

Influence of nearshore hydrodynamics on larval abundance and settlement of sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* in the Oregon upwelling zone

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ABSTRACT: Patterns of larval abundance and early juvenile recruitment of the sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* were examined throughout spring and summer of 1994 and 1995 at 2 sites in southern Oregon, USA, lying within the northern region of the California Current System. Sea temperature and coastal wind records were used as indicators of local upwelling and relaxation events and combined with a method of aging young sea urchin recruits to link specific settlement events with hydrographic events. In 1994 sea urchin larvae were found in plankton collections from April to July, while in 1995 larvae were found from March to July and occurred in a higher percentage of the collections than in 1994. At the 2 sites, settlement occurred from April to August, was variable between years and sites, but most consistently occurred in June. Larval occurrences in the plankton and settlement events in 1994 and 1995 were associated with water masses between 11 and 12°C. Peak settlement in both years was associated with warm water events characterized by a mixed water column and northward wind stress. Settlement rates were low during warm events characterized by a stratified water column and low wind stress. During the summer flow regime, onshore transport of larvae may be linked to relaxation events forced by wind from the south and onshore Ekman flow.

KEY WORDS: Sea urchin · Larvae · Juveniles · Recruitment · Settlement · Upwelling · Relaxation · *Strongylocentrotus franciscanus* · *S. purpuratus* · Oregon · California Current

INTRODUCTION

Variation in recruitment for many marine organisms has been attributed to numerous physical processes that influence larval supply (e.g. Gaines & Roughgarden 1985, Roughgarden et al. 1988, Shanks 1995). In particular, the influence of nearshore currents on larval supply has been the focus of numerous studies (e.g. Banse 1955, 1956, 1986, Scheltema 1986, Farrell et al. 1991, Roughgarden et al. 1991, Wing et al. 1995a, b). Investigations of the link between nearshore hydrodynamics and larval supply and settlement are fundamental to understanding variability in recruitment to local populations. One approach to studying this link is to measure settlement of larvae from the plankton in conjunction with physical parameters. Some hydro-

graphic processes, such as coastal upwelling and relaxation, are associated with characteristic patterns of temperature, salinity, and wind stress. Concurrent measurements of larval settlement and physical parameters may permit correlation of events and provide a link between hydrographic processes and larval supply to a specific region (e.g. Farrell et al. 1991 for barnacle recruitment and Wing et al. 1995a, b for crab and sea urchin recruitment).

In California and Oregon, USA, recruitment of the sea urchins *Strongylocentrotus franciscanus* (A. Agassiz) and *S. purpuratus* (Stimpson) varies spatially and between years (Ebert 1983, Pearse & Hines 1987, Ebert & Russell 1988, Rowley 1989, Ebert et al. 1994). In California, Ebert et al. (1994) found more regular and higher magnitudes of settlement occurring at sites south of Point Conception, California, compared to more northern sites. These differences were attributed

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to greater retention of water in the Southern California Bight and more energetic offshore advection of water in northern California. Along the southern Oregon coast, Ebert (1983) measured strong recruitment of 1 yr old *S. purpuratus* in 1963, but found little or no recruitment from 1964 to 1978. A large recruitment of 1 yr old *S. purpuratus* was observed in southern Oregon in 1994, but no significant recruitment was found in 1995 or 1996 (authors' pers. obs.). Further north at Tatoosh Island, Washington, Paine (1986) reported substantial recruitment of *S. purpuratus* in only 4 years between 1963 and 1985. These studies suggest that annual recruitment within the northern portion of the California Current System and more northern waters may, in part, be limited by larval supply.

Studies by Ebert et al. (1994) and Wing et al. (1995b) suggest that spatial and temporal patterns of sea urchin settlement may be closely linked to patterns of onshore and offshore transport of coastal waters. Wing et al. (1995b) found that sea urchin settlement near Bodega Bay, California, appeared to be associated with relaxation of upwelling. However, most of the sample intervals (weekly) in that study included some phase of both upwelling and relaxation events. Because the age of recruits was not known, it was not possible to make a precise connection between settlement events and specific hydrographic events.

This study examines spatial and temporal patterns in abundance and vertical distribution of sea urchin larvae in nearshore (<30 m depth) water along the southern Oregon coast. Spatial and temporal patterns of sea urchin recruitment are presented for 2 sites over 2 years, and a method of estimating the age of recently settled *Strongylocentrotus franciscanus* and *S. purpuratus* (Miller 1995) is used to link specific settlement events to hydrographic events. Sea temperature and coastal wind records are used as indicators of local upwelling and relaxation events and to interpret observed patterns of larval abundance and recruitment. An experimental field outplant of juveniles from lab-reared larvae was also conducted to provide an estimate of survivorship and retention of juveniles on field settlement collectors.

METHODS

Study sites. This study was conducted at 2 sites along the southern Oregon coast. One site (43° 20.4' N, 124° 22.7' W) was located at Gregory Point, north of Cape Arago, and a second site (42° 44.1' N, 124° 30.4' W) was located 1 km west of the port of Port Orford, 67 km south of Gregory Point (Fig. 1). Both sites were fully exposed to winter winds and swell from the west and south and partially protected from north-

west winds and ocean swell which predominate in the summer months.

Plankton sampling. Plankton was sampled at both study sites from late January to August in 1994, and from March to August in 1995. In 1994, plankton samples were collected at ca 1 wk intervals at both sites. In 1995, plankton samples were collected at Gregory Point every other day (weather permitting, $n = 69$ sample days). Samples were collected at Port Orford at ca 2 wk intervals in 1995, in conjunction with sampling settlement collectors. Samples at both sites were collected 200 to 300 m offshore, near the settlement collectors. Three replicate tows of 5 min duration were made at 5 m depth with a 0.25 m diameter, 202 μ m mesh net. Sample volume was measured using a calibrated mechanical flowmeter with a low-speed impeller (General Oceanics, Inc., Miami, FL, USA, Model 2030R2). Plankton samples were preserved and stored in 1.5% formaldehyde in seawater and buffered with excess sodium borate. Samples were sorted using cross-polarized light which highlighted the birefringent calcareous arm rods of sea urchin larvae. Samples that contained very high densities of zooplankton or diatoms were subsampled with a plankton splitter.

