LARVAL ABUNDANCE AND EARLY JUVENILE RECRUITMENT OF ECHINOIDS, ASTEROIDS, AND HOLOTHUROIDS ON THE OREGON COAST

by

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Dr. Richard B. Emlet

Larval abundance and settlement of red sea urchins (*Strongylocentrotus franciscanus*) and the purple sea urchins (*S. purpuratus*) was found to be variable over a two year period on the southern Oregon coast. A method of estimating age of early juvenile sea urchins was developed, based on temperature-dependent developmental rates of specific juvenile traits. This method was used to correlate sea urchin settlement to several relaxation events during the summer upwelling season. Occurrence of larvae and peak settlement events were linked to relaxation events characterized by warm water, a mixed water column, and strong northward wind. Occurrence of planktonic larvae of asteroids and holothuroids coincided with settlement. Asteroid and holothuroid settlement occurred regularly during the upwelling season, suggesting these groups may recruit by different mechanisms than those for sea urchin larvae.

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GENERAL INTRODUCTION

In the last decade, the linkage between early life history stages, including larvae and early juveniles, and adult populations has received considerable attention (Underwood & Fairweather 1989, Roughgarden *et al.* 1988, Botsford *et al.* 1994). In some circumstances, variation in abundance and survival of early life history stages may control recruitment, the infusion of a new age or year class into a population. Variation in recruitment is of interest not only to marine ecologists, but also to fishery managers who must establish guidelines for sustainable harvest of commercially important species.

Populations of red and purple sea urchins support an important commercial fishery along the west coast of North America. In this fishery, sea urchins are harvested from wild populations that rely solely on natural populations of planktonic larvae. Since 1990, commercial landings have steadily declined in northern California, Oregon, and Washington as the most accessible virgin stocks have been harvested (N. Richmond, Or. Dept. Fish and Wildlife, pers. comm.). This declining trend suggests northern coastal populations may be overexploited, and has highlighted the need for information about recruitment and knowledge of long-term population trends. Annual recruitment is known to be variable within the geographic range of both species (Ebert & Russel 1988, Ebert *et al.* 1994). The seasonal patterns of nearshore hydrodynamics also vary between regions within this same broad range (Beardsley 1987), and presumably have different effects on larval transport and subsequent recruitment of juveniles to adult populations within each region. Determining the regional variation in recruitment success and corresponding physical factors that influence recruitment are fundamental to understanding population dynamics of sea urchins.

Chapter I of this thesis presents results of a two year study on early life history stages of sea urchins within the northern region of the California Current System. Physical parameters are used to interpret spatial and temporal patterns of larval abundance and early juvenile recruitment. These patterns form the basis for several proposed mechanisms that influence larval supply and recruitment variability within the Oregon upwelling zone of the California Current System.

Previous studies have measured recruitment of sea urchins, but the methods used in each case have precluded linking settlement events to specific hydrographic events. A key component of the interpretive process in Chapter I was the development of a method that permits association of settlement and hydrographic events within a sampling period. This method, described in Chapter II, is based on temperature-dependant developmental rates of early juvenile traits. The desciptive morphology of juvenile red and purple sea urchins in Chapter II should also prove useful for identification of early juveniles from the field.

While sea urchins were the primary focus of these studies, data on other groups of echinoderms, including asteroids and holothuroids, were collected concurrently with data on sea urchins. Little work has been done on larval and early juvenile ecology of these other echinoderm groups in the northeast Pacific. Collection of these data provided an opportunity to report spatial and temporal patterns of larval abundance and recruitment of asteroids and holothuroids for an open coastal region. These data, presented in Chapter III, also suggest these groups may recruit by different mechanisms than those influencing sea urchins. It is hoped that data presented in Chapter III will stimulate further investigation of asteroid and holothuroid recruitment within a coastal upwelling system.

Chapters I and II are written as self-contained studies. Chapter III focuses on asteroids and holothuroids, but Chapter I is referenced for field sampling methods, and the comparison of larval and recruitment patterns for these groups with patterns for sea urchins discussed in Chapter I are emphasized. An appendix is provided that summarizes natural history notes recorded throughout the course of field and laboratory studies.

