper graph) and their spatial distribution in relation to bottom depth from the average catches of positive tows (lower graph).

Spawning time and seasonal variation in larval length. Based on egg abundance in the plankton the majority of Dover sole began spawning in late April and continued until mid-June (Fig. 8). The smallest larvae (6.0–10.0 mm) were caught from late April to July. The largest Dover sole larva collected was 29 mm in late September. In the case of rex sole, the majority of spawning began in mid-April and continued until mid-June (Fig. 8). For rex sole larvae, a seasonal increase in the length frequency was more obvious and we caught more large larvae in our surveys. The largest rex sole larva captured was 59 mm in late September.

3.3. Immature fish

From 6536 shrimp trawl hauls taken over 32 years, 3539 immature Dover sole were captured in 216 hauls and 10 273 immature rex sole were captured in 960 hauls. Immature Dover sole were concentrated near-shore in bays (Fig. 2e) with lesser numbers in relatively shallow waters over the continental shelf. By contrast,

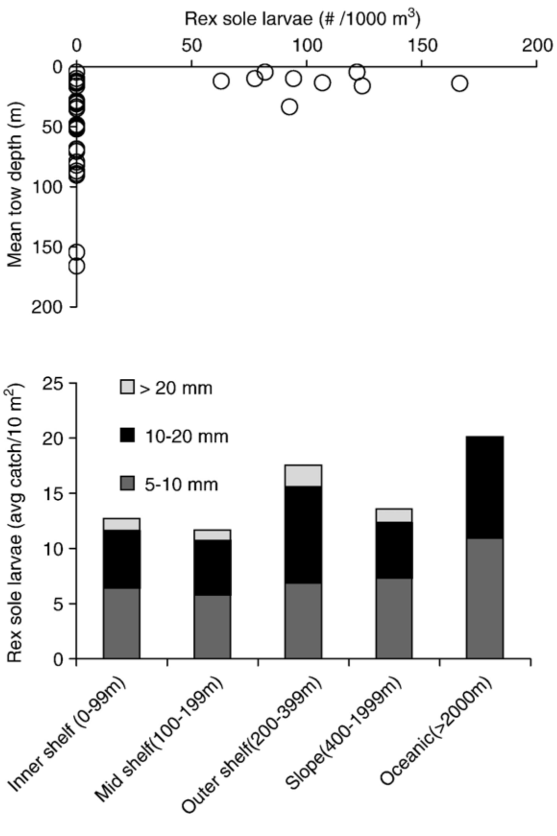

Fig. 7. Vertical distribution of rex sole larvae in the water column (upper graph) and their spatial distribution by size category in relation to bottom depth from the average catches of positive tows (lower graph).

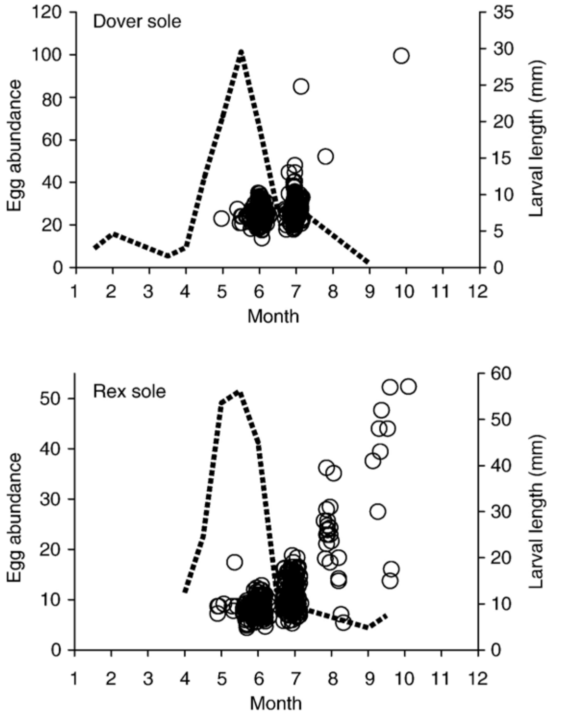

Fig. 8. The average bimonthly abundance of eggs (catch per 10 m^2) in positive catches is shown with the dashed line corresponding to the primary y-axis. Dover sole eggs were collected from late January to late September (upper graph) and rex sole eggs were collected from April to late September (lower graph). Individual larval lengths (mm) are plotted in open circles according to date, and length values are shown on the secondary y-axis. Months are denoted numerically on the x-axis.

immature rex sole were more widely distributed over the shelf and also in bays (Fig. 3e).