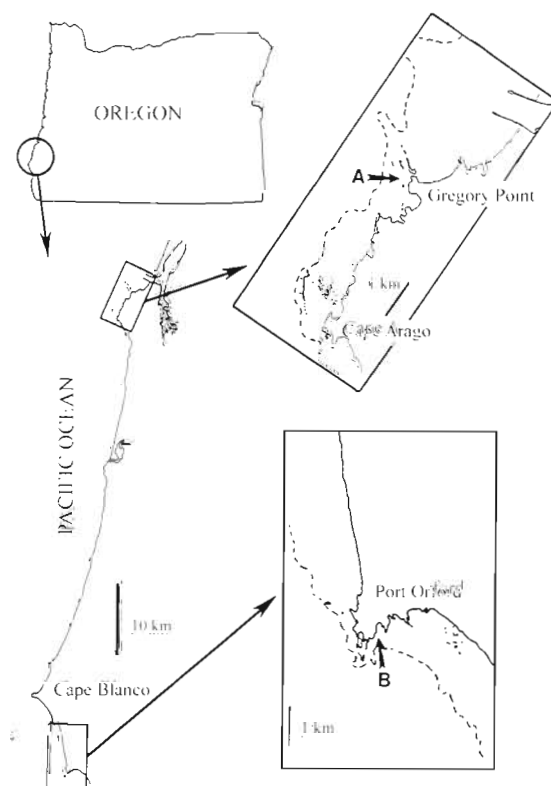


Fig. 1 Location of study sites at Gregory Point (A) and Port Orford (B) along the Oregon coast, USA. North is toward the top of the figure. Dashed lines: 10 fathom contour

A series of depth-stratified plankton samples was collected on 3 dates in 1995 when sea urchin larvae were abundant. Plankton was sampled with a 0.5 m diameter, 202 μm mesh net with a close-open-close mechanism to collect samples from discrete depths. Tows were 4 min in duration and sampled between 12 and 30 m^3 . Samples were processed as described above for temporal patterns. On each sample date, 3 replicate samples were collected and temperature was recorded at each depth. In order to minimize variation in larval abundance along the horizontal axis due to alongshore currents, all tows were made adjacent to a drogue suspended 5 m below a surface buoy. Samples were collected at Gregory Point on 2 dates in March, in an 18 to 22 m depth water column, and at Port Orford on 1 day in June, in a 30 m depth water column. Sampling was conducted during calm conditions with 1.0 to 1.5 m swell and winds $< 4 \text{ m s}^{-1}$.

Recruitment monitoring. Recruitment was measured using settlement collectors that were deployed over the same time periods described for plankton sampling. An attempt was made to sample the collectors at 2 wk intervals, but sea conditions caused sample intervals to range from 9 to 35 d in 1994, and from 12 to 28 d in 1995. Recruitment on collectors was assumed to be influenced by a time-dependent survival rate, with lowest survival for juveniles that settled early in a sample interval. In this report, the term 'recruitment' is used as a measure of settlement and represents the sum of larval settlement, minus post-settlement mortality, for each sample interval.

Settlement collectors consisted of buoyant PVC cylinders (80 cm long \times 15 cm diameter) with 4 panels (21.5 cm \times 29 cm) of Astroturf™ (Monsanto Co.) attached in pairs around the outer circumference of the cylinder (Fig. 2). Each collector held a total of 0.25 m^2 of Astroturf™ substratum. At each study site, three 90 kg concrete moorings were placed on the bottom 10 m apart, at 22 m depth at Gregory Point and 18 m depth at Port Orford. Two settlement collectors were suspended above each mooring, the lower collector suspended 1 m above the bottom and the upper collector suspended at 4 m below the surface (at mean lower low water).

Replacement settlement panels were seasoned in coarse-filtered seawater for at least 1 wk prior to deployment to encourage growth of a microbial film. Settlement panels on each collector were retrieved and replaced using SCUBA. Sampled panels were soaked in freshwater for 5 min, killing all sea urchins, then spray washed over a 300 μm mesh screen to recover juvenile sea urchins. Samples were preserved in 1.5% formaldehyde in seawater buffered with excess sodium borate. Samples were sorted using cross-polarized light to highlight the calcareous test plates and spines of juvenile sea urchins. Because sample intervals varied, all data on ju-

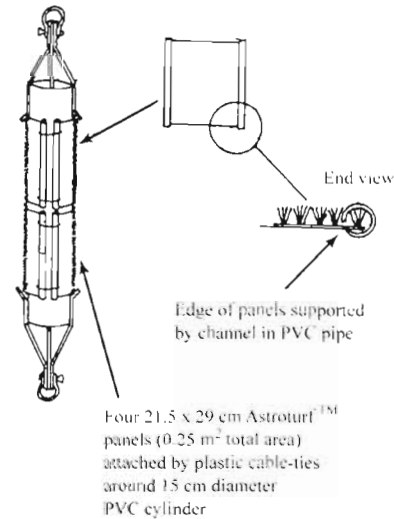


Fig. 2. Design of collectors for sea urchins deployed at Gregory Point and Port Orford

veniles were adjusted to a settlement rate ($\text{no. m}^{-2} \text{ d}^{-1}$) and plotted on the last day of each sample interval.

Settlement within each sampling interval could not be directly linked to a specific hydrographic process because the specific day of settlement was not known. Such links were made indirectly, however, by calculating the timing of settlement during a sampling interval based on the estimated age of juveniles on the sample date. The age of juveniles on the sampling date was estimated by staging them according to the development of certain traits (e.g. spines, pedicellariae, functional gut) and knowing the time it takes to develop to a given stage. Miller (1995) developed this aging method by rearing juveniles in the laboratory at a range of temperatures (8, 11, and 14°C), establishing stages (10 or 11, depending on species) based on a set of traits, and determining the temperature-dependent developmental rates (stage d^{-1}) for juveniles in the first 2 wk after metamorphosis. For application to this field study, the aging methods (Miller 1995) were modified by combining juvenile stages after field-sampled juveniles were assigned to single stages. For *Strongylocentrotus franciscanus*, stages were combined in consecutive pairs older than stage 2 (Σ juveniles in stages 3 and 4, ..., 9 and 10). For *S. purpuratus*, stages older than stage 1 were combined (Σ juveniles in stages 2 and 3, ..., 10 and 11). Stages were combined in this manner so that some of the uncertainty in staging juveniles could be disregarded. The dates of settlement were calculated for 6 sampling intervals that represent the majority of recruitment measured in 1994 and 1995. Dates of settlement were not calculated for sampling intervals when few recruits were found. The relative proportion of settlers shown for each sampling interval was also adjusted using a survival curve calculated for

outplanted juvenile *Strongylocentrotus franciscanus* (see 'Outplant experiment'). This adjustment was made by dividing the number of juveniles in a given age group by the mean of the daily survival values for that age group. The survival curve for age 1 to 14 d old *S. purpuratus* was assumed to be the same as that calculated for *S. franciscanus*.

Water temperature was recorded at 36 min intervals at the depths of the upper and lower settlement collectors at both study sites using intercalibrated submersible temperature loggers (Onset Computer Corp., Pocasset, MA, USA). Wind data recorded at Gregory Point were obtained from NOAA National Oceanographic Data Center archives (<http://www.nodc.noaa.gov>).