CHAPTER I

THE INFLUENCE OF NEARSHORE HYDRODYNAMICS ON LARVAL ABUNDANCE AND SETTLEMENT OF THE RED SEA URCHIN, *Strongylocentrotus franciscanus*, AND PURPLE SEA URCHIN, *S. purpuratus*, IN THE OREGON UPWELLING ZONE

Introduction

The red sea urchin , *Strongylocentrotus franciscanus* (A. Agassiz), and purple sea urchin, *S. purpuratus* (Stimpson), are important members of rocky intertidal and shallow subtidal communities in the northeast Pacific. Grazing by dense populations of these urchins may decrease diversity and alter structure of benthic communities by removal of macroalgae and sessile invertebrates (Duggins 1980, Lawrence & Sammarco 1982). Heavily grazed areas become dominated by encrusting coralline algae, but are recolonized by macroalgae when released from grazing pressure (Ebeling *et al.* 1985). Natural controls on local densities of sea urchins include predation, adult migration, storm events, and recruitment of juveniles (Harrold & Pearse 1987).

A primary factor influencing population structure of sea urchins is the magnitude and variability of juvenile recruitment. Recruitment is a general term that ususally refers to the first size or age class that can be detected or measured, thus the definition of recruitment depends on the method used to detect juveniles. For sea urchins, juvenile recruitment may be generally defined as the number of juveniles produced in any interval of time, and is a function of larval settlement and survival rates.

Levels of juvenile recruitment are dependent on both pre-settlement and post-settlement processes. Pre-settlement processes determine the magnitude of larval supply to an area and include number of zygotes produced from adult spawners (Pennington 1985, Levitan *et al.* 1991), mortality in the plankton (Pennington *et al.* 1986, Rumrill 1990), and hydrodynamics that transport competent larvae to suitable habitats (Giese *et al.* 1978, Ebert & Russell 1988). The relative importance of these factors to determining larval supply in any year is not known. Post-settlement mortality is also an important determinant of juvenile recruitment (Cameron & Schroeter 1980, Keough & Downes 1982, Rowley 1989,1990), but the relative importance of pre and post-settlement processes is also not clear, and may differ between species and between years.

Numerous authors have discussed or demonstrated the role of nearshore currents in determining larval supply to coastal areas (Day & McEdward 1984, Banse 1986, Scheltema 1986, Farrel *et al.* 1991, Roughgarden *et al.* 1991, Shanks 1995). Along the northern California and Oregon coasts, the California Current System has a major influence over nearshore proccesses (Hickey 1979, Beardsley 1987). During the interval from mid-April to September, predominant winds from the north force a southward current and create periods of upwelling driven by offshore Ekman transport of surface water. Also during this interval, periods of onshore transport may occur due to relaxation of north winds, southerly winds, or tidally-forced internal waves (Huyer *et al.* 1975, Shanks 1983, Shanks & Wright 1987, Pineda 1991). This time interval coincides with the 1 to 5 month planktonic larval period of *Strongylocentrotus franciscanus* and 1 to 3 month larval period of *S. purpuratus* (Strathmann 1978, 1987, Ebert *et al.* 1994).

Echinoid larvae have a limited ability to vertically migrate (Mileikovsky 1973, Pennington & Emlet 1986). They probably behave more as passive particles and may remain associated with a particular water mass for the length of the larval period (Day & McEdward 1984, Banse 1986, Possingham & Roughgarden 1990). Thus, alongshore currents may transport larvae hundreds of kilometers from their origin and offshore transport due to upwelling may move larvae away from suitable nearshore habitats. Echinoid larvae have the ability to delay metamorphosis (Strathmann 1978, Rumrill 1989), but at a cost of higher mortality in the plankton and possibly reduced post-metamorphic survival (Highsmith & Emlet 1986).

In California, sea urchin larval settlement varies spatially and between years (Ebert 1983, 1988, Pearse & Hines 1987, Ebert *et al.* 1994). Ebert *et al.* (1994) found regional differences in settlement, with higher densities and more regularly annual settlement south of Point Conception compared to more northern sites. This difference was attributed to greater retention of water in the Southern California Bight, south of Point Conception, and more energetic offshore advection of water in northern California. Ebert (1983) measured strong recruitment of *Stongylocentrotus purpuratus* on the southern Oregon coast in 1963, but found little or no recruitment from 1964 to 1978. These studies suggest that recruitment strength is highly variable in northern California and Oregon, and that annual recruitment may, in part, be limited by larval supply.