4. Discussion

In the central GOA, the peak spawning period for Dover sole based on egg collections is from April to mid-June, with eggs present from late January to July. Based on histological analysis of ovarian tissue, Abookire and Macewicz (2003) estimate the spawning season for Dover sole to extend from at least February to May, noting that January collections were absent. Egg collections corroborate this spawning window and, because incubation time of Dover sole eggs averages 18 days between 8° and 12 °C (Butler et al., 1996), they indicate that the spawning season for Dover sole likely commences in January. Surprisingly, rex sole egg collections indicate a more abbreviated spawning season than the October to May spawning period estimated from histological analysis of ovarian tissue (Abookire, 2006). The incubation time for rex sole eggs is unknown, and there is no clear answer to reconcile the different estimates of rex sole spawning season. However, we note the relative paucity of ichthyoplankton sampling in the GOA from October to March. As well, ichthyoplankton samples with the most eggs were collected offshore of where most of the histology samples were taken, and the spatial and depth differences in spawning areas may account for some of the discrepancy between estimates of spawning season.

Adult Dover sole and rex sole are widely distributed in the central GOA from the inner shelf to outer slope during the non-spawning season and undergo a marked migration to spawn. Dover sole spawn exclusively on the continental slope and rex sole, although apparently less site specific, also concentrate spawning along the slope. Similar patterns of adult distribution were observed along the Oregon coast where Dover sole spawn in specific offshore sites along the slope (Hagerman, 1952; Hunter et al., 1990) and rex sole spawn in deep water but do not appear to have specific spawning sites (Pearcy et al., 1977). At southern latitudes, both Dover and rex sole larvae fit the life history pattern typical for flatfish that are spawned offshore; they spend a longer time in the plankton, metamorphose at a larger size, and display higher variability in size-at-settlement (Minami and Tanaka, 1992). At the northern extent of their range, these species may behave differently and remain pelagic for a shorter duration.

4.1. Dover sole

Two distinctive features of Dover sole development include the uncoupled process of metamorphosis approximately 3–6 months after settlement to bottom habitats (Markle et al., 1992), and the irregular growth rates among larval stages (Butler et al., 1996). Larval Dover sole grow rapidly in length during the first 200 days, then growth abruptly stops for the next 100 days during a compensatory shrinkage phase, after which growth slowly resumes during the remaining larval stages which can span an additional 400 days (Markle et al., 1992; Butler et al., 1996). Additionally, the early life history of Dover sole seems to be extremely complex with pelagic juveniles reported by Butler et al. (1996) and benthic larvae referred to by Toole et al. (1993).

Dover sole larvae remain in the plankton for over a year off the U.S. West coast (Pearcy et al., 1977; Markle et al., 1992; Butler et al., 1996); however, the absence of large larvae in GOA spring ichthyoplankton collections suggests the possibility of a more condensed pelagic larval phase. The largest Dover sole larva collected in this study was 29 mm, which is much smaller than the maximum size of 74.9 mm SL reported by Markle et al. (1992). It is possible that our primary sampling gears (Tucker and bongo nets, n=9927) were inadequate to collect large Dover sole larvae overwintering offshore. Pearcy et al. (1977) sampled with both bongo nets and Isaac–Kidd midwater trawls (IKMT) and demonstrated a striking difference in the selectivity of the gears. Additionally, Toole et al. (1997) used a bottom trawl to successfully sample late stage larvae and newly settled juvenile Dover sole. However, our analysis of 849 IKMT and Methot tows during spring and summer GOA surveys also indicated the absence of large Dover sole larvae in plankton samples one year after being spawned. As well, nearly 400 oblique tows using a pelagic anchovy trawl with a 3 mm mesh codend liner during night and day over the continental shelf in September 2001, 2003, and 2005 (Wilson et al., 2006) failed to catch age-0 Dover sole (Matt Wilson, NMFS/AFSC, unpub. data).

Furthermore, we have reports of 39–50 mm Dover sole collected in the GOA in bottom trawls. Norcross et al. (1998) captured a 39 mm Dover sole with a small-meshed beam trawl in September in Kachemak Bay, Alaska. In addition, during the small-mesh shrimp trawl survey described in the methods four Dover sole larvae (46–50 mm TL) were captured (Dave Jackson, Kodiak ADF and G, unpub. data). Examination of the otoliths from one of these Dover sole (46 mm TL) collected nearshore in Izhut Bay (Fig. 1) in late October had 176 increments and thus was likely spawned in April. This specimen had secondary primordia that had formed between 110–120 increments on the otoliths which is indicative of settling in September (Toole et al., 1993). The absence of Dover sole larvae larger than 29 mm in 30 years of ichthyoplankton collections combined with the presence of 39–50 mm Dover sole in bottom trawls may indicate that in the GOA they adopt a benthic existence at a smaller size and after a shortened pelagic phase than observed at southern latitudes. We are missing 30–39 mm individuals from samples either because of gear selectivity (both bottom and pelagic trawls), sampling location (not enough sampling in the right areas) or sampling intensity (not enough sampling given the low abundances). In any case, the absence of larger Dover sole larvae in our pelagic samples precludes definitive determination of the minimum time to settle from the plankton.