Outplant experiment. Juvenile survivorship on field settlement panels was estimated by outplanting juvenile *Strongylocentrotus franciscanus* that were reared in the lab. Survivorship was then measured over a 2 wk period. Three buoyant PVC cylinders (60 cm long \times 10 cm diameter), similar in construction and function to the field settlement collectors, were moored 1 m apart at 4 m depth in the mouth of Coos Bay, 3 km north of Gregory Point. This site was exposed to diminished ocean swell entering the bay mouth and to moderate tidal currents ($<0.5 \text{ m s}^{-1}$). Larvae of *S. franciscanus* were reared using methods modified from Leahy (1986) and Strathmann (1987), and induced to metamorphose using methods modified from Pearse & Scheibling (1994). Juveniles 24 h old were pooled from laboratory settlement containers and 50 juveniles were pipetted onto each of twelve 225 cm^2 AstroTurf™ panels. Juveniles were given ca $\frac{1}{2}$ h to attach to the substratum, then each panel was placed in a plastic bag. Panels were deployed on the subtidal moorings using SCUBA. Bags were resealed following removal of the panels so that the number of juveniles not attached to the panels could be counted (mean number/panel outplanted = 47, range = 41 to 50). Six bare control panels, with no juveniles, were also deployed on the moorings to measure any natural settlement of larvae. After 1 wk in the field, 6 outplant panels and 3 control panels were randomly sampled and juvenile sea urchins were removed from panels and processed as in 'Recruitment monitoring' for settlement collectors described above. After 2 wk in the field, the remaining 6 outplant and 3 control panels were retrieved and processed for number of juvenile sea urchins.

RESULTS

Physical parameters

Sea temperature patterns differed between years but were synchronous among sites in each year (Figs. 3

to 6). These patterns were characterized by aperiodic changes in temperature that began in March or April and continued throughout each study period. Changes in water temperature corresponded to changes in wind-forcing, with colder water associated with wind from the north and warmer water associated with periods of calm or winds from the south (Fig. 7).

Low-amplitude cycles of upwelling and relaxation occurred at both sites in March 1994, but in 1995, upwelling did not begin until late April (Figs. 3 & 4). This pattern was consistent with sea level recorded at Crescent City, California (available from NOAA archives, Sea and Lake Levels Branch, Silver Spring, MD, USA). Sea level records for Crescent City provide a good index of sea level in southern Oregon because alongshore currents are generally coherent in northern California and Oregon (Huyer et al. 1979). A drop in sea level is correlated with the onset of upwelling during spring (Huyer et al. 1979). In 1994, mean monthly sea level at Crescent City gradually decreased from 2.33 m in February to 2.13 m in April. In contrast, sea level in 1995 increased from 2.35 m in February to 2.43 m in March, then dropped to 2.18 m in April, indicating delayed onset of upwelling compared to 1994.

In 1994, strong upwelling dominated from late June to mid-July at both sites. After mid-July, relatively warm water predominated at Gregory Point, while periods of upwelling continued at Port Orford. In 1995, prolonged upwelling was not observed in June and July; instead, shorter upwelling events occurred through the sampling period.

The water column was stratified for longer periods and displayed a stronger thermal signal at Gregory Point than at Port Orford (Figs. 3i, j & 4i, j). The degree of stratification also varied in response to different phases of upwelling. During strong upwelling, the water column was mixed or weakly stratified, with cold water at all depths. When upwelling-favorable winds relaxed, stratification increased. Stratification was strongest during relaxation events, but stratification lagged surface warming during some relaxation events. During strong relaxation events in mid-June of both years, warm water was found at all depths during the early phase of the events. The warm, mixed water column indicated influx of a warm water mass that displaced colder water on the bottom (Figs. 3g, h).

Spatial and temporal abundance of sea urchin larvae

Fewer sea urchin larvae overall were found in nearshore plankton in 1994 than in 1995. Although sampling frequency differed between years, larvae of *Strongylocentrotus franciscanus* and *S. purpuratus*