Studies by Ebert *et al.* (1994) and Wing *et al.* (1994) suggest that spatial and temporal patterns of sea urchin settlement may be closely linked to patterns of onshore and offshore transport of coastal waters in the northern portion of the California Current System. Wing *et al.* recorded sea surface temperature, salinity, and subsurface pressure at a settlement monitoring site near Bodega Bay. Sea urchin settlement appeared to be associated with relaxation of upwelling, as indicated by increasing temperature, but most of the sample intervals (weekly) that included sea urchin settlement also included some phase of both upwelling and relaxation events, and the connection of settlement to specific hydrographic events was not clear.

Previous studies of *Strongylocentrotus franciscanus* and *S. purpuratus* recruitment have focused on settlement and post-settlement processes. Rumrill (1987) measured larval abundance of *S. franciscanus* and *S. purpuratus* during a two month period in Barkley Sound, British Columbia, but no attempt has been made to measure temporal trends in larval abundance along the open coast and relate those trends to patterns of settlement and nearshore hydrodynamics.

This study presents temporal trends in abundance for early and competent stages of sea urchin larvae during 1994 and 1995 at two sites along the southern Oregon coast. The vertical distribution of sea urchin larvae in nearshore (<30m depth) water was also measured. Spatial and temporal patterns of sea urchin recruitment for the same time periods and sites are presented, including within-site vertical recruitment patterns. Sea temperature records are used as indicators of local upwelling and relaxation events and to interpret observed patterns of larval abundance and recruitment. A method of estimating the age of recently settled *Strongylocentrotus franciscanus* and *S. purpuratus* based on temperature-dependent developmental rates of juvenile traits (see Chapter II) is used to link specific settlement events to hydrographic events.

Previous studies of sea urchin recruitment have used a variety of artificial substrata to induce settlement, but none of these studies have measured the effectiveness of artificial substratum to induce settlement and metamorphosis, relative to natural substrata.

In this study, lab-reared larvae were used in two experiments designed to test alternative methods of seasoning artificial substratum to produce a microbial film that induces metamorphosis in sea urchins (Cameron & Hinegardner 1974). A field experiment was also conducted to determine survival rate of juvenile sea urchins on artificial substratum under conditions simulating the settlement collectors. Recently settled (age 24 hr) lab-reared juvenile *Strongylocentrotus franciscanus* were placed on artificial substratum and outplanted to a subtidal site. Survival estimates from this experiment provide an upper bound to the total number of juveniles that may have settled if settlement occured early in a sampling period.

Methods

Field Sampling

Study Sites

Two study sites were chosen that were accessible by small boat and provided partial protection from northwest wind and ocean swell that predominates during summer months. Both sites were fully exposed to wind and swell from the west and south. The Gregory Point site was located at the mouth of a broad cove on the south side of Lighthouse Island, north of Cape Arago along the southern Oregon Coast (Figure 1A). A second site was located in Nellies Cove, 67 km south of Gregory Point, at the base of a steep headland 1 km west of the port of Port Orford (Figure 1B).

Temporal Patterns in the Plankton

Plankton was sampled at Gregory Point between January 31 and August 5 in 1994, and between March 1 and August 30 in 1995. At Port Orford, plankton was sampled between January 29 and August 6 in 1994, and between March 16 and August 29 in 1995. Sampling frequency differed between years. In 1994, plankton samples were collected at approximately one week intervals at both sites. In 1995, samples were collected at a higher frequency at one site to correlate larval abundance to high frequency hydrographic events. Plankton samples were collected at Gregory Point on a schedule of every other day in 1995 ($n = 69$ sample days), although heavy seas occasionally forced modifications of this schedule. Samples were collected at Port Orford in conjunction with sampling settlement collectors in 1995, at approximately two week intervals. Samples at both sites were collected in the vicinity of the settlement collectors, 200 to 300 m offshore.

Plankton was sampled with a 0.25 m diameter net with 202 μm mesh. Three replicate oblique tows were made from 0 to 5 m depth, although the major portion of each tow was collected at 5 m depth. Tows were five minutes in duration and generally sampled 8 to 15 m^3. During periods of diatom blooms, lower volumes were sampled. Sample volume