Dover sole eggs rise quickly into the surface layer. This leads to wide dispersal across the shelf and slope either through onshore advection of surface waters during predominant downwelling or periodic spring and summer upwelling events which lead to offshore transport (Ladd et al., 2005). Most of the Dover sole larvae in our collections were small (5–15 mm) and distributed over depths from 50–500 m, while the largest Dover sole larvae (15–29 mm) were collected much further offshore over depths of 1000 m. Given that Dover sole larvae in the GOA demonstrated no organized migration from offshore spawning grounds toward coastal nursery areas, our data indicate facultative settling. Similarly, off the Oregon coast the extended pelagic life for some, but not all, Dover sole larvae indicates facultative settling whereby larvae have the ability to delay metamorphosis and postpone their settlement to the bottom until favourable oceanographic conditions occur (Pearcy et al., 1977; Markle et al., 1992).

It is unclear where Dover sole settle in the GOA, but immature Dover sole were concentrated in bays (Fig. 2e) and ancillary studies of juvenile flatfishes have collected age-1 Dover sole nearshore in bays in August (Norcross et al., 1998; Abookire et al., 2001). A possible mechanism for transporting Dover sole larvae from the outer shelf and slope to nearshore bays is an accelerated Alaska Coastal Current that could entrain offshore waters up troughs and direct larvae in the GOA toward inshore nurseries (Schumacher and Reed, 1980). The GOA is predominantly a downwelling system with a peak in surface water transport onshore in winter (Ladd et al., 2005). The lack of strong upwelling in summer in the GOA compared to the Oregon coastal region may result in less transport of larvae offshore in the northern range of Dover sole. Ekman transport of Dover sole larvae inshore in autumn and winter could contribute to early settlement of larvae in the GOA. Larvae overwintering offshore in the Alaskan Stream would likely be transported far westward at speeds up to 100 cm/s (Stabeno and Reed, 1991; Stabeno et al., 2004). If this is the case, settlement checks on otoliths from juveniles caught downstream in the Aleutian Islands might demonstrate that they have experienced a longer pelagic life.

4.2. Rex sole

Off the Oregon coast, rex sole spawn in late winter and their larvae can grow to 89 mm SL during an extended pelagic phase which lasts approximately 12 months (Pearcy et al., 1977). Rex sole larvae undergo a consistent progression of growth through the first year and most growth in length occurs before the left eye begins to migrate (Pearcy et al., 1977). Size-at-transformation for rex sole is 49–72 mm and larvae presumably utilize wintertime onshore Ekman currents after nearly a year in the plankton to reach nurseries over the shelf (Bailey et al., 2005). In the GOA, newly hatched rex sole larvae are widely distributed in June from the inner shelf to the outer slope, and by autumn larger larvae (20–57 mm) concentrate over the shelf. The prolonged spawning season likely accounts for the wide range of larval lengths captured in August and September. Given that GOA ichythoplankton collections contained only one size-class of larvae in each month, rex sole apparently remain in the plankton for less than 9 months rather than 12 or more months as found off the coast of Oregon by Pearcy et al. (1977). Because GOA ichythyoplankton collections contained large rex sole larvae (up to 59 mm) it seems unlikely that the reduced pelagic duration observed at the northern extent of their range is solely a result of gear effects. Furthermore, only 2 confirmed rex sole larvae were caught in the collection of pelagic anchovy trawls in September (see above). Rather, the strategy of rex sole larvae in the GOA seems different from southern latitudes and may be a result of hydrography or seasonality.

Ichthyoplankton collections in the GOA indicate a cross-shelf pattern of larval transport for rex sole, where larvae may settle over the shelf in late autumn. Settled rex sole as small as 69 mm were captured nearshore with a beam trawl in August in Kachemak Bay (Abookire et al., 2001). Exactly where and when rex sole larvae settle remains unknown, as well as what happens between settlement and the immature stage. Fluctuations in transport of the Alaska Coastal Current system influence cross-shelf flux of slope water onto the shelf (Parker, 1989). The downwelling conditions of alongshore and cross-shelf winds may generate transport conditions from the slope and outer shelf to nearshore. In the vicinity of the GOA near eastern Kodiak Island, increased winter wind energy can produce onshore transport in the upper 20–50 m and provide larvae with accelerated trajectories cross-shelf toward shallow waters (Parker, 1989).

Given the general similarities in spawning time and area and egg and larval vertical distributions of Dover and rex sole, the difference in transport patterns across the shelf is a conundrum. It is possible that Dover sole take advantage of strong winter downwelling conditions and stay in the plankton longer to facilitate transport further inshore in bays. We believe that fine-scale sampling of the vertical migratory behaviour with simultaneous measurements of current speeds and directions might reveal subtle differences in mechanisms of transport. There is also a need for more research on timing of settlement using small-mesh trawls in winter and spring combined with otolith ageing of specimens, and sampling offshore waters in winter with appropriate sampling gear for large pelagic larvae to better understand the biology of these animals.

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