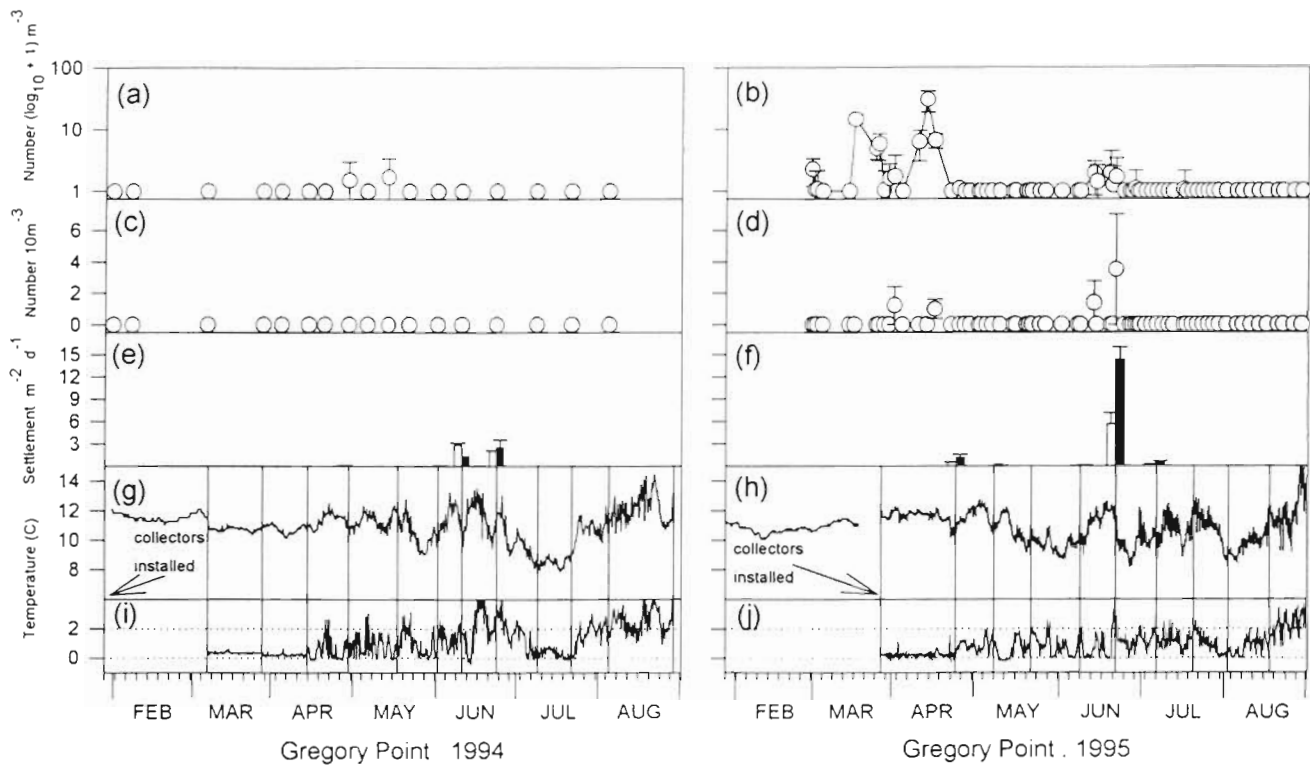


Fig. 3. *Strongylocentrotus franciscanus*. Larval abundance and settlement rates (mean \pm SE, $n = 3$) and sea temperature at Gregory Point in 1994 and 1995. (a, b) Density of larvae in plankton; (c, d) density of competent larvae in plankton; (e, f) cumulative settlement (normalized for sample interval) on upper (clear bars) and lower (black bars) collectors for each sample period, and plotted on date of sample; (g, h) sea surface temperature (4 m depth); (i, j) difference between surface and bottom (22 m depth) temperature. Vertical bars on temperature plots delineate settlement sampling periods

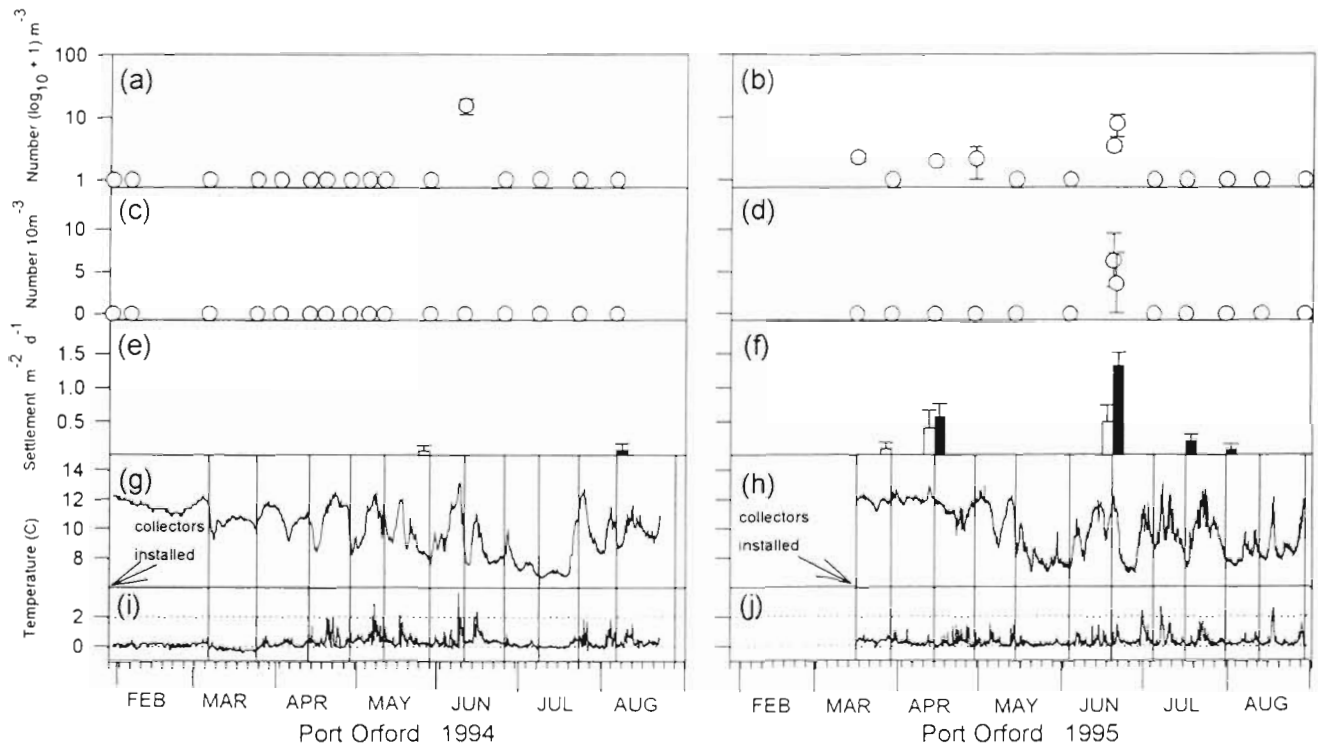


Fig. 4. *Strongylocentrotus franciscanus*. Larval abundance and settlement rates (mean \pm SE, $n = 3$) and sea temperature at Port Orford in 1994 and 1995. (a) to (j) as in Fig. 3, except in (i) and (j) bottom depth = 18 m

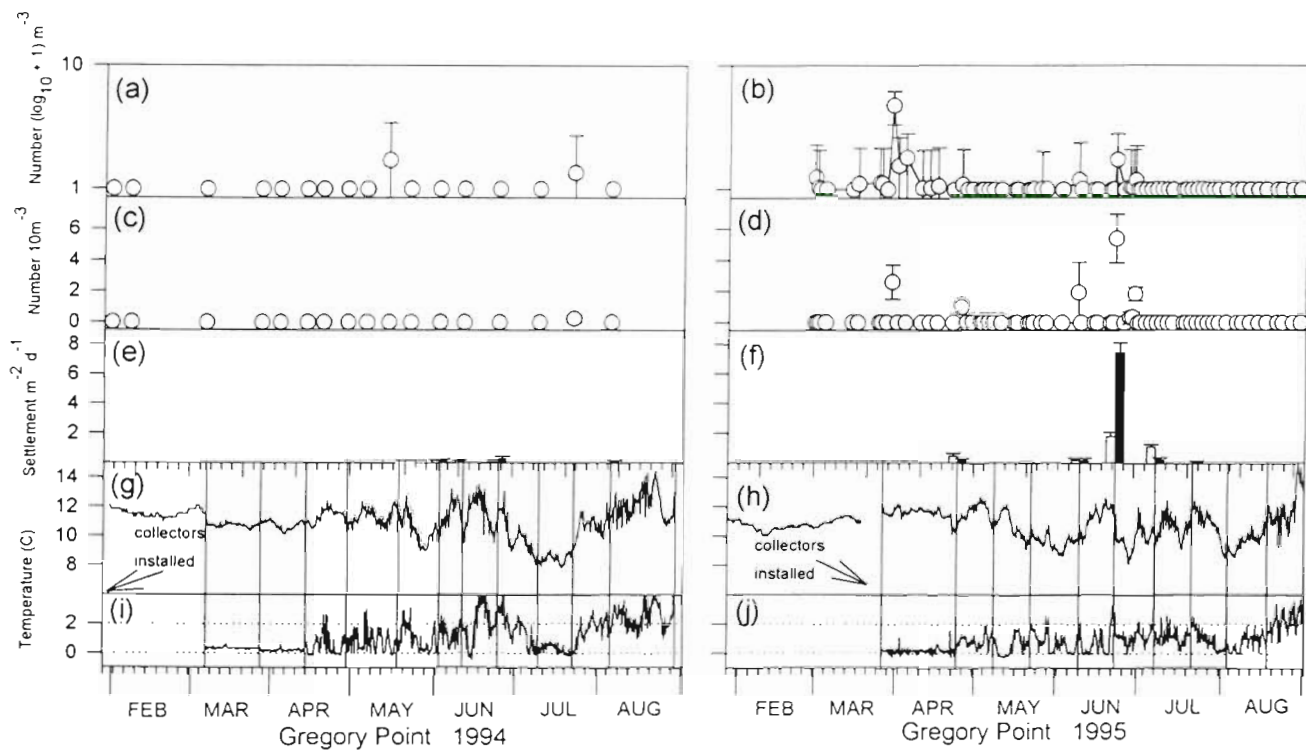


Fig. 5. *Strongylocentrotus purpuratus*. Larval abundance and settlement rates (mean \pm SE, $n = 3$) and sea temperature at Gregory Point in 1994 and 1995. (a) to (j) as in Fig. 3

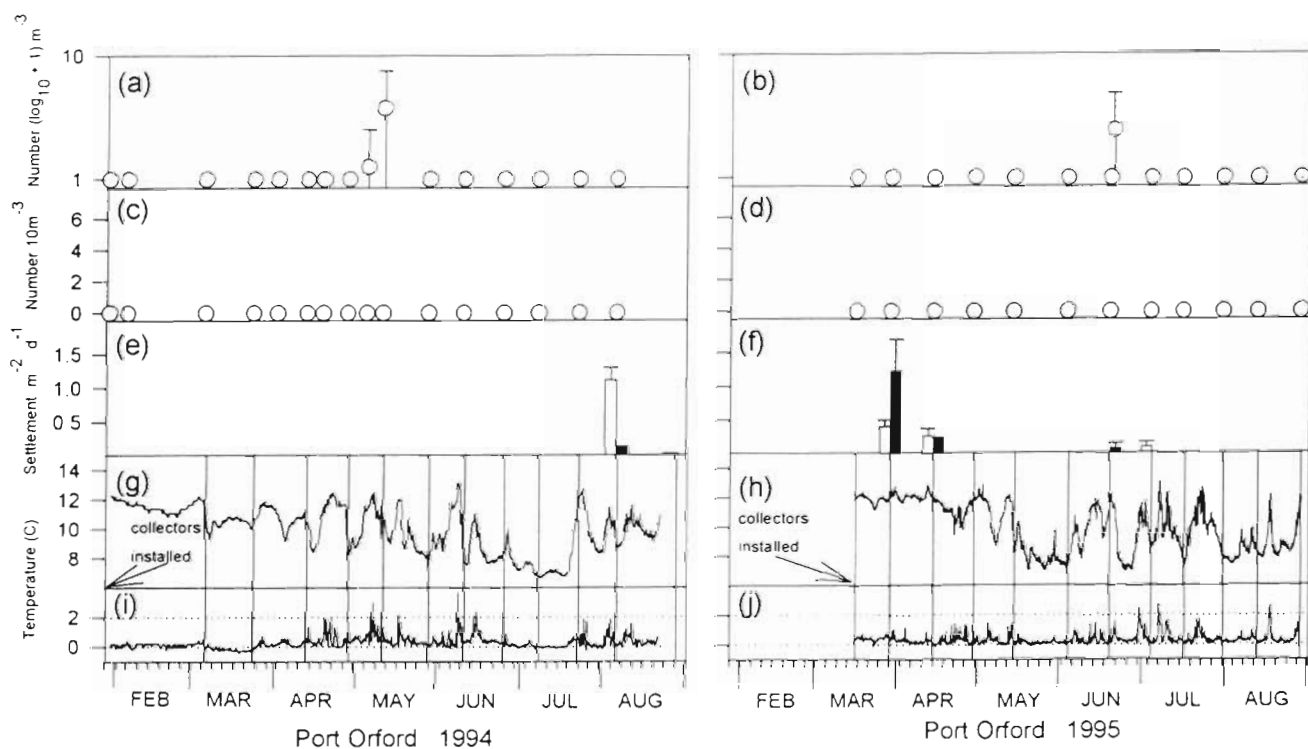


Fig. 6. *Strongylocentrotus purpuratus*. Larval abundance and settlement rates (mean \pm SE, $n = 3$) and sea temperature at Port Orford in 1994 and 1995. (a) to (j) as in Fig. 3, except in (i) and (j) bottom depth = 18 m

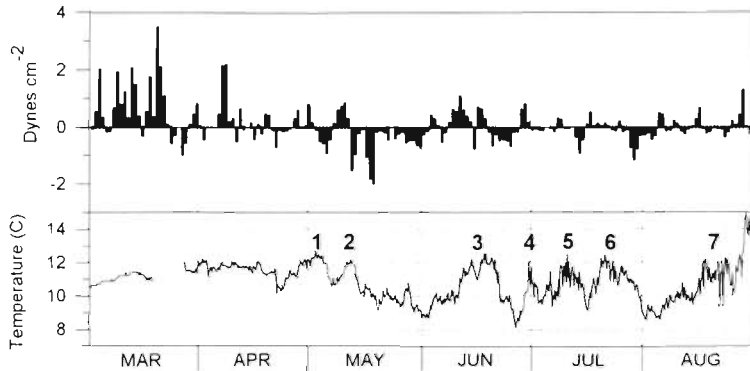


Fig. 7. Alongshore wind stress and surface water temperature (4 m depth) at Gregory Point in 1995. Daily mean alongshore component of wind stress recorded at Cape Arago Lighthouse (Gregory Point) C-MAN station (CARO3). Values > 0 represent northward wind stress, values < 0 represent southward wind stress. Recorded wind direction was rotated 17° (clockwise) from north. Numbers 1 to 7 denote relaxation events referenced in 'Discussion'

were found on 27.5 and 24.6% of dates sampled at Gregory Point in 1995, respectively, compared to 11.8% for both species in 1994. At Port Orford, larvae of *S. franciscanus* were found on 38.5% of dates sampled in 1995 compared to 6.3% in 1994, while larvae of *S. purpuratus* were found on 7.7 and 12.5% of dates sampled in 1995 and 1994, respectively (Figs. 3 to 6).

In 1994, all larvae found were precompetent 4- to 8-armed stages except for a single competent larva of *Strongylocentrotus purpuratus* found on July 22. Competency was judged based on the presence of a fully developed juvenile rudiment.

In 1995, larvae of both species were found earlier in the year and at higher densities than in 1994. Four- and six-armed stages of both species were found during the first week of March. Larvae reach the 4- and 6-armed stages after approximately 4 to 10 d at 11 to 12°C (Strathmann 1987, Miller unpubl.). This suggests that larvae found in the first week of March were spawned in late February. At Gregory Point, highest larval abundance of both species occurred from late March to mid-April and during June. A similar temporal pattern was found at Port Orford for larvae of *Strongylocentrotus franciscanus*. A total of 5 larvae of *S. purpuratus* (all 4-armed) were found at Port Orford, all on June 20. Most competent larvae were found in June at both sites when highest settlement rates were found, but competent larvae of both species were also found in April at Gregory Point (Figs. 3d, 4d & 5d).

Plankton was sampled over a wide range of water temperatures, from 7 to 15°C , but sea urchin larvae were most abundant and most frequently found in water between 11 and 12°C (76 and 73% of dates on which *Strongylocentrotus franciscanus* and *S. purpuratus* were found, respectively; Fig. 8).

Larvae of *Strongylocentrotus franciscanus* were found at all depths in depth-stratified samples, but were most abundant at 10 to 15 m depth in water depths of 20 and 30 m. The same distribution was observed for larvae of *S. purpuratus* on March 26 and June 20, but on March 30 most larvae were found at 1 m depth (Fig. 9). There was no apparent relationship between larval stage and depth distribution. The water column was mixed on March 26 and 30, with the bottom temperature only 0.1°C colder than the surface.

The water column was weakly stratified on June 20, with a 0.6°C difference between the surface and bottom temperature.

Spatial and temporal patterns of recruitment

Recruitment of *Strongylocentrotus franciscanus* at Gregory Point was highest in mid-June in both 1994 and 1995 (Fig. 3). Few recruits of *S. franciscanus* were found at Port Orford in either year (Fig. 4). Although recruitment at Port Orford was low in 1995, the timing of settlement was consistent with that observed at Gregory Point.

Recruitment of *Strongylocentrotus purpuratus* at Gregory Point was very low in 1994. These recruits were found almost entirely in June (Fig. 5). In 1995, settlement occurred as early as April but, like that of *S.*

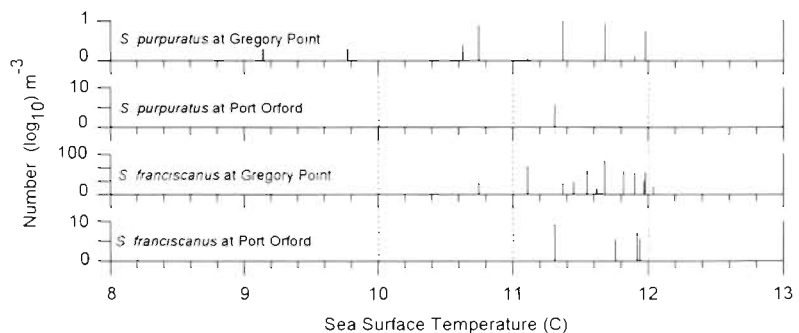


Fig. 8. *Strongylocentrotus franciscanus* and *S. purpuratus*. Surface temperature (4 m depth) of water mass in which larvae were found in plankton samples from Gregory Point and Port Orford in 1994 and 1995. Relative densities for each species at each site are plotted on a log scale

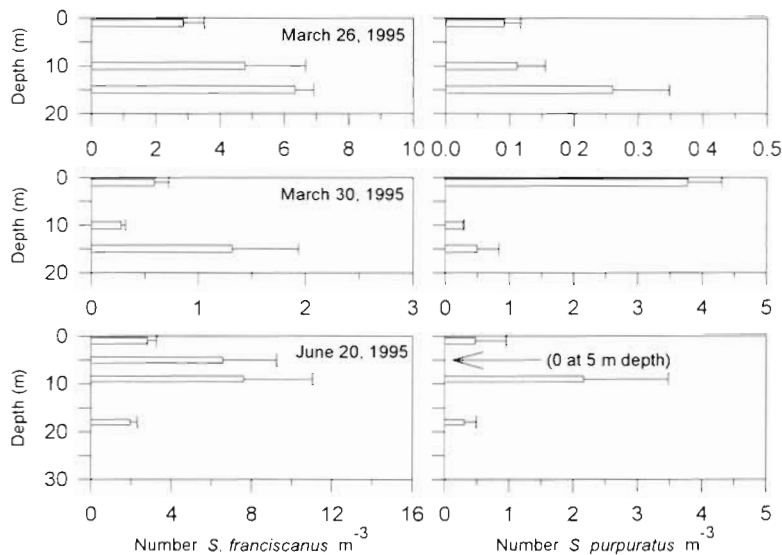


Fig. 9. *Strongylocentrotus franciscanus* and *S. purpuratus*. Vertical distribution of larvae of (mean \pm SE, $n = 3$ tows per strata) at Gregory Point (March 26 and 30) and Port Orford (June 20) in 1995. Depth of water column was 18 to 22 m at Gregory Point and 30 m at Port Orford

franciscanus, peaked in June. At Port Orford the settlement pattern of *S. purpuratus* was very different between years. Settlement was low in both years, but occurred entirely in late July and early August in 1994 and primarily in March and April in 1995.

Outplant experiment

The percent recovery (survival) of early juvenile *Strongylocentrotus franciscanus* outplanted on subtidal moorings was 80.7% (95% confidence interval, CI = 66.0 to 91.6%) after 7 d, compared to 46.7% (95% CI = 22.6 to 67.6%) after 14 d. Group means for each recovery date were significantly different (Student's *t*-test on arc-sine transformed data; $p < 0.001$, $df = 10$; Sokal & Rohlf 1981). The daily survival function (y) for 1 to 14 d is represented by the regression equation: $y = 100 - 1.707x - 0.15x^2$, where x = age in days. No natural settlement was found on control panels. Settlement of other taxa on the panels was not quantified but was similar in composition to that found at the settlement monitoring sites. The survival rate determined from this experiment provided the basis for adjusting the number of juveniles that may have settled during any interval of a sampling period.

Settlement timing

The calculated timing and magnitude of settlement based on the estimated age of recruits indicate most

settlement of *Strongylocentrotus franciscanus* occurred when surface water temperature was $\geq 10^\circ\text{C}$, with highest settlement in water between 11 and 12°C (Figs. 10 & 11). This is consistent with larval occurrence in water between 11 and 12°C . Settlement of *S. purpuratus* in each year was also highest when surface temperature was between 10 and 12°C , but larvae continued to settle when temperature decreased below 10°C (although at lower rates).

The calculated timing of settlement in Figs. 10 & 11 is depicted as the range of days over which settlement occurred, but this does not imply that settlement was continuous over this range. For the majority of settlement events, however, 4 or 5 age groups of juveniles were identified for each 2 wk interval. This suggests that settlement occurred over a period of several days within each sampling period and implies a residence time of several days of

a water mass containing competent larvae at each site. Thus, settlement rates measured at each site are a function of residence time of the water mass delivering the larvae, the density of competent larvae, and time-dependent survivorship.

DISCUSSION

Larval abundance and settlement patterns

Temporal patterns of larval abundance were consistent with previous reports of the spawning period. *Strongylocentrotus purpuratus* spawns from January to March off the Oregon coast (Gonor 1973) and from December to June off northern California (Pearse 1981). *S. franciscanus* are reported to spawn from March to May in northern California (Bennett & Giese 1955, Pearse 1981). In 1995, a single 4-armed larva of *S. franciscanus* was found at Gregory Point in mid-July, indicating at least some spawning as late as July.

Larval densities of both species were $<10 \text{ m}^{-3}$ on all but 2 dates and were generally an order of magnitude less than larval densities of these species found in Barkley Sound, British Columbia, Canada (Rumrill 1987). Highest larval abundance in 1995 was found in March and early April when recruitment was low, but most of these larvae were precompetent. Larvae of all stages were also found during the period of highest recruitment in mid-June, but competent larvae were most abundant during this period. Different stages of larvae concurrently in the same water mass could

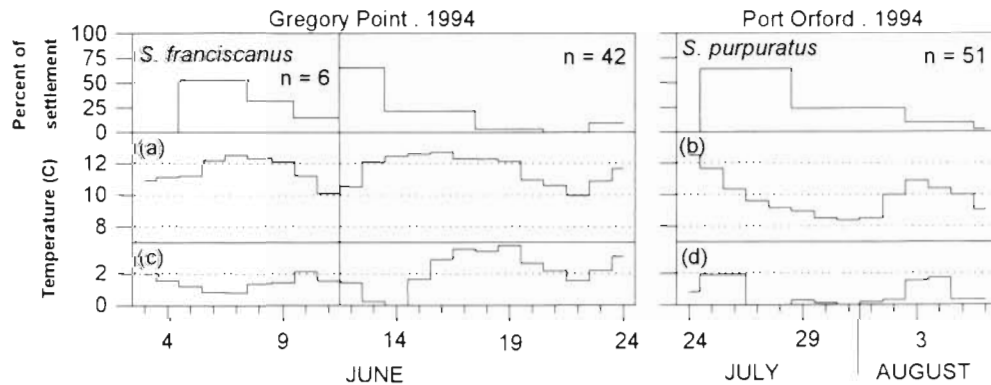


Fig. 10. Calculated timing of settlement for 3 sampling intervals at Gregory Point and Port Orford in 1994. Settlement timing was inferred from estimated age of juveniles on sampling day. Magnitude of settlement was adjusted for survivorship over the interval (see text). (a, b) Daily mean water temperature at upper settlement collectors (4 m depth); (c, d) temperature difference between upper and lower settlement collectors

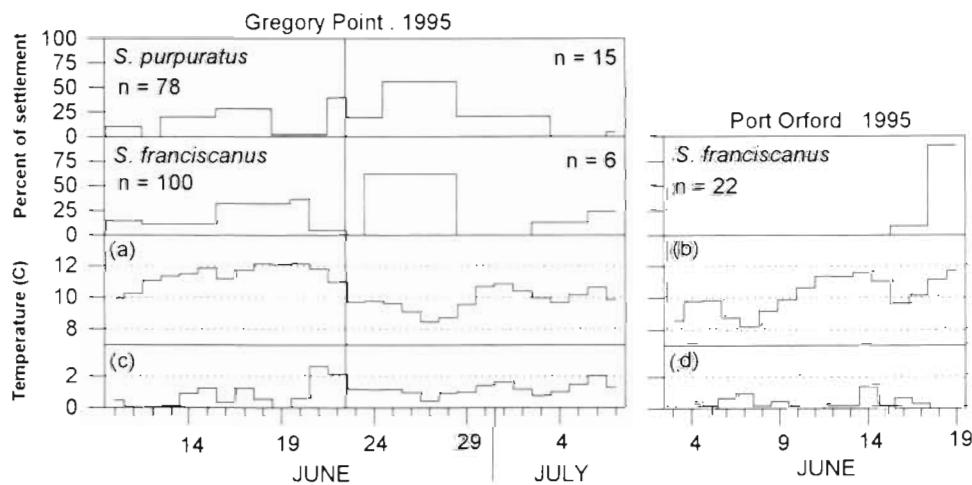


Fig. 11. Calculated timing of settlement for 3 sample intervals at Gregory Point and Port Orford in 1995. See legend of Fig. 10 for explanation

result from at least 2 processes, these being (1) spawning as water containing older larvae is advected over adult populations, and (2) large-scale horizontal mixing between water masses containing larvae of different ages.

Recruitment was higher on collectors near the bottom in most sample intervals. Dissolution of gypsum blocks attached to the collectors indicated that water flux past upper and lower collectors was not significantly different (Miller 1995), thus differential water flux did not account for the observed recruitment patterns. Recruitment of both species was higher on the upper collectors when the bottom temperature was 1 to 2°C colder than the surface, and higher on the lower collectors when the water column was mixed or weakly stratified (<1°C difference). Stratified plankton sampling showed that larvae of both species were gen-

erally more abundant at 10 to 15 m depth under conditions of weak thermal stratification, but were found throughout the water column at relatively shallow (<20 m) depths. The recruitment patterns and vertical distribution of larvae suggest depth of settlement is influenced by the thermal structure of the water column, with lower settlement rates below the thermocline in stratified water.

Influence of nearshore hydrodynamics on larval supply and recruitment

Water masses that may carry sea urchin larvae are influenced by distinct winter and summer regimes of wind and current patterns in the northern portion of the California Current System. During the winter

regime, nearshore currents off northern California and Oregon are from the south (Hickey 1979) and are strongest very near shore (Huyer et al. 1979). A brief transition period between winter and summer flow regimes occurs during late March to early April in most years (Huyer et al. 1979, Strub et al. 1987). During this transition period, the onset of southward-flowing surface currents may occur over a day or two during a single event of north wind stress and upwelling (Allen 1983).

Following the spring transition, mean alongshore flow is southward in April and May, but may oscillate in direction at event scales of several days (Huyer et al. 1975). After May, predominant winds from the north force a southward flow from June to September (Huyer et al. 1975, Smith 1981). Flow velocities offshore (5 to 25 km) can reach 0.4 m s^{-1} , but mean flow velocities are less nearshore, generally $<0.1 \text{ m s}^{-1}$.

Some inference of the source of urchin larvae in Oregon waters may be made from records of water temperature, sea level, and observed patterns of larval abundance. The transition from mean north- to south-flowing currents during spring is highly correlated with a drop in sea level, thus sea level records may be used to determine timing of the shift in flow regimes (Huyer et al. 1979). The relatively high sea level at Crescent City, California, and warm water temperature during March and early April in 1995 suggest strong northward and mean onshore flow. Competent larvae and settled juveniles of both species were found during the March and early April pre-transition period in 1995. Larvae of *Strongylocentrotus purpuratus* reared in the laboratory generally require at least 45 d at 11 to 12°C to reach competency, while larvae of *S. franciscanus* reach competency in slightly less time (Miller unpubl.). If the larval period is this long in the plankton, larvae could be transported hundreds of kilometers in nearshore currents. This suggests a larval source in northern California and southern Oregon for settlement that occurs in Oregon before the spring transition in flow regimes.

The relatively low alongshore current velocities and frequent decay or reversal of wind-forcing in April and May (Huyer et al. 1975) suggest that larvae produced in early spring may not disperse as far alongshore as larvae produced earlier or later in the year. Settlement during the summer period of mean southward currents could be from 2 sources, either from late spawners to the north, or from larvae transported to the north earlier in the year and returned by southward currents.

While alongshore advection patterns may be a major determinant of larval source, cross-shelf transport strongly influences whether competent larvae reach suitable habitat. During the winter flow regime or periods of strong wind reversal during the summer flow regime, Ekman transport deflects surface currents

toward the coast. During the period of mean southward wind stress from spring to fall, the nearshore southward surface current is transported offshore and replaced by colder, more saline water from below the pycnocline. The layer of mean offshore-directed flow off Oregon is less than 20 m deep and upwelled water comes from mid-depths of 20 to 80 m (Moore et al. 1976, Smith 1981). Stratified plankton sampling in 1995 showed that sea urchin larvae were found throughout the upper 20 m of the water column, although distribution below this depth was not determined. Other echinoid larvae also are found in surface waters above the pycnocline (see Rumrill 1987 for *Strongylocentrotus droebachiensis*, also Emlet 1986 and Pennington & Emlet 1986 for larval sand dollars *Dendraster excentricus*) and remain associated with a particular water mass (Banse 1986). The apparent confinement of echinoid larvae to water between 11 and 12°C in 1995 supports this view. Thus, forces driving the movement of surface waters also control the cross-shelf transport of echinoid larvae.

Larvae of both species settled during late March and early April in 1995. This period was characterized by relatively warm water (11 to 12°C), a mixed water column, relatively high sea level, and a predominantly northward alongshore component of wind. This suggests that wind-forced onshore Ekman transport contributed to the delivery of larvae to study sites during this period.

No settlement occurred during May 1995 following the spring transition. Upwelling and offshore Ekman transport, as evidenced by predominantly southward wind stress and progressively colder surface water, was probably the mechanism that accounted for the absence of larvae and settlement during this period.

Settlement during summer was associated with several relaxation events in both years. The relaxation phase has been described as a cross-shelf advection of heat when winds relax or reverse and the inclined and surfacing isopycnals are advected or relax dynamically toward a more level state (Smith 1968, Gill & Clarke 1974, Halpern 1976). Others have reported that the return of higher temperatures may proceed in an entirely different manner. Nearshore warming events in northern California (Send et al. 1987, Wing et al. 1995a) and Oregon (Huyer et al. 1974, Halpern 1976) were attributed to net solar heat flux and alongshore advection of warmer water from the south.

Several warm water events were observed during the summer flow regime (after mid-April) at Gregory Point in 1995. Warm water events labeled 5, 6 and 7 in Fig. 7 occurred during periods of calm winds and generally sunny weather. The water column was stratified (1 to 2°C colder on the bottom) during these events, suggesting the heat influx was due to either onshore

flow of a thin surface layer or to surface heating. The 1 to 2°C daily variation in surface temperature during these events was at a tidal frequency, due to the temperature recorder (at a fixed height from the bottom) dipping into the thermocline at high tide. This also suggests the warm water was confined to a thin layer. No larvae were found in the plankton nor did settlement occur during these events.

In contrast, warm water events labeled 1, 2, 3 and 4 in Fig. 7 occurred following periods of northward wind stress. The water column was weakly stratified or mixed during these events. The depth of the warm layer suggests these events resulted from onshore (Ekman) advection of a warm water mass, forced by wind from the south. Most of the settlement observed during the summer flow regime in 1995 occurred during the mid-June warming event when the water column was mixed. In 1994, most settlement also occurred during warm water events when stratification was weak. Thus, the majority of settlement in both years was tied to warm water of sufficient mass to displace colder bottom water over a period of several days.

If sea urchin settlement is linked to onshore advection of warm water during cessation or reversal of upwelling-favorable winds, the characteristics and behavior of larvae and these warm water masses may control urchin recruitment in Oregon. Echinoid larvae are relatively weak swimmers ($<1 \text{ mm s}^{-1}$, Mileikovsky 1973; 0.3 mm s^{-1} for sand dollar larvae *Dendraster excentricus* Podolsky & Emlet 1993) and are distributed to at least 20 m depth. Echinoid larvae behave more as passive particles and may be widely dispersed in the water mass into which they were spawned. These water masses, characterized by relatively warm water and low salinity, are displaced offshore during upwelling. Recruitment occurs when the forcing mechanism of onshore transport, such as wind or relaxation of inclined isopycnals, is sufficiently strong to move the water mass containing larvae far enough onshore that it contacts the coast. Settlement is a function of the density of competent larvae and the onshore residence time of the water mass.

This study suggests variability in sea urchin recruitment in Oregon may be linked to 2 processes: (1) timing of spawning, which places larvae within the hydrodynamics of winter or summer flow regimes, and (2) variability of hydrodynamics within each flow regime. This study supports findings by Ebert et al. (1994) that urchins settle from March through August in the northern portion of the California Current System, showing spawning time is highly variable. Recruitment during the winter flow regime is influenced by the magnitude of northward flow and onshore Ekman transport, and the timing of the spring transition in flow regimes. Recruitment during the

summer flow regime is influenced by the frequency, timing, and forcing mechanism of relaxation events. Relaxation events accompanied by wind reversal and onshore Ekman transport of surface water may contribute most to recruitment events in Oregon.

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