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Recruitment Dynamics of Metamorphosing English sole, *Parophorys vetulus,* to Yaquina Bay, Oregon

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English sole, *Parophrys vetulus,* spawn in shelf waters off the west coast of North America and early development occurs in coastal waters. Near metamorphosis, however, larvae recruit to nearshore and estuarine nursery areas, an uncommon life-history feature for a species in this region. Recruitment of larval *P. vetulus* to Yaquina Bay, Oregon, was sampled with moored nets on a weekly basis. Recruitment began during night flood tides in late February and was characterized by three peaks during the season. Planktonic recruitment continued into June, whereas benthic juveniles began to emigrate from the estuary in late May.

The data suggest that two developmental stages of recruits immigrated to Yaquina Bay. The first are newly transforming larvae which enter the bay earliest within each peak of recruitment; peaks of abundance are related to onshore Ekman transport. This transport also brings larvae to shallow areas along the open coast where they settle. These transforming stages are still capable of pelagic swimming activity and continue to recruit to the estuary, typically swimming deeper in the water column than the early stages. Estuarine factors, particularly bottom salinity at the end of ebb tide, are most strongly correlated with recruitment of these stages. It seems that tidal stream transport is the primary mechanism used by English sole to recruit to the estuary, but the mechanism of locating the estuary and timing of entry is relatively complex.

Introduction

Shallow-water estuarine nursery areas are important to the young of many fish and shellfish species; as many as 50–70% of the commercially exploited species of fishes in the western Atlantic, for example, utilize estuarine nursery habitats (McHugh, 1967; Clark *et al.,* 1969). The reasons for estuarine residence by young stages of predominantly offshore species include increased food availability and decreased predation rates (McHugh, 1967; Rosenberg, 1982). Many of these species spawn in offshore waters, where egg and early larval stages may be dependent upon prevailing current patterns for transport to nearshore areas (Nelson *et al.,* 1977; Miller *et al.,* 1984). The mechanism by which larvae locate and enter estuaries, however, is unknown. The high densities of larvae and juveniles

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within estuaries suggest that the mechanism requires active behavioural orientation by the larvae to specific characteristics of the estuaries, including salinity, tidal flushing and olfactory cues (Creutzberg, 1961; Creutzberg *et al.*, 1978; McCleave & Kleckner, 1982).

Only 10–20% of the Pacific coast is estuarine, as compared to 80% of the Atlantic and Gulf coasts (Emery, 1967). Thus, although estuarine utilization is more limited for Pacific than Atlantic coast fishes (McHugh, 1967; Pearcy & Myers, 1974), the problem of estuarine entry may be particularly acute for Pacific coast fishes whose young inhabit these nursery areas. Pacific estuaries are important to several fish species, including Pacific herring, *Clupea harengus pallasi*, which migrate to, and spawn in, estuaries (Rounsefell, 1930), and anadromous salmon which utilize estuaries as nurseries during their migration to the sea (Healey, 1980). Few offshore Pacific species, however, use estuaries as nurseries after metamorphosis (McHugh, 1967). Pearcy and Myers (1974) and Krygier and Pearcy (1986) concluded that Yaquina Bay, Oregon, was an important nursery area for several flatfish species that spawn offshore, because newly metamorphosed juveniles moved into the estuary in large numbers. The dominant species of juvenile flatfish in Yaquina Bay is the English sole, *Parophrys vetulus*.

The spawning season for *P. vetulus* is extended and annually variable, with peak spawning occurring as early as September and as late as April (Laroche & Richardson, 1979; Kruse & Tyler, 1983). Larvae hatch from pelagic eggs in 3–12 days, depending upon temperature (Alderdice & Forrester, 1968), and are the dominant species in the winter–early spring ichthyoplankton assemblage which occurs from nearshore to approximately 28 km seaward (Richardson & Pearcy, 1977; Mundy, 1984). Metamorphosis begins at approximately 16–18 mm and is complete by 20–22 mm SL (Ahlstrom & Moser, 1975; Rosenberg & Laroche, 1982); these lengths correspond to ages of approximately 70–100 days (Rosenberg, 1982), and recruitment to estuaries occurs at this stage (Misitano, 1976). It was previously believed that 0-group juveniles inhabited only estuaries and shallow protected inland coastal areas (Ketchen, 1956; Olson & Pratt, 1973). More recent sampling off the Oregon coast has shown the presence of populations in 15–50 m of water off the open coast as well (Laroche & Holton, 1979; Krygier & Pearcy, 1986). In the offshore area, newly settled juveniles are present from October to July; in Yaquina Bay they first appear in November and are last captured in June (Krygier & Pearcy, 1986). Peak immigration to Yaquina Bay apparently occurs from mid-January to late May, but may vary from year to year with timing of spawning.

Estuaries and shallow coastal areas appear to be important nurseries for *P. vetulus*, but the mechanism of recruitment to estuaries is not understood (Rogers, 1985; Krygier & Pearcy, 1986). Species with larval distributions offshore must first reach nearshore waters. Peterson *et al.* (1979) proposed a mechanism by which copepod populations could be maintained in the coastal zone despite offshore transport associated with upwelling. The recruitment season for *P. vetulus*, however, occurs prior to the upwelling season off Oregon, when onshore convergence is prevalent. The situation may thus be more similar to that for larval Atlantic menhaden, *Brevoortia tyrannus*, which are estuarine-dependent and apparently use onshore transport to reach estuaries (Nelson *et al.*, 1977).

In this paper, we present the results from a field study of temporal patterns of English sole recruitment to Yaquina Bay. However, rather than taking an approach concerned with interannual variability (Nelson *et al.*, 1977; Bailey, 1981), a finer temporal scale within a single year was considered. The relationship of estuarine entry to two types of environmental factors is described; the first type is offshore factors such as onshore Ekman transport, concerned with transport of larvae to the nearshore. The second group is