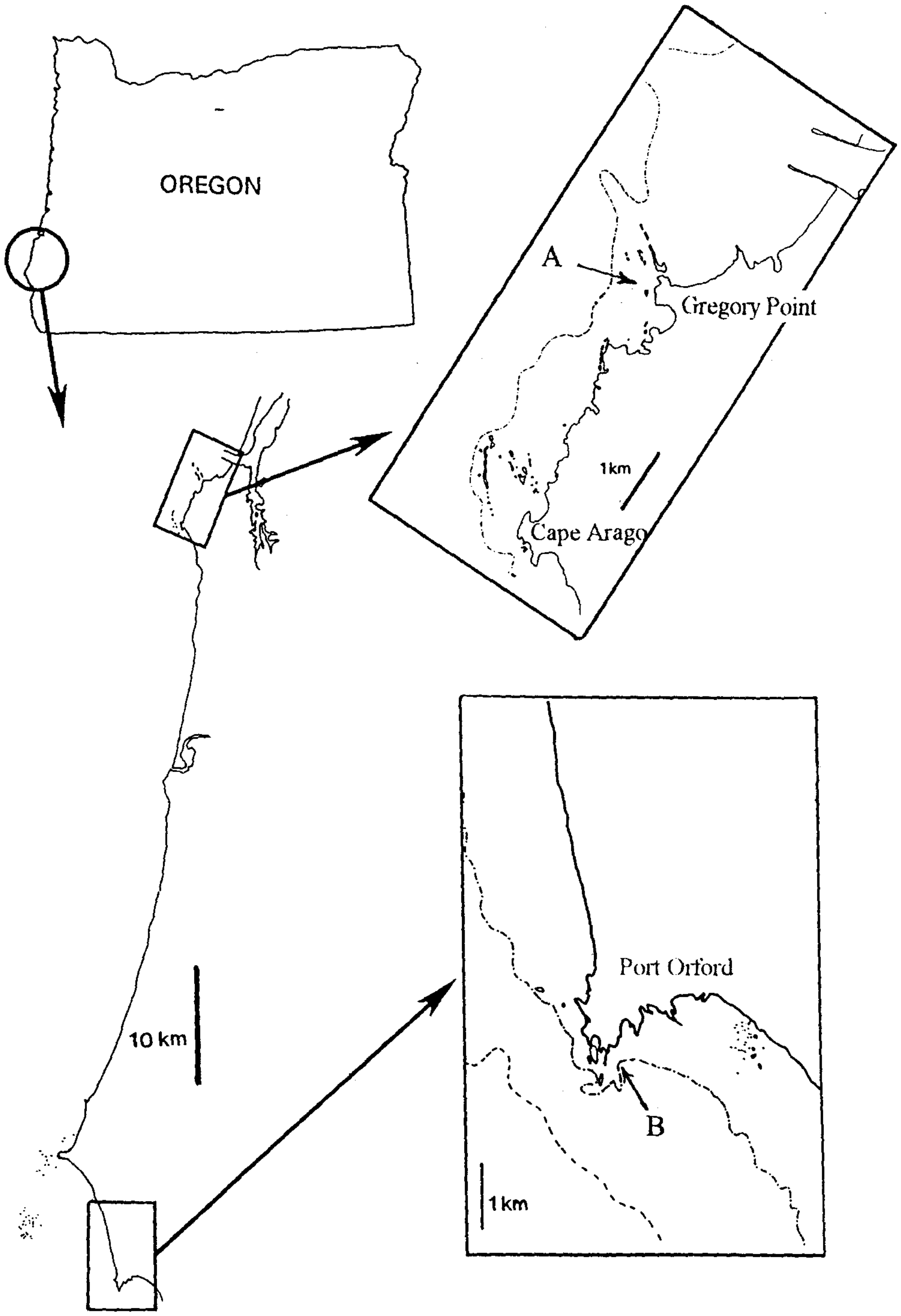

FIGURE 1. Location of study sites at Gregory Point (A) and Port Orford (B) along the Oregon Coast. Solid line represents shoreline, dot-dash line represents 10 fathom contour, dash line represents 20 fathom contour.

was measured using a calibrated mechanical flowmeter with a low-speed impeller (General Oceanics, Inc., Model 2030R2). Plankton samples were preserved and stored in 1.5% formaldehyde in seawater and buffered with excess sodium borate. Samples were sorted under a binocular dissecting microscope using cross-polarized light to highlight the birefringent calcareous arm rods of sea urchin pluteus larvae. Samples that contained very high densities of zooplankton or diatoms were subsampled with a plankton splitter.

Stratified Plankton Sampling

A series of stratified plankton samples were collected on three dates in 1995 when prior sampling indicated sea urchin larvae were present. Plankton was sampled with a 0.5 m diameter net with 202 μm mesh and a close-open-close mechanism to collect samples from discrete depths. Tows were four minutes in duration and sampled between 12 and 30 m^3. Sample volume was measured with a calibrated mechanical flowmeter (General Oceanics, Inc., Model 2030R2). Samples were processed as described above for temporal patterns.

