

Evidence for resource partitioning and competition in nursery estuaries by juvenile flatfish in Oregon and Washington

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Resource partitioning among co-occurring species can provide evidence that density-dependent survival can be a function of interspecific competition. Of the early life history stages of flatfish, the juvenile phase is thought to be the most susceptible to density-dependent mortality, and intraspecific competition among individuals is thought to lead to decreased survival of extremely strong year classes (Iles and Beverton, 2000). Juveniles of multiple flatfish species are often observed to coexist in a single nursery area (e.g., Burke et al., 1991; Henderson and Holmes, 1991; Reichert and van der Veer, 1991; Norcross et al., 1997), but evidence for interspecific competition is rarely examined. We examined evidence for resource partitioning and interspecific competition among juvenile flatfish species co-occurring in nursery areas.

Flatfish species often have juvenile nursery areas that are segregated from the adult population. In many cases, juveniles use shallow nearshore habitats as nursery areas, and adults are found in deeper offshore habitats (Gibson, 1994; van der Veer et al., 2000). On the Pacific coast of North America, estuaries are typically smaller and occur less frequently than in other areas such as the Atlantic coast of North America. Possibly because of the limited estuarine habitat on the West Coast, fewer species of marine fish and

invertebrates use coastal estuaries for nursery areas. In our study, we examined the spatial distribution of co-occurring juvenile flatfish populations within Pacific coast estuaries. The four species examined were English sole (*Pleuronectes vetulus*), Pacific sanddab (*Citharichthys sordidus*), sand sole (*Psettichthys melanostictus*), and starry flounder (*Platichthys stellatus*). Juveniles of these species are found in Oregon and Washington estuaries during the summer, and adults of each of these species contribute to a lucrative trawl fishery on the coastal shelf.

To date, estuarine residency of juvenile English sole has been well documented (Krygier and Pearcy, 1986; Gunderson et al., 1990; Rooper et al., 2003); however, this is the first comparison of the spatial distribution of the three other species within estuaries, and is the first study to encompass such a wide region of coastal estuaries (ranging over 400 km of coastline). The goal of this study was to compare the summer distribution of juvenile English sole, starry flounder, sand sole, and Pacific sanddab within nursery estuaries over three years, to determine whether the four flatfish species were spatially partitioning the nurseries. We also examined the summer distribution in relation to the abundance of species across years and habitats in order to deter-

mine the potential for interspecific competition.

Materials and methods

Study area

This study was carried out at four estuaries on the Oregon and Washington coasts: Grays Harbor, Willapa Bay, Coos Bay, and Yaquina Bay (Fig. 1). Seventeen to 20 trawl sites were chosen within each estuary, and each trawl site was classified into three habitat types: lower main channel, lower side channel and upper estuary. Habitat delineations were previously identified by principle component and discriminant function analysis (Rooper et al., 2003). The lower estuarine sites were on average deeper (depth=5.1 m), colder (13.6°C), and more saline (28.5 ppt) than upper estuarine sites because of their proximity to the mouth of the estuary. On average, lower side channel sites were slightly warmer (15.6°C), shallower (depth=3.7 m) than the lower estuarine sites, and had extensive tide flats that surrounded the sites and were exposed during low tides. Upper estuarine sites were typically shallow (depth=4.0 m), very warm (17.0°C), less saline (25.1 ppt), and had a large sediment size and a smaller area of surrounding tidal flats (Rooper et al., 2003).

Sampling procedures

Trawl surveys of all four estuaries were conducted in both June and August from 1998 through 2000. In each month all four estuaries were sampled over two and a half weeks and a total of 431 trawl hauls were completed over the three summers. The same sites were resurveyed throughout all years of sampling; however the exact trawl location varied somewhat between sampling