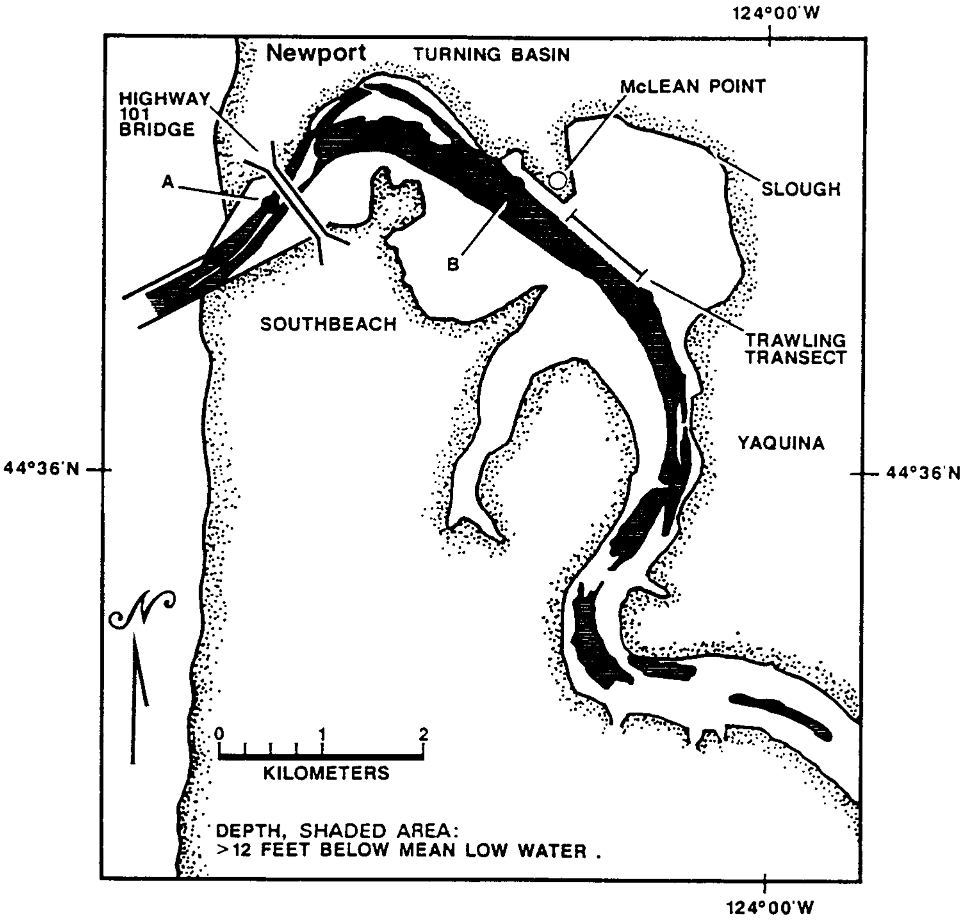

Figure 1. Yaquina Bay, Oregon, site of sampling for early stage *Parophrys vetulus*. Prior to 23 February, samples were taken west of the bridge (A), but after that date were at point B after excessive current caused repeated anchor failure. Shaded areas in the bay indicate 3·16 m below mean low water.

associated with estuarine entry and includes river discharge, temperature and salinity differences, lunar phase and tidal currents. We discuss the relationship of the estuarine and offshore juvenile populations of English sole.

Materials and methods

Study area

Yaquina Bay, Oregon (44°36'N, 124°00'W) is a small estuary with an area of 11·6 km^2 (Figure 1). Sloughs and the river channel comprise 65% of this area; the remainder is tidelands (Percy *et al.*, 1974). The channel is maintained by dredging to a depth of 9 m from the narrow entry, between two breakwaters, to the ship turning basin at McLean Point (Figure 1), approximately 5 km from the mouth. Upriver of McLean Point, the channel depth is 3·6 m. Average monthly river discharge at Newport is 36 m^3 s^{-1} with an average low near 2 $m^3 s^{-1}$ in August and an average high near 70 $m^3 s^{-1}$ in December–January (U.S. Army Corps of Engineers, 1970). Mixed semidiurnal tides with a tidal range of 1·7 m occur in the bay (Kulm & Byrne, 1967); flushing times are approximately 13·3 tidal cycles in the summer and the exchange ratio is 52% (Zimmerman, 1972). The estuary is partially mixed from November to May and well mixed from June to October (Burt & McAlister, 1959; Kulm, 1965). Temperatures in Yaquina Bay range from about 7 to 17 °C. Lowest temperatures occur in January and February, and the highest (but most variable) temperatures occur in summer, when high temperatures produced by local warming alternate on a tidal basis with cold, upwelled water from offshore (Bourke, 1969; Frolander *et al.*, 1973). Salinity depends upon freshwater input and reflects the ocean salinity from June to October in the lower bay; values are lower and more variable in the months of high freshwater runoff (Frolander *et al.*, 1973). Dissolved oxygen does not vary markedly with depth in the lower bay (W. DeBen, U.S. Environmental Protection Agency, Newport, OR 97365, unpubl. data).

Larval collections

Weekly collections of larval and juvenile *P. vetulus* were made from the 11-m RV *Sacajawea* on night flood tides from 14 January to 23 July 1982. Pelagic larvae were collected with moored nets (0·5-m mouth diameter, 0·75 mm mesh) modified from Graham (1972) as described by Weinstein *et al.* (1980). The nets were attached by pivots to aluminium collars and orienting vanes bolted to a nylon rope (1·25-cm diameter) suspended from a buoy. The line was attached to a 41-kg cement block shackled to a chain with a 9·1-kg anchor; a tag line and float on the anchor were used for retrieval. Three nets were set on each string, at 1·5 m below the surface, halfway between the surface and bottom, and 1 m above the bottom. The volumes of water filtered were measured with calibrated General Oceanics model 2030-R2 (large-rotor) flowmeters mounted in the centers of the net frames. Nets were set after slack low water and fished for 0·6–4·4 h, with the fishing time being dependent on the current velocity. Two strings of nets were initially set west of the bridge on the north side of the boat channel (Figure 1, Site A). Strong currents over hard substrates at these sites occasionally caused the nets to move. After 23 February, the sampling locations were moved farther into the estuary (Figure 1, Site B), to avoid movement of the nets and boat traffic. However, English sole larvae did not enter the bay in large numbers until about 3 March, so the change in location did not bias the catches. Furthermore, the two sites are similar in plankton composition because of high tidal exchange in the bay (Frolander *et al.*, 1973). Additional samples were taken to assess the abundance patterns of larvae by setting the anchored nets on both ebb and flood tides over 24-h periods on 17–18 March and 9–10 April 1982.

Detritus, mostly of terrestrial origin, occasionally clogged the nets and fouled the flowmeters. These problems were most severe in the bottom nets. Samples containing more than 4 l of total sample volume (including detritus), or in which the ratio of sample volume (l) to water volume filtered (m^3) exceeded 0·03 were discarded due to net clogging and excluded from further analysis. When flowmeter readings were missing due to fouling or other problems, filtered water volumes were estimated. Linear regressions were calculated from samples with reliable readings to estimate flowmeter readings from each net based upon readings from other nets on the same string. Only nine readings were estimated in this manner.

Demersal English sole were collected with a 1·5 m wide beam trawl (Kuipers, 1975) equipped with a 1-m diameter odometer wheel (Krygier & Pearcy, 1986) and a net with

1·6 mm bar mesh liner. Four replicate 5-min tows were taken while the anchored nets fished, except on dates when concurrent Tucker trawl samples were taken (9 April and 27 May); on those dates, beam trawl samples were taken within 48 h of the plankton samples. All trawl samples were taken on a transect south of a large slough, along the north edge of the boat channel at a depth of 4·5–8·0 m (depending on tidal stage) from a point opposite buoy 14 to the east edge of McLean Point (Figure 1). All tows were taken at night against the flooding tide. When fish were highly abundant (>5 per 10 m^2), density estimates were made from a single haul because our data showed little intersample variability in density, as noted by Krygier and Pearcy (1986). When fish were moderately abundant ($\geq 1·5$, $\leqslant 5$ per 10 m^2), estimates were made from two samples.