On each sample date, three replicate tows were made at each depth sampled. All tows were made adjacent to a drogue suspended 5 m below a surface bouy, to sample the same water mass and minimize variability due to horizontal patchiness. On March 26 and 30, tow depth was calculated from meters of wire out and angle, and water samples were collected at each depth to measure temperature. On June 20, a temperature and depth recording data logger (VEMCO, Ltd., North Falmouth, MA) was attached to the net to record profiles of each tow. Samples were collected at Gregory Point in March, in an 18 -

22 m depth water column, and at Port Orford in June, in a 30 m depth water column. Sampling was conducted during calm conditions with 1.0-1.5 m swell and winds < 4 m sec^{-1}.

Recruitment monitoring

Sea urchin settlement 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.

Recruitment was measured at Gregory Point from January 30 to August 29 in 1994, and from March 27 to September 1 in 1995. At Port Orford, recruitment was measured from January 29 to August 28 in 1994, and from March 16 to August 29 in 1995. Settlement collectors were sampled at two week intervals at both sites except for the first sample period at Gregory Point, when heavy seas prevented sampling for a four week period in both years.

Settlement collectors consisted of PVC pipe (80 cm long x 15 cm diameter) with four 21.5 cm x 29 cm panels of Astroturf™ (Monsanto Co.) attached in pairs around the outer circumference of the cylinder. Foam floats inside each cylinder kept the collectors suspended in the water column. Each collector held a total of 0.25 m^2 of substratum (Figure 2).

At each study site, three 90 kg concrete moorings were placed on the bottom 10 m apart. A wire cable connected each mooring to facilitate locating adjacent moorings when sampling underwater. Moorings were deployed at 22 m depth at Gregory Point and at 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 datum level). A small buoy attached by a 10 m line to the upper collector marked the location of each mooring.

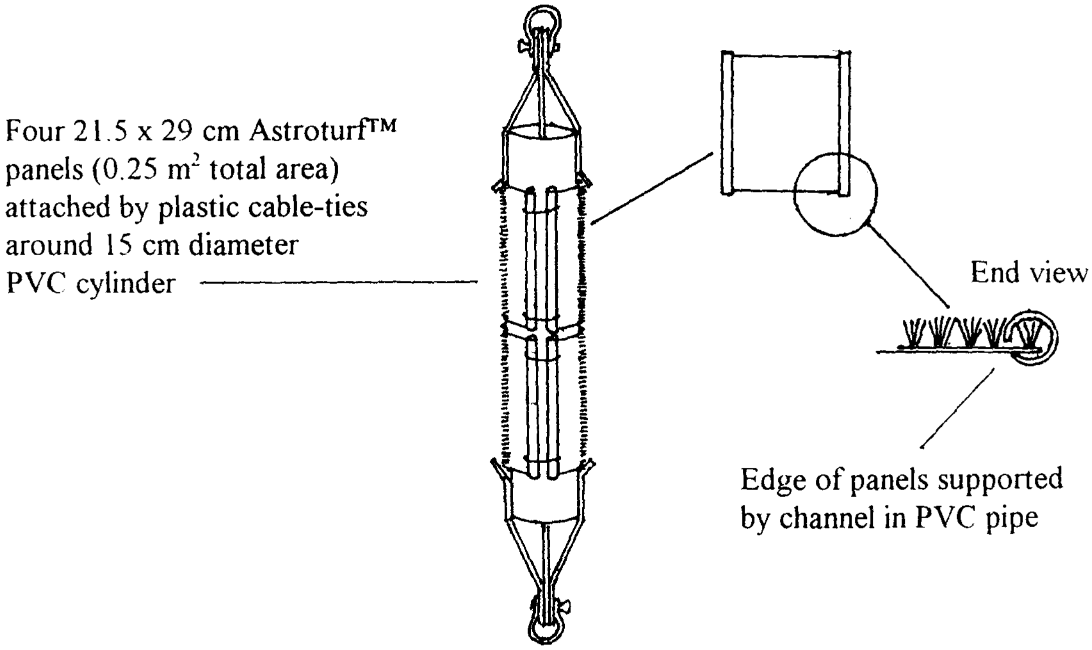

FIGURE 2. Design of larval settlement collectors deployed at Gregory Point and Port Orford.

Replacement settlement panels were seasoned in coarse filtered seawater flowing through the lab for at least one week prior to deployment to encourage growth of a microbial film on the artificial substratum. Settlement panels on each collector were retrieved and replaced using SCUBA. All four panels from a single collector were placed in a plastic container with a tight lid for transport to the surface and back to the lab.

Organisms were removed from each settlement panel by soaking in freshwater for five minutes, effectively killing all juvenile sea urchins, then spray washing to dislodge organisms from the substratum. This method was tested using known numbers of lab-reared sea urchin juveniles and was found to be effective in removing all juveniles from the substratum with little or no physical damage. Organisms were preserved in 1.5% formaldehyde in seawater and buffered with excess sodium borate. Samples were sorted under a binocular dissecting microscope using cross-polar light to highlight the calcareous ossicles and spines of juvenile sea urchins. All sea urchins were identified to species and enumerated. Because sample intervals varied, all juvenile data was adjusted to a "settlement rate" (number m^{-2} day^{-1}) and plotted on the day of sample.

Physical Parameters

Sea Temperature

Water temperature was recorded at 36 minute intervals at the depth of upper and lower settlement collectors using temperature recording data loggers (Onset Computer Corp.). Data loggers were intercalibrated (at 0, 8 and 12°C) against a lab thermometer accurate to ± 0.1°C. Temperature data downloaded from each data logger were adjusted by the error value determined for each unit.

Water Flux

The relative flux of seawater moving past the collectors was determined by attaching blocks of gypsum ($CaSO_4$) and measuring the change in mass due to dissolution over a fixed time period. Eckman *et al.* (1989) used this method to measure flux due to water currents near the ocean bottom. At each site, a rectangular gypsum block (160 to 205 gm) mounted to a plexiglass plate was attached to each of two upper and two lower collectors. In the first two trials, partially dissolved gypsum blocks deployed for 13 days at Port Orford were retreived, while blocks deployed for 14 and 19 days at Gregory Point had completely dissolved. On a third trial, blocks were deployed and retrieved from both sites after seven or eight days. Blocks were dried at 50° C for three days before weighing.

Laboratory and Field Experiments

Outplant Experiment

The survival rate of lab-reared juvenile *Strongylocentrotus franciscanus* on Astroturf™ substratum was measured over a two week period under field conditions. Three bouyant PVC cylinders (60 cm long x 10 cm diameter), similar in construction and function to the field settlement collectors, were attached 1 m apart to a weighted steel bar moored at 4 m depth in the mouth of Coos Bay, 3 km north of Gregory Point. This site was more accessible than the Gregory Point study site during heavy seas, permitting recovery of experimental substratum on a fixed schedule. This Coos Bay site was exposed to diminished ocean swell entering the bay mouth and to moderate tidal currents ($<0.5 m\ sec^{-1}$).

Larvae of *Strongylocentrotus franciscanus* were reared to a stage competent to metamorphose (see methods under laboratory studies, below). Larvae were induced to metamorphose in a solution of seawater and 30 mM KCl and and an extract of encrusting coralline algae scraped from subtidal rocks (KCl method modified from Pearse & Scheibling 1994). Juveniles 24 hours old were pooled from lab settlement containers and 50 juveniles were pipetted onto each of twelve 225 cm^2 Astroturf™ panels. Juveniles were given several minutes to attach to the substratum, then each numbered panel was placed in a plastic bag. Panels were immediately transported to the field outplant site and deployed on the subtidal mooring using SCUBA. Panels were carefully removed from each bag and the bags immediately resealed so that the number of juveniles not attached to the panels could be counted. The sealed bags were returned to the lab, the contents filtered, and all juvenile urchins counted (mean number per panel outplanted = 47, range = 41 - 50). Six bare control panels, with no juveniles, were also deployed on the moorings to measure any natural settlement of larvae. After one week in the field, six outplant panels and three control panels were chosen at random , removed, and transported to the lab in plastic bags. Organisms were removed from panels (and treated like the settlement collectors mentioned above) and juvenile *S. franciscanus* were counted. After two weeks in the field, the remaining outplant and control panels were retreived and processed for number of juvenile urchins..

Evaluation of Artificial Substrate

Two laboratory experiments were conducted to evaluate the effectiveness of Astroturf™ substratum to induce settlement of sea urchin larvae. The first experiment was designed to test the effectiveness of seasoning Astroturf™ panels in the lab prior to deployment in the field. The second experiment was designed to test whether the depth at which panels seasoned in the field, simulating the depth of upper and lower settlement collectors, influenced settlement rate.

In both experiments, larvae of *