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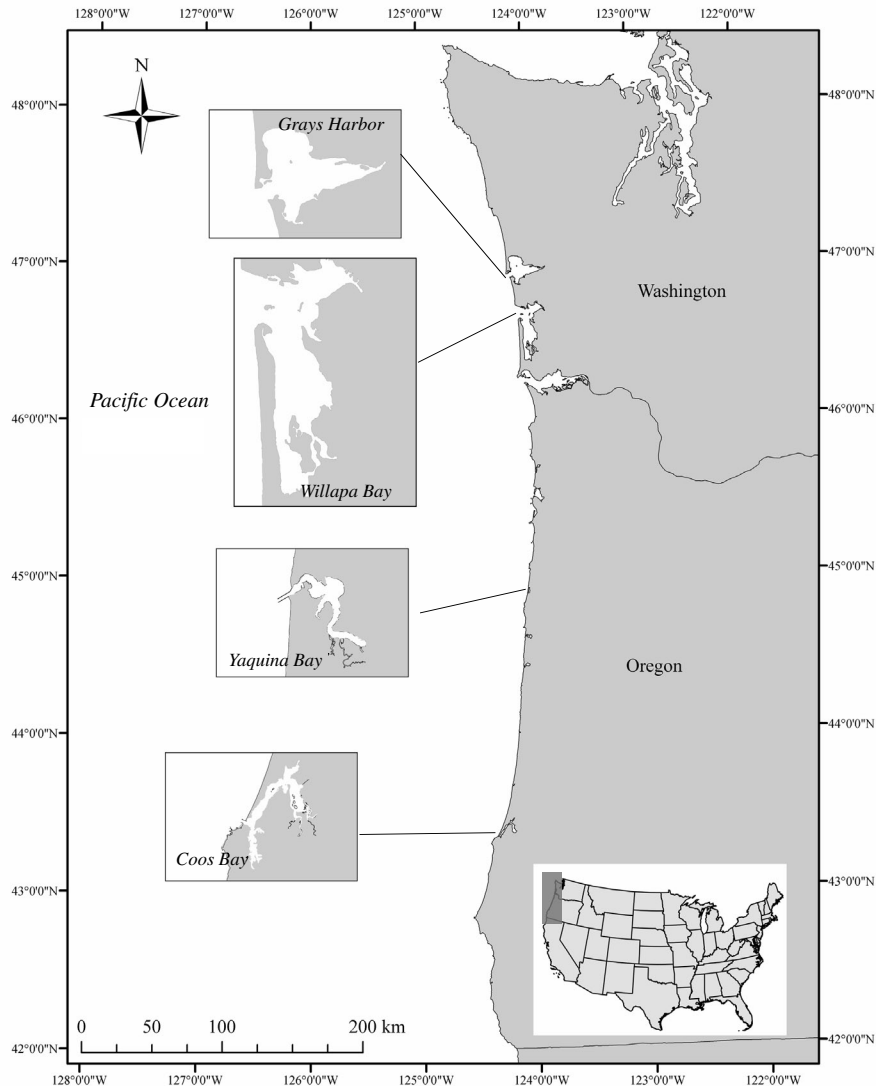


Figure 1

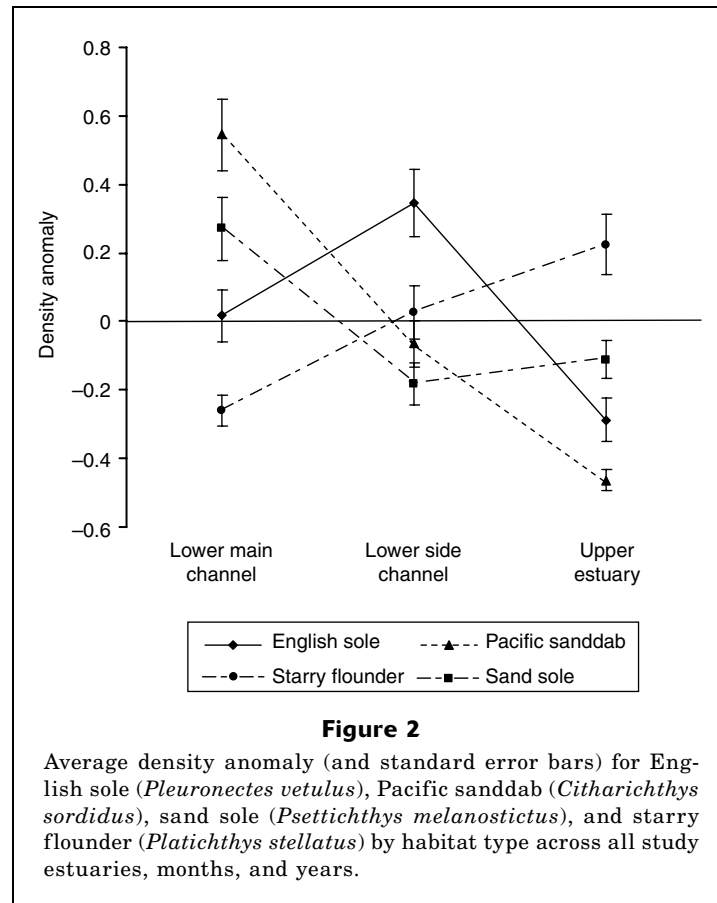
Map of coastal Oregon and Washington with insets showing the four estuaries studied: Grays Harbor (total subtidal area=8545 ha), Willapa Bay (total subtidal area=11,200 ha), Yaquina Bay (total subtidal area=471 ha), and Coos Bay (total subtidal area=1195 ha).