Pelagic larvae were also collected with a 1 × 1 m Tucker trawl (Clarke, 1969) with an effective mouth area of 0·71 m^2 when fished at an angle of 45° (Boehlert *et al.*, 1985). The trawl consisted of three nets and a double-release mechanism operated with messengers; each net was 5 m long with 0·505-mm mesh and an effective open-area : mouth-area ratio of 6 : 1. The filtered water volumes were measured with calibrated General Oceanics model 2030 flowmeters mounted in the center of each net. A wire angle of 45° was maintained during each tow, and depths of tow were maintained by adjusting the amount of wire let out by predetermined amounts for each depth. Tucker trawl tows were made against the prevailing tidal current through the center of the boat channel and turning basin from approximately 400 m east of the bridge to the east edge of the turning basin (Figure 1). For each sample set, the water column was divided into three equal strata and 10-min oblique tows were taken throughout the surface, midwater and bottom strata. Duplicate samples were taken at each depth during flood, ebb, and on slack tides during the diel sampling on 9–10 April 1982, and during night flood/ebb tide comparisons on 20–22 and 27–28 May 1982. Additional single samples at each depth were taken during day flood and ebb tides without concurrent moored net samples on 4 May 1982.

All samples were preserved in the field with 10% formalin in seawater buffered with sodium borate. *Parophrys* larvae larger than 10 mm were sorted from the samples. Standard lengths of larvae were measured to the nearest 0·1 mm and lengths of juveniles (>22 mm SL) to the nearest 1·0 mm with dial calipers following the method of Laroche and Richardson (1979). Larvae were classified by developmental stages A–F using criteria modified from Tsuruta (1978). These stages are based upon the stage of metamorphosis and not on length, because transforming larvae were observed in early stages between 15·3 and 23·0 mm SL. The modifications from Tsuruta include a slightly different definition of stage F and an additional juvenile stage. The stage F used in this work includes fish in which the left eye has reached its final position, but the snout is not yet elongate and the lateral line had not begun to form; also, the left eye is once again visible from the left side. The additional juvenile stage of *Parophrys* includes those fish in which the lateral line has begun to form and the snout has begun to elongate, with the snout appearing pointed rather than rounded.

Observations of the duration of the stages were taken between 20 March and 9 April 1984. Thirteen *Parophrys* in early stage C were collected with the beam trawl on 20 March. They were maintained in a tank with a flow-through system using filtered water from the bay with ambient temperatures (10·4–14·0 °C) and salinities from 28–30·3‰. The fish were fed a mixture of *Brachionus, Tigriopus,* and *Artemia* nauplii *ad libitum* daily. Daily observations were made of stages and single fish were preserved every other day.

Surface and bottom temperatures and salinities were taken at the beginning and end of each anchored net set. Salinity samples were analysed with a Guildline Autosalinometer model 8400. Water depth was measured at the moored net stations at the beginning and end of sampling. Tidal heights, maximum current velocities, time of maximum and minimum currents, time of high and low water, and lunar phase were obtained from tide and tidal current tables (National Ocean Survey, 1981*a*,*b*). Daily mean values of Yaquina River discharge ($m^3 s^{-1}$) were obtained from C. G. Kroll (United States Department of the Interior Geological Survey, Water Resources Division, Pers. comm., 31 August 1982). Weekly values of the coastal divergence (upwelling) index were provided by A. Bakun (Pacific Fisheries Environmental Group, National Marine Fisheries Service, NOAA, Monterey, CA 93942). Six-hour estimates of adjusted sea level, related to alongshore water transport (Marthaler, 1977) were provided by A. Huyer (Oregon State University, College of Oceanography).

Results

Gear comparison

Catches of the moored nets and Tucker trawl were compared to determine if avoidance of the moored nets occurred. Too few larval *Parophrys* were taken in daytime samples by either gear to determine if avoidance was greater for the moored nets during daylight. In night samples, however, no significant difference was found between the mean catches of the moored nets and Tucker trawl in paired samples at each depth on each tide (*t*-test; d.f. = 23; $p < 0{\cdot}05$) or in the mean lengths of larvae in those samples (*t*-test; d.f. = 28; $p < 0{\cdot}05$). Avoidance of the moored gear relative to the towed nets was thus not observed, which is similar to results of gear comparisons for larvae and juveniles of other species of estuarine fishes (M. P. Weinstein, LMS Engineers, pers. comm., 5 October 1983).

Duration of stages

The transitions from stage C to D and D to E were each observed in the laboratory to occur with 24–48 h. The transition from stage E to stage F occurred in 5–10 days, while that from stage F to the juvenile stage is gradual, occurring in the 3 to 9 days after the left eye reached its final position. We infer that stages B–D are of short duration, lasting a few days, while stages E-F last from 1 to 2·5 weeks.

The relative duration of the stages partially explains why stages E and F dominated the catch as each recruitment peak progressed, and as the season of recruitment progressed. The short duration of stages C and D make their contribution to the catch more important than standing stocks alone would indicate.

Hydrographic measurements

Surface temperatures were consistently between 8·5 and 10·0 °C from January through March but after April were higher and more variable than in the first half of the study [Figure 2(a)]. Bottom temperatures were more similar at the start and end of sampling and were less variable in the second half of the sampling than were surface temperatures [Figure 2(b)]; they showed a pattern similar to surface temperatures but were usually 1–2 °C less. Generally, initial surface temperatures reflect those of the riverine system, with the final bottom temperatures being those of ocean temperatures. Surface salinities were variable from January through April, but were uniformly high in May–July [Figure 2(c)]. Bottom salinities were almost always high [Figure 2(d)] with a gradual increase through the sampling season.