periods by approximately 50 m. Benthic organisms, including the four target flatfish species, were collected during daylight with a beam trawl (Gunderson and Ellis, 1986). The beam trawl had an effective opening width of 2.3 m and a height of 0.6 m. The net was towed at a speed of 0.8–0.9 m/s behind a 6.4-m research vessel with a minimum 5:1 scope of line out to depth. The distance towed averaged 139 m in 1998–2000. Trawls were made against the prevailing current over a variety of tide stages, although efforts were made to conduct trawling near the time of daylight slack low water. Sampling was not conducted at high current velocities during maximum ebb and flood tides to ensure the greatest adherence of the beam trawl to the substratum. All fish

and invertebrates captured were identified to species and English sole were measured for total length (TL) to the closest 1.0 mm. Other species of flatfish were measured (TL) only in 1999 and 2000.

Data analysis

There was considerable variability in the data associated with each sampling period that was not related to habitat use. This variability was due to other factors, such as patterns in interannual variability in recruitment to individual estuaries or to differences in overall abundance among the four flatfish species. To minimize the effect of this variability on the analyses, it was



necessary to standardize the data within each estuary. We used the normalized anomaly (Zar, 1974) of flatfish densities as the dependent variable to compare use of habitats within estuaries for each species, where

$$a_i = \frac{x_i - \bar{x}_{emy}}{sd_{emy}}$$

In this equation the subscript i refers to an individual density from a trawl survey site within an estuary-month-year combination, emy refers to the estuary-month-year combination where a trawl survey occurred, and \bar{x} and sd are the mean and standard deviation of all trawl surveys occurring in that estuary-month-year combination. By using the anomaly of the densities, we reduced the variation in the data that was attributed to estuarine, seasonal, and interannual sources in order to concentrate solely on the within-estuary component of variation. For example, if the average catch of Pacific sanddab was 1000/ha for the Grays Harbor estuary in June 2000, individual trawl hauls from Grays Harbor in June 2000 with catches <1000/ha would have a negative density anomaly, whereas trawl hauls with Pacific sanddab catches >1000/ha would have a positive density anomaly.

The density anomalies were analyzed by using analysis of variance (Zar, 1974). The full model used to analyze spatial distributions of each species included the main effects of habitat type, month of survey, year of survey, and estuary, as well as estuary-habitat, month-habitat, and year-habitat interaction terms. The interaction terms were specifically included to test the hypotheses that spatial distribution of each flatfish species was consistent across estuaries, years, and months. All significant ($P < 0.05$) main effects and interactions were compared for significant differences among effect levels by using the least squares mean approach as a *post hoc* test with a Tukey's adjustment for multiple comparisons (Zar, 1974).

Results

Juvenile Pacific sanddab collected during the trawl surveys ranged in length from 23 to 150 mm TL. The analysis of Pacific sanddab density anomalies for habitat types within estuaries resulted in significant differences among habitats in the estuaries. There were significantly higher density anomalies in lower main channel habitats and significantly lower anomalies in upper estuary sites (Fig. 2). Lower side channels usually had

negative density anomalies—the most notable exceptions being Willapa Bay and Grays Harbor in 1998 (Fig. 3). This pattern produced significant interactions between habitat and both year and estuary.