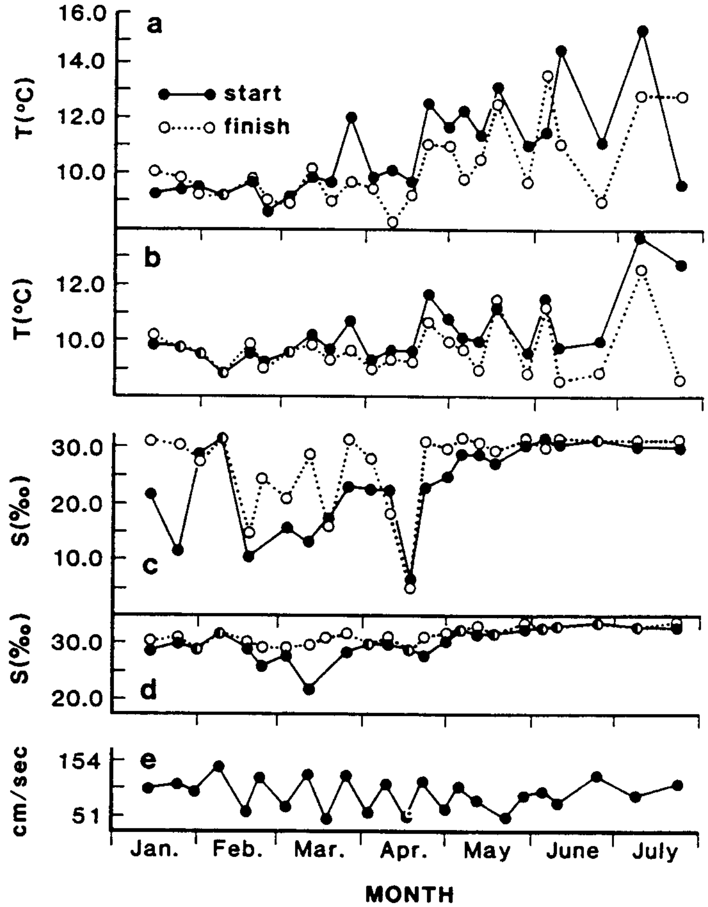

Figure 2. Physical features of Yaquina Bay during the sampling period. For temperature and salinity measurements, the sampling location was at the moored net sampling site; initial values (●) were taken at the start of the flood tides when the moored plankton nets were set, and final values (○), near the end of flood tide when the nets were retrieved. a, Surface temperature (taken with a bucket thermometer). b, Bottom temperature (from Niskin bottle samples). c, Surface salinity. d, Bottom salinity. e, Maximum current speed (cm s^{-1}) taken from tidal current charts (National Ocean Survey, 1981*b*).

Maximum flood tide current speeds (National Ocean Survey, 1981*b*) indicate that our sampling coincided with alternating spring and neap tides from February through April, but was offset from this cycle in May–July [Figure 2(e)]. River discharge was variable with high flow following rainfall on three dates [Figure 3(a)]. The high discharge values show close temporal correlations with low surface salinity values at the start of sampling [Figure 2(c)]. After April, discharge declined to low ($< 4{\cdot}0\ m^3\ s^{-1}$) summer levels after the end of the winter rains.

The strength of onshore and offshore Ekman transport is estimated by the 'coastal upwelling index' [Bakun, 1975; Figure 3(b)]. The transition between winter onshore transport and summer offshore transport (upwelling) occurred in late April, although

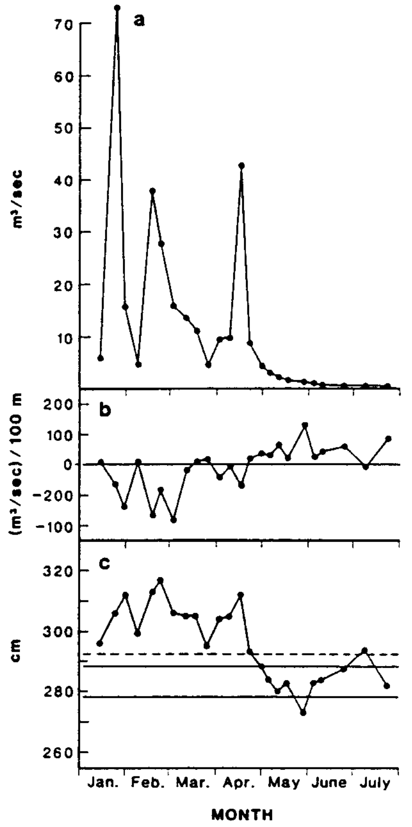

Figure 3. Riverine and ocean conditions during the sampling period. a, Yaquina River freshwater discharge on the day of sampling. b, Bakun upwelling index for 45°N, 125°W. c, Mean sea level at Yaquina Bay. The dashed line in (c) indicates the annual mean sea level (Pittock *et al.*, 1982) and the lower two solid lines represent the range of sea levels associated with zero alongshore current speed (Marthaler, 1977). Values of upwelling index and sea level are means for the seven days preceding the day of sampling.

weeks of reduced zonal transport were found in all months [Figure 3(b)]. Coastal sea level is correlated with current speed and direction over the Oregon shelf (Marthaler, 1977; Kruse & Huyer, 1983). Sea level measurements in 1982 indicate a transition from the winter regime of northward, onshore transport to the summer regime of southward, offshore transport during late April [Figure 3(c)]. A general correlation among river discharge, upwelling index, and sea level is apparent in Figure 3. Moreover, a correlation matrix of the physical factors considered between 23 February and 24 July (Table 1) shows a high degree of intercorrelation of variables, with relatively few being nonsignificant.

Size, stage, and seasonality of larval recruitment

Recruitment of *P. vetulus* to the estuary occurred during transformation; the mean length of pelagic larvae in stages A–F was 19·1 mm SL, and no trend in changing mean length was found over the season of recruitment. Catches of pelagic larvae from surface and midwater

TABLE 1. Pearson correlation matrix of physical factors considered in the study of recruitment of larval *Parophrys vetulus* to Yaquina Bay, Oregon[a]

	FW	SL	UPW	UPW4	BS	BT	SS	ST	DS
DT	0·50[b]	0·65[b]	−0·49[b]	−0·45[b]	−0·74[b]	−0·48[b]	−0·60[b]	−0·86[b]	0·54[b]
DS	0·77[b]	0·75[b]	−0·35	−0·60[b]	−0·71[b]	−0·37	−0·99[b]	−0·54[b]	—
ST	−0·51[b]	−0·63[b]	0·46[b]	0·50[b]	0·54[b]	0·78[b]	0·60[b]	—	—
SS	−0·78[b]	−0·81[b]	0·41[b]	0·64[b]	0·74[b]	0·41[b]	—	—	—
BT	−0·36	−0·39[b]	0·35	0·32	0·27	—	—	—	—
BS	−0·41[b]	−0·71[b]	0·30	0·86[b]	—	—	—	—	—
UPW	−0·39[b]	−0·72[b]	0·30	—	—	—	—	—	—
UPW4	−0·36	−0·53[b]	—	—	—	—	—	—	—
SL	0·66[b]	—	—	—	—	—	—	—	—

[a] FW, freshwater input to Yaquina Bay; SL, sea level at Newport; UPW, Bakun upwelling index at 45°N 125°W (FW, SL and UPW are all averaged for the 7 days prior to sampling); UPW4, mean upwelling for the previous week; BS, bottom salinity at beginning of sampling; BT, bottom temperature at beginning of sampling; SS, surface salinity; ST, surface temperature; DS and DT, values of the difference between ocean and bay salinity and temperature, respectively, calculated by the difference between the final bottom salinity and temperature and the initial surface values.
[b] Significant correlation ($p < 0·05$).

collections indicate that larvae enter the bay pelagically as the left eye migrates across the dorsal surface of the head, but before the juvenile pigment develops, as found for *Kareius bicoloratus* (Tsuruta, 1978).

An ontogenetic change in depth distribution of pelagic fish was observed [Figure 4(a–c]. Stages A and B comprised a larger proportion of the catch at the surface than at midwater or the bottom, stages C and D were abundant at all depths, and stages E and F were most abundant in the midwater and bottom nets. Thus, later stage larvae may not swim as high in the water column as earlier stage larvae. As shown by the beam trawl collections, however, stages B–F occurred within 0·3 m of the bottom.

Three peaks of larval recruitment were observed in 1982 (Figure 4). The first, 4–25 March, was largest with stages C and D dominating the catch (Figure 4). Initially within this peak, surface densities were greatest; catches in midwater and bottom nets peaked progressively later (Figure 5). After 4 March, however, larval densities were almost always greatest in the bottom net, and larval densities in midwater were generally greater than those at the surface. The second peak occurred from 16 to 22 April. During this brief peak, surface densities were higher in the first week but lower than midwater in the second week. This peak was dominated by stage D at the surface and stages E and F at the bottom. The third peak, from 5 May to 9 June, was more extended than the first two, and larvae were never abundant at the surface. These data suggest that entry into the estuary occurs at all depths, but with a trend for a greater proportion of the larvae to occur deeper in the water column during the course of each peak in larval recruitment. Also fewer larvae are captured at the surface at the beginning of each recruitment peak as the season progresses (Figure 5). Larvae at later stages of eye migration (E and F) composed a greater proportion of the catch as each peak progressed.

Benthic larval densities

The temporal trend in abundance of the larval English sole caught in the beam trawl generally matches that from the moored nets. The three peaks of abundance (during

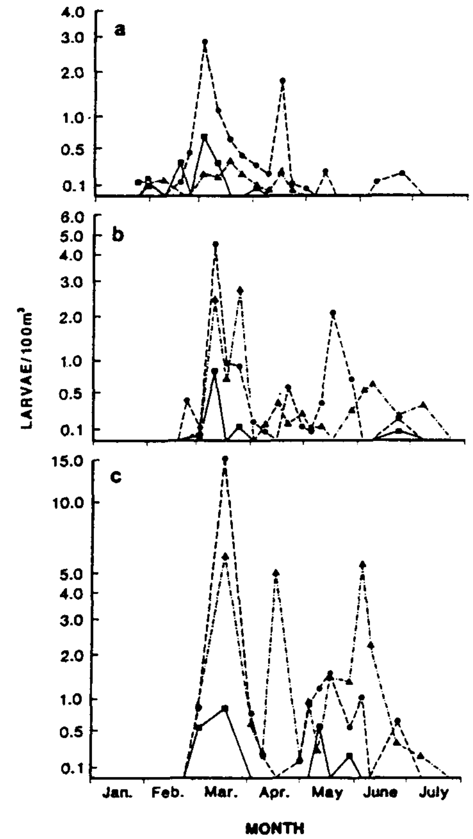

Figure 4. Seasonality of recruitment of different larval stages in surface (a), midwater (b), and bottom (c) moored ichthyoplankton nets. Density estimates shown are the mean of the two replicate samples at each depth. Densities of larval stages: A and B (■), C and D (●), E and F (▲).

March, April, and May) were found in the beam trawl catches, and are reflected in the abundance of stage D–F larvae (Figure 6). Larvae were present in trawl samples at all stages except A. Early stage larvae were rare compared to their relative abundance in the plankton. This suggests that early larvae are either not available to the sampling gear, are flushed from the bay, that the transformation process in early stages is rapid, or that the earliest stages are more vulnerable to predation. Our observations of stage durations support the third hypothesis.

The abundance of completely transformed juveniles followed the temporal pattern of stages B–F in beam trawl samples until late March (Figure 6). After 18 March, the densities of juveniles increased in proportion to those of younger stages. High densities ($> 1\ m^{-2}$) of juveniles were found from 7 April through 9 June, indicating that the strongest cumulative recruitment of young-of-the-year English sole to the estuary occurred prior to this time and was strongest in March–April. Declining abundances in June and July indicated that emigration from these stations and mortality exceeded recruitment, despite continued catches in the moored net samples in June (Figures 4 and 5).

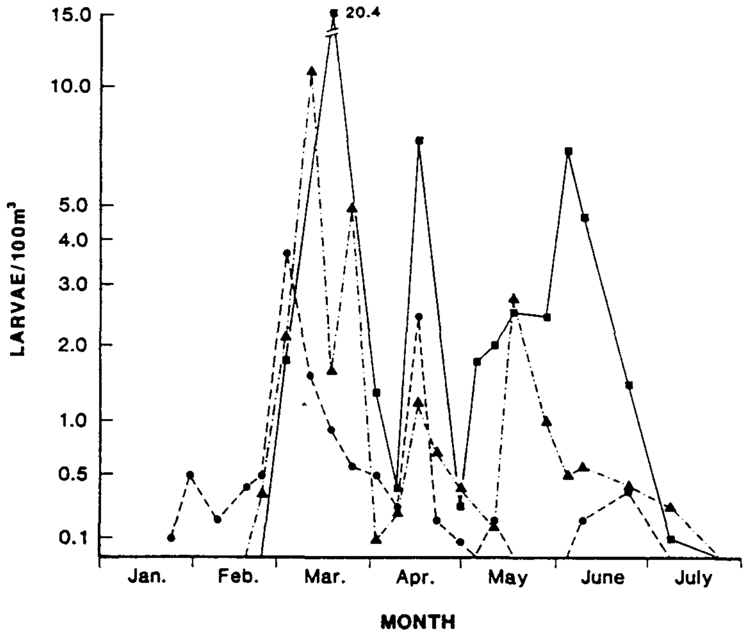

Figure 5. Seasonal densities (larvae per 100 m^3, all stages combined) or larval *Parophrys vetulus* during the 1982 migratory season, as a function of depth of capture. Each value represents the mean of two replicate samples. ●, Surface nets; ▲, midwater nets; ■, bottom nets.

Fortnightly oscillations in the catches of juveniles were superimposed on the seasonal pattern of February–May (Figure 6). High abundances generally occurred on spring tides followed by lower abundances on the neap tides the following week. The oscillation was not apparent after recruitment decreased in June. To test for the relationship of abundance with the neap–spring tidal cycle, the moving average (weighted by one adjacent point earlier and one adjacent point later) for each point of juvenile abundance, from 23 February to the end of the season, was determined. Then, the deviation of these values from observed values was calculated and divided by the moving average for scale. Regressing this value on maximum values of current speed (National Ocean Survey, 1981*b*) during collections shows a significant relationship of scaled abundance with current speed (Figure 7), suggesting that densities are low at the stations during neap tides (when current speed is low). High current speed may result in greater bottom scour in the mid-channel areas; during these times juveniles may seek more protected shallows such as our sampling area. The same relationship, only weaker, held for benthic larvae in stages B–F.

Diel recruitment patterns

Diel sampling on different tides demonstrated that larval *P. vetulus* were only abundant during night flood tides on 17–18 March and 9–10 April (Table 2), supporting the choice of sampling times. No *Parophrys* larvae were taken in daylight ebb and flood tide Tucker trawl samples on 4 May, although they were found in night flood tide moored net collections on 5 May. This trend for highest catches during night flood tides thus occurred

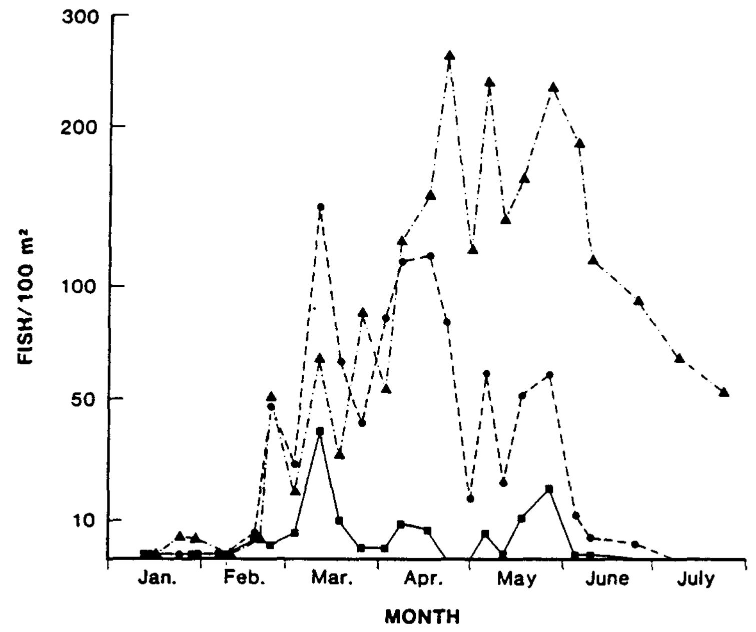

Figure 6. Densities of benthic larval and juvenile *Parophrys vetulus* (numbers per 100 m^2) taken during beam trawl sampling in 1982. ■, Densities of larval stages B–D combined; ●, larval stages E and F; ▲, juvenile fish.

throughout the early part of the season of recruitment. This pattern was not observed during the night ebb and flood tide collections later in the season, when night ebb tide catches were high (Table 3). Very high densities of *Parophrys* larvae were found in Tucker trawl samples from the slack high tide on 20–21 May, relative to densities in Tucker trawl and moored net samples from the ebb tide on 20–22 May and slack low and flood tides on 27–28 May. In addition, densities from bottom moored net samples during the ebb tide on 20–21 May were greater than the densities from bottom moored net and Tucker trawl samples during the slack low and flood tides on 27–28 May. While no simple pattern is seen in these data, it is clear that the pattern of high abundance only during night flood tides was not found in late May. The high abundance from the slack high tide on 20–21 May was found during a week of spring tides, while the lower abundance from the flood tide a week later was found during a neap tide. The occurrence of high abundance during a spring tide is similar to our results from beam trawl catches. Two seasonal factors may be pertinent to the change in pattern of diel abundance near the end of recruitment. Upwelling began in late April (Figure 3), which may have affected the behaviour of *Parophrys* larvae. Emigration of early juveniles from Yaquina Bay began in late May and June (Figure 6; Krygier & Pearcy, 1986), which could have altered the pattern and abundance over the tidal cycle, particularly near the bottom, even though immigration of stages D–F continued during the study (Figure 4).

The relationship of environmental factors to estuarine recruitment of Parophrys vetulus

Parophrys vetulus larvae and juveniles accumulated in Yaquina Bay during 1982 with recruitment extending over a prolonged season, from February to June (Figures 5 and 6).

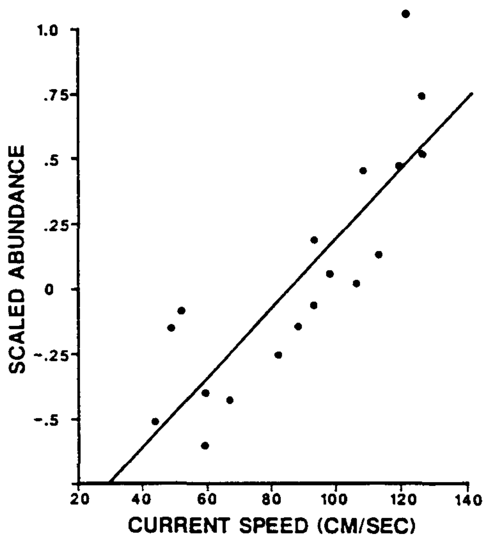

Figure 7. Densities of juvenile *Parophrys vetulus* collected in the beam trawl as a function of current speed. Maximum current speeds were taken from National Ocean Survey (1981*b*). Data points represent sampling times between 23 February and 9 July. Observed abundances were changed to moving averages weighted by one point earlier and later; this value was then subtracted from the observed value and divided by the moving average for scale. Thus positive scaled abundances are greater than expected, negative abundances less than expected. The line is represented by the linear fit scaled abundance = 0·0135 (current speed) − 1·14. $N = 18$, $r^2 = 0{\cdot}71$.

During this season, most of the fish entered in pulses. Planktonic larvae entered at all depths, but the proportion of larvae entering at the surface was usually greatest earlier in the peak than later. Benthic juvenile density increased from February through April but not as rapidly in March as would be expected from the large pulse of pelagic and benthic larvae (Figures 5 and 6). The major increase of benthic juveniles occurred in April, during the second peak of recruitment which was the least pronounced of the three for pelagic larvae. Although the third peak of pelagic larval recruitment was prolonged, from mid-May through mid-June, densities of benthic juveniles declined during that time.

Accumulation of larval *P. vetulus* in nearshore areas by onshore Ekman transport appeared to be important during the period of larval recruitment from mid-February to June (Figures 5 and 6). A period of onshore transport [Figure 2(b)] preceded the first peak of larval recruitment by a week (Figure 4). The strongest peak of onshore transport (in early March) coincided with the greatest recruitment of pelagic larvae at the surface, and preceded the largest peak of benthic larval recruitment by a week. The final two periods of onshore transport (in April) coincided with the major increase in abundance of benthic larvae and juveniles. The relationship was not observed during the final pulse of recruitment in May and June, when surface water transport was offshore; these recruits were typically later stages which may have come from nearshore nursery areas (Figure 4). The sea level record [Figure 3(c)] matched the recruitment of *Parophrys* in the same way as the upwelling index record, but the relationship of peaks in transport to pulses of recruitment was not as clear.

A direct relationship of river discharge [Figure 3(a)] to recruitment was not found. The largest peak in discharge preceded recruitment of *Parophrys* in January. The next peak in

TABLE 2. Density of *Parophrys vetulus* larvae (individuals per 100 m^3) taken at each depth on each tide during diel sampling[a]

	Moored nets			Tucker trawl		
	Depth			Depth		
Date 1982/Tide	S	M	B	S	M	B
17–18 March						
Day flood	0	0	0	—	—	—
Day ebb	0·91	—	—	—	—	—
Night flood	0·90	1·60	19·75	—	—	—
Night ebb	0	0	0·64	—	—	—
9–10 April						
Day slack low	—	—	—	0	0	0
Day flood	0·04	0	0	0	0	0
Day slack high	—	—	—	0	0	0
Day ebb	0	0	0	0	0	0
Night slack low	—	—	—	0	0	0·92
Night flood	0·26	0·20	0·43	0	1·28	2·06
Night slack high	—	—	—	0	0	0
Night ebb	0·07	0	0·20	0	0	0·12
4–5 May						
Day flood	0	0	0	0	0	0
Day ebb	—	—	—	0	0	0
Night flood	0	0·17	1·73	—	—	—

[a] Each value is the mean of two samples. S, Surface; M, midwater; B, bottom nets; ——, no sample.

TABLE 3. Density of *Parophrys vetulus* larvae (individuals per 100 m^3) taken at each depth on each tide during night sampling from 20 to 28 May 1982[a]

	Moored nets			Tucker trawl		
	Depth			Depth		
Date 1982/Tide	S	M	B	S	M	B
20–21 May						
Night slack high	—	—	—	8·17	5·93	8·96
Night ebb	0·31	0·27	4·87	—	—	—
22 May						
Night ebb	0·34	0·65	—	0·43	0·64	0·26
27–28 May						
Night slack low	—	—	—	0·45	0·12	0
Night flood	0	0·96	2·40	0·12	0·22	0·42

[a] Each value is the mean of two samples. S, Surface; M, midwater; B, bottom; ——, no sample.

TABLE 4. Pearson correlation matrix of larval densities with physical factors[a]

	FW	SL	UPW	UPW4	BS	BT	SS	ST	DS	DT
ADS	0·68[b]	0·65[b]	−0·68[b]	−0·60[b]	−0·62[b]	−0·47[b]	−0·77[b]	−0·63[b]	0·76[b]	0·56[b]
ADM	0·04	0·19	−0·18	−0·46[b]	−0·61[b]	−0·08	−0·34	−0·22	0·34	0·37
ADB	−0·01	0·17	0·02	−0·25	−0·41[b]	−0·23	−0·28	−0·36	0·30	0·40
AD	0·16	0·27[b]	−0·19	−0·37[b]	−0·48[b]	−0·22[b]	−0·38[b]	−0·36[b]	0·39[b]	0·40[b]
EFS	0·49[b]	0·56[b]	−0·29	−0·38[b]	−0·45[b]	−0·37	−0·65[b]	−0·38[b]	0·67[b]	0·29
EFM	0·07	0·18	−0·07	−0·26	−0·51[b]	−0·17	−0·30	−0·18	0·32	0·15
EFB	0·17	0·08	0·12	0·05	−0·20	−0·12	−0·23	−0·05	0·25	0·11
EF	0·11	0·10	0·02	−0·06	−0·22[b]	−0·11	−0·20	−0·08	0·21	0·10

[a] ADS, ADM, ADB, AD, log-transformed densities of stages A–D at surface, midwater, bottom, and all nets combined, respectively. EFS, EFM, EFB, EF, log-transformed densities of stages E and F in surface, midwater, bottom, and all nets combined, respectively. For description of physical factors, see Table 3.

[b] Significant correlation ($p < 0·05$).

discharge, in late February, coincided with the onset of estuarine recruitment. Discharge was moderate during the peak of larval recruitment in March. The final discharge peak, in mid-April, coincided with the second pulse of recruitment, when juvenile *Parophrys* accumulated in the bay. Discharge declined to low spring and summer levels in May and June, during the final pulse of recruitment.

Clear differences exist in the times and depths at which different stages recruited to the estuary (Figure 4), so it is not unexpected that relationships between physical factors and recruitment will vary among stages and in the different nets. To examine the differences, densities of pelagic larvae were combined by stages A–D and by stages E and F to correlate with the physical variables (from Table 1). Correlations of the physical factors with early stage (A–D) densities are stronger than for the late stage (E and F) densities (Table 4). This may be due to the duration of the stages, with the more ephemeral early stages showing a closer relationship with conditions at the time of their capture. Secondly, within both groups, correlations are typically significant in the surface net samples, but poor in the midwater and bottom nets.

As described above, onshore transport brings transforming larvae to nearshore areas and is responsible for the major pulses of early stage larval recruitment (Figures 4–6). This is reflected in the negative correlation between mean upwelling for the week of sampling (i.e. offshore transport) and early stage larval densities in surface samples (Table 4). The lack of significant correlation between upwelling and later stage larval recruitment suggests that other factors influence their recruitment. Larvae recruited to nearshore nursery areas (Laroche & Holton, 1979; Krygier & Pearcy, 1986) begin the transformation process, and may use a different mechanism for locating and recruiting to the estuary. This is supported by the stronger correlation of upwelling lagged by a week to the various larval densities (Table 4).

For this group, which we call the nearshore recruitment pool, the strongest correlation is with bottom salinity at the start of sampling (BS, Table 4), which shows a strong negative correlation with densities of virtually all groups. While this might infer that freshwater input to the estuary is the causative factor, the correlation of input with recruitment is weak, with the exception of surface catches (Table 4). As expected, surface salinity shows a similar trend, with greater surface recruitment during times of low salinity. Bottom salinity is weakly correlated with freshwater input as compared to surface salinity, but strongly correlated with sea level and with lagged upwelling (Table 1). This suggests that lowered bottom salinity as the ebb tide begins may play a role in the movement of animals from the nearshore recruitment pool.

Discussion

Several studies have documented a relationship between physical factors and recruitment of fishes, generally by correlating onshore transport with year class strength (Nelson *et al.*, 1977; Bailey, 1981). The implication is that larval drift in the wrong direction prevents movement to the appropriate nursery areas (whether coastal or estuarine) and that the resultant cohort will show poor survival; this concept dates back to Hjort (1914) and has been placed in the context of current patterns of the west coast of North America by Parrish *et al.* (1981). This type of relationship is unclear for *P. vetulus*. Ketchen (1956) showed an inverse correlation between temperature during development and subsequent year-class strength; he inferred that lower temperatures delayed development, resulting in extended pelagic existence and more complete drift to nursery areas before metamorphosis. Higher temperatures presumably resulted in rapid metamorphosis prior to availability of habitat for settlement, which may cause high mortalities (Marliave, 1977).

Subsequent studies dealing with a larger body of fishery data have not made the situation clearer for *P. vetulus*. Hayman and Tyler (1980) suggested that upwelling during the fall delayed spawning and that this was in some way linked to stronger cohorts. Kruse (1984), with a more sophisticated model, did not link recruitment success to either storm effects or starvation (as reflected in primary production), but to indices of larval transport. Larval *P. vetulus*, however, are consistently found in the coastal assemblage of fish larvae (within 28 km of shore) under various environmental regimes (Richardson & Pearcy, 1977; Laroche & Richardson, 1979; Richardson *et al.*, 1980; Mundy, 1984). Therefore, this species may control its onshore–offshore distribution through some form of modulated transport akin to the mechanism proposed by Peterson *et al.* (1979) and Rothlisberg and Miller (1983). The general picture of planktonic population maintenance over continental shelves, however, is probably more complex; Sundby (1984) showed that eddies produced by flow–topography interactions may retain fish eggs on the continental shelf of Norway. On the shelf off the west coast of North America, a similar phenomenon may occur because most cross-shelf transport occurs in localized jets (Mooers & Robinson, 1984). Within a given year, however, our data suggest that onshore transport is important in the pulses of recruitment to Yaquina Bay (Figures 3 and 5). Transforming larvae are abundant in neuston collections within 30 km of shore, where densities reached 75 per 10^3 m^2 (J. Shenker, Bodega Bay Marine Laboratory, Sonoma, CA 94923, pers. comm., 9 May 1985). Larvae occurring in the neuston may be subject to a greater probability of onshore transport by wind-driven advection than larvae occurring throughout the water column (Parrish *et al.*, 1981); further, Shanks (1983, 1985) has shown that neustonic species may accumulate and be transported onshore in surface slicks associated with internal waves.

A comparison of the life history of *P. vetulus* with many of the species subject to offshore transport effects (hake, menhaden) shows that one important difference is in timing of spawning. English sole are unlike other marine species in that the spawning season is prolonged and variable from year to year, apparently subject to thermal conditions in the benthic habitat; Kruse and Tyler (1983) found that spawning occurred between September and April, with a peak lasting 1–3 months within this interval. As spawning is triggered by warming of shelf waters, it coincides with periods of onshore transport which may maintain eggs and early larvae in the nearshore zone. Further, feeding ecology may play a role in larval survival. Gadomski and Boehlert (1984) demonstrated that larval English sole depend upon appendicularians as prey organisms. Appendicularians show peaks of abundance which are also associated with periods of onshore transport of low salinity water (Peterson & Miller, 1976) and are often highly aggregated (Alldredge, 1982). Thus an understanding of the year-class strength of this species may require further analysis of the match–mismatch hypothesis of Cushing (1975). Despite several studies considering environmental factors and year-class strength (Ketchen, 1956; Hayman & Tyler, 1980; Kruse, 1984), the stage at which year-class strength is determined for English sole has not been clearly defined. However, in the most comprehensive study to date comparing mortalities of pelagic and estuarine demersal stages of a flatfish, van der Veer (1986) noted that overall year-class strength in plaice was determined prior to settlement but that density-dependent mortality in the estuary served a modulating effect, significantly decreasing the variability in year-class strength.

Estuarine dependence for species with eggs and larvae spawned offshore is rare on the Pacific coast of North America. By comparison, Miller *et al.* (1984) showed that five fishes representing 85% of the commercial fisheries catch in North Carolina have this life history pattern. It is significant in this regard that the one marine species with an estuarine-dependent juvenile stage on the Pacific coast is a flatfish. We have suggested a dual pattern of estuarine recruitment, with the earliest pulses being transforming pelagic larvae and then continued recruitment of a nearshore recruitment pool of older larvae. This interpretation agrees with data in Krygier and Pearcy (1986), who observed a dcrease in density of juveniles in nearshore nursery areas concurrent with density increases in Yaquina Bay. Near metamorphosis, flatfishes undergo significant morphological and behavioural changes (Finger, 1976; Tsuruta, 1978; Kawamura & Ishida, 1985) which allow transition from pelagic to benthic existence. Maintenance of a nearshore pool of recruits would be difficult for fishes not associated with the bottom, such as the estuarine recruiting sciaenids and clupeids of the Atlantic and Gulf coasts. Flatfish, however, can remain on the bottom, like recruiting *Anguilla* (Creutzberg, 1961; McCleave & Kleckner, 1982) or shrimps (Hughes, 1969; Staples, 1980), as demonstrated by the abundance of transforming pelagic larvae in our beam trawl samples (Figure 6). This group of larvae can affect their horizontal distribution by moving into the water column, as transforming flatfish may show an ambivalence between pelagic and benthic behaviour (Fluchter, 1965).

While initial recruitment is related to onshore transport, subsequent entry to the estuary by the nearshore pool of recruits is apparently related to estuarine factors, as recruitment occurs primarily on night flood tides (Table 2). Larvae in stages E and F are most indicative of this pattern, and the dominant factor correlated with larval abundance is bottom salinity at the start of sampling. While this is not strongly correlated with freshwater input, as one would suspect, it may instead be a function of turbulence within the estuary. Locating the estuary may thus be a function of low salinity water flowing out near the bottom, which could result in activity patterns such as pelagic swimming (Creutzberg *et al.*, 1978). Reference to either the bottom or endogenous, rhythmic activity may then signal the end of flood tide and of pelagic activity (Boehlert & Mundy, in press). Such behaviour would increase the probability of transport into the estuary (Tsuruta 1978; Rijnsdorp *et al.*, 1985). This movement is a form of tidal stream transport and can save up to 90% of the energy necessary for migration (Weihs, 1978). That it is a directed movement is obvious by comparing densities of transforming larval *Parophrys* in the estuary with passively recruited larvae of other species (Pearcy & Myers, 1974; Boehlert & Mundy, in press). When samples from the present study were later sorted for smaller larvae, only five *Parophrys* larvae smaller than 10 mm SL were found (Mundy & Boehlert, unpubl. data); these early larvae apparently enter the estuary by passive movement.

While the sampling did not expressly study emigration from the estuary, the data on juvenile abundance (Figure 6) suggest that emigration began in late May while immigration of larvae was still occurring (Figures 4 and 5). Pelagic emigrants in late May (Table 3) did not differ in development stage from immigrants seen at the same time period. Early in the season, virtually all pelagic activity by larvae takes place on night flood tides (Table 2), whereas late May samples show activity by larvae on night slack high and the following ebb tide (Table 3). This contrasts with the observations of Rijnsdorp *et al.* (1985) and van der Veer (1986), who noted that early-stage larvae recruited on flood tides but were often flushed from the estuary on the following ebb tide. Development of behaviour patterns with age is probably an important factor in estuarine retention (Fortier & Leggett, 1982; Epifanio *et al.*, 1984). While the study involved too few samples to determine the relationship of temperature, salinity, or other factors with the difference between the early and late season samples, the pattern of juvenile abundance (Figure 6) and its relationship with the spring–neap cycle (Figure 7) may help explain the difference. It is possible, for example, that the increased densities during periods of high current speed may be from movement of fish from farther up the estuary to the region sampled near the mouth (Figure 1). Rijnsdorp *et al.* (1985) found higher larval densities correlated with increased suspended material and suggested that larvae are 'swirled up from the bottom' like the suspended matter, and perhaps flushed from the estuary. While this is possible, it was not observed in this study [Tables 2 and 3; Figure 2(e)].

The recruitment dynamics of English sole to Yaquina Bay show a more complex pattern than those reported for many Atlantic species using larger estuarine nursery areas (Creutzberg, 1961; Weinstein *et al.*, 1980; Miller *et al.*, 1984). Accumulation of *P. vetulus* larvae in nearshore areas, and the initial pelagic recruitment to estuaries, is related to onshore transport in a relatively simple way. Recruitment to the estuary, however, also appears to occur from some of the later stage larvae and juveniles which have settled in open coast areas (Rogers, 1985; Krygier & Pearcy, 1986). A more complicated relationship exists between recruitment and reduced bottom salinities, perhaps in connection with moderately high river discharge. The reduced salinity may serve not only to influence behaviour that would enhance tidal stream transport of recruits entering the estuary directly (Creutzberg *et al.*, 1978), but may also influence fish recruiting to the estuary from coastal areas. This more complex recruitment pattern may enhance the ability of *P. vetulus* to use the relatively small, isolated west coast estuaries as juvenile nursery areas.

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