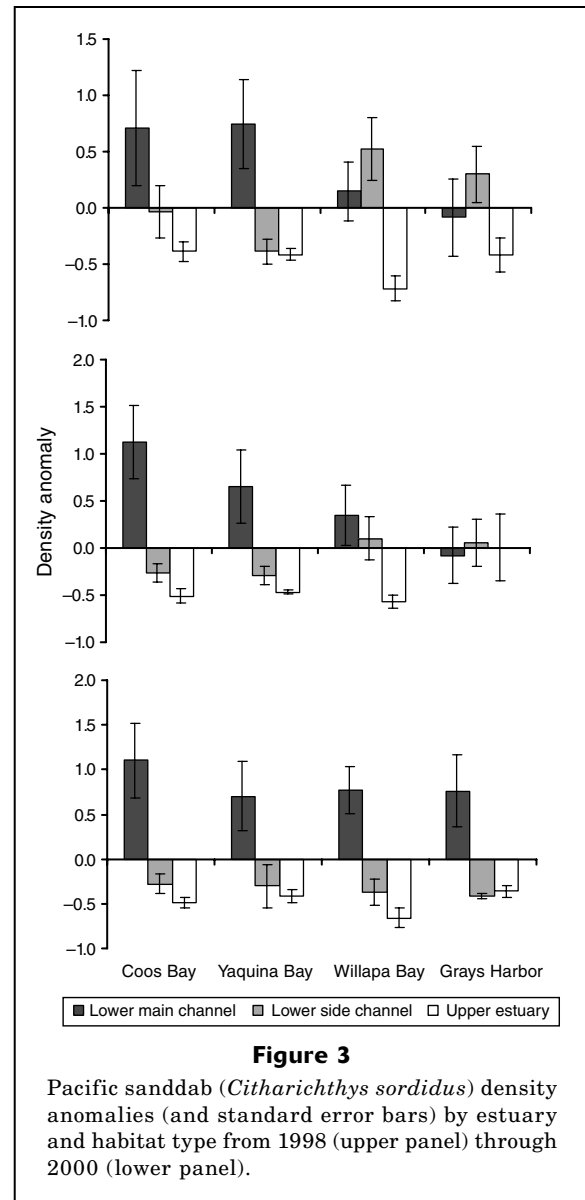
The lengths of sand sole captured by trawling were comparable to those for Pacific sanddab, ranging from 20 to 234 mm TL, and only 12 specimens longer than 150 mm TL. Sand sole catch was highly variable across all systems, and there were 318 zero catches over the total 431 trawls. Sand sole density anomalies followed a pattern similar to those of Pacific sanddab. Density anomalies were significantly higher at lower main channel sites than at other sites within the estuary (Fig. 2). Density anomalies were similar between upper estuary sites and lower side channel sites. There were no significant interaction terms between estuary or year and habitat type; thus the pattern in spatial distribution of sand sole appeared to be consistent across estuaries and years.

Starry flounder were the least common species of flatfish captured in the study estuaries. The starry flounder captured were larger than the other species of flatfish, ranging from 49 to 376 mm TL, and 44 individuals were >150 mm TL. Density anomalies were highest at upper main channel sites (Fig. 2). As with sand sole, there were no significant interaction terms between habitat type and either estuary or year. The effect of habitat type on starry flounder densities was thus a consistent effect observed across all estuaries and years.

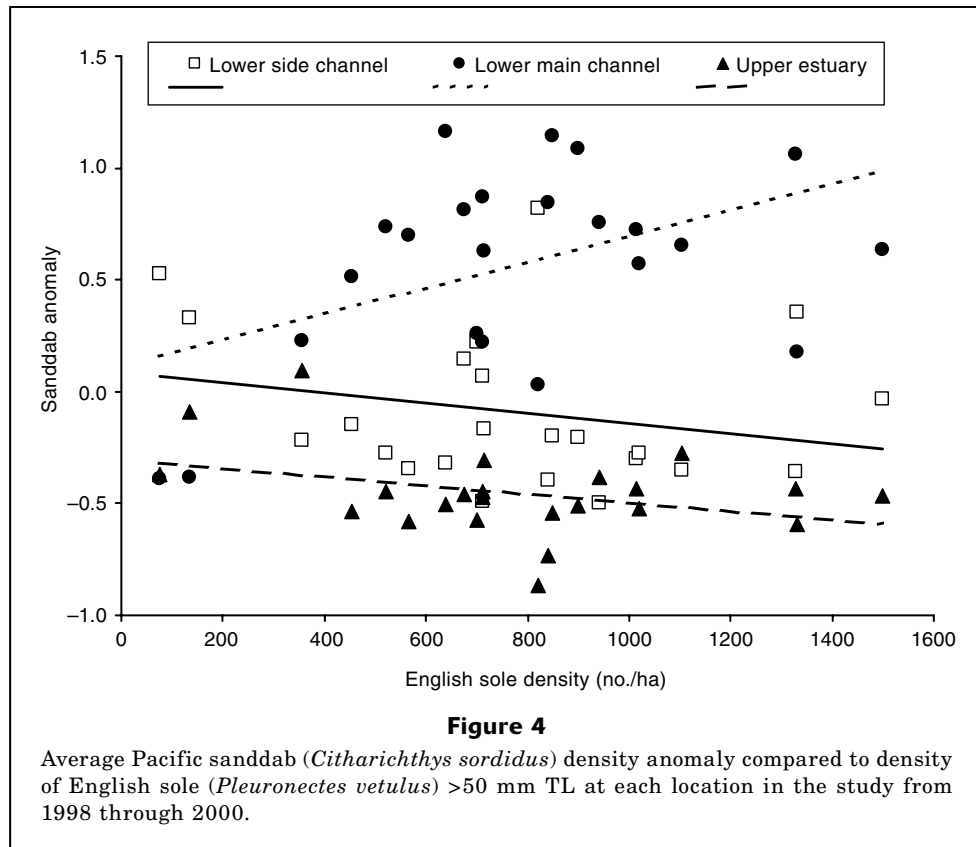
English sole lengths ranged from 14 to 200 mm TL and only 12 individuals were greater than 150 mm TL. English sole density anomalies were significantly higher at lower side channel sites than at other estuarine locations (Fig. 2). There was also a significant interaction term between habitat type and month. In August there was no significant difference between density anomalies in lower side channel and lower main channel sites, while in June density anomalies were much larger in lower side channels than at all other locations. The significant month and habitat type interaction in the analysis of English sole density anomalies was most likely due to habitat changes observed in juvenile English sole as they grow (Rooper et al., 2003). A carrying capacity for large (>50 mm TL) English sole was observed in the study estuaries, and large English sole distribution expanded when densities were high (Rooper et al., 2003). The expansion of English sole distribution when densities were large corresponds to an increase in the density anomalies of Pacific sanddab in lower main channel areas (Fig. 4). Conversely, as large (>50-mm-TL) English sole densities decreased, Pacific sanddab appeared to increase their distribution in the estuaries, as observed in higher density anomalies in lower side channels.

Discussion

We observed evidence for resource partitioning in four species of co-occurring juvenile flatfish in west coast nursery estuaries. The analysis of density anomalies



indicated that the four flatfish species exploit different areas of estuaries. The spatial segregation among juvenile flatfish observed in our study is consistent with results of other studies and indicates the potential for interspecific competition among the four species. Surveys of flatfish assemblages in Puget Sound, Washington have revealed spatial segregation of juvenile flatfish by depth, although the pattern was not consistent among sites (Thornburgh, 1980). In Thornburgh's study, spatial segregation may have been driven by differences in sediment type at the sites and by differences in settling times among the dominant species: English sole, sand sole, Pacific sanddab, and rock sole (*Lepidopsetta bilineata*). Distinct patterns in spatial distribution have also been observed for juvenile flatfish assemblages beyond the Pacific Northwest. In estuaries along the California



Bight, diamond turbot (*Hypsopsetta guttulata*) settle in the upper portions of bays during January and March, whereas California halibut (*Paralichthys californicus*) are found closer to bay entrances and the open coast, settling from March to September (Kramer, 1991). Settlement timing has also been found to be an important partitioning factor for common dab (*Limanda limanda*) and plaice (*Pleuronectes platessa*) in a small Scottish bay, where plaice settle earlier in the year than dab (Steele and Edwards, 1970). Depth has been identified as an important factor in partitioning nursery areas for the common dab and age-0 plaice (Edwards and Steele, 1968; Gibson, 1973). Juvenile flatfish in Alaskan inlets have also been found to segregate with depth and a number of other factors, such as temperature and sediment type (Norcross et al., 1997). Habitat type has also been found important in determining the spatial segregation of northeast Atlantic flatfish assemblages; ontogenetic shifts in habitat use occur in some species (Walsh et al., 1999; Phelan et al., 2001).

These studies indicate that flatfish species that exist together in nursery areas can partition resources in a number of ways according to biological (i.e., diet) or physical (i.e., depth or salinity) requirements, or according to a combination of both biological and physical requirements. Studies of shallow water habitats have generally indicated that flatfish in nursery areas are not limited by food resources (Evans, 1983). In west coast

estuaries food resources can be quite high, especially in intertidal areas (Gunderson et al., 1990; Dumbauld et al., 2000). After review of diet studies documenting feeding differences among Pacific sanddab and English sole (Hogue and Carey, 1982; Thornburgh, 1980), as well as the abundance of food within the nursery area, we do believe it is unlikely that direct competition for food is solely responsible for the apparent pattern in estuarine distributions between the two species. We suggest that the segregation observed in northwest estuaries is most likely caused by differences in physical conditions of the habitat.

The four species of flatfish observed in the present study probably partition the nursery estuaries along gradients of salinity and temperature. Starry flounder were found in upper reaches of the estuary to a greater degree than the other species—a finding that is consistent with their ability to tolerate low salinity (Orcutt, 1950). Starry flounder were most abundant in Yaquina Bay, where the coverage of trawl survey sites extended farther up the estuarine salinity gradient than in other estuaries. The average salinity in June was 16–18 ppt at the uppermost Yaquina Bay sites, whereas the average June salinity at sites in other estuaries was always greater than 19 ppt. Salinity has been found to be an important determinant of the distribution of other flatfish species (Coggan and Dando, 1988; Marchand, 1988; Kerstan, 1991; Gibson, 1994; Marshall and Elliot, 1998).

The temperature preferences of English sole may allow them to exploit areas of the estuary not used extensively by Pacific sanddab. Temperatures less than 17.5°C have been observed to lead to high English sole growth (Yoklavich, 1982). These temperatures were observed in lower side channels of the study estuaries. For the speckled sanddab (*Citharichthys stigmæus*), a close relative of the Pacific sanddab, maximum growth has been observed from 8° to 13°C (Ehrlich et al., 1979). This temperature range is closer to the temperatures found in lower side channels, and lower than the temperature range found in lower main channels in our study area. Thus, the Pacific sanddab, if it has temperature tolerances similar to those of its congener, may be limited to lower main channel locations in order to optimize growth rates, whereas optimal English sole growth occurs at the higher temperatures found in lower side channels.

An alternative explanation for Pacific sanddab distribution may be found in its response to high English sole density. The changing distribution of Pacific sanddab, when confronted by high densities of English sole, provides evidence that competition may occur between these two species. When English sole densities are high, Pacific sanddab seem to be limited in distribution to lower main channel locations (sites not preferred by English sole), and when English sole densities are low, Pacific sanddab appear to be more evenly distributed throughout the estuary. This pattern does not apply to starry flounder or sand sole, whose distributions remain the same regardless of English sole density. The implication of this resource partitioning is that English sole year-class strength may be affecting the ability of Pacific sanddab to use areas of the estuaries where conditions are optimal for flatfish growth.

Distinct patterns of habitat use by juvenile English sole, starry flounder, sand sole, and Pacific sanddab were observed in all four estuaries that we examined. Highest densities of Pacific sanddab and sand sole were found in lower main channel sites, highest densities of English sole were found in lower side channels, and highest densities of starry flounder were found in upper estuarine sites. These patterns of spatial segregation were consistent from 1998 through 2000. The patterns were consistent across the four estuaries encompassing 400 km of coastline. Resource partitioning is probably based primarily on temperature and salinity tolerances and growth preferences of the individual flatfish species; however, there is evidence of competition between English sole and Pacific sanddab when their spatial distributions are examined in response to their relative abundances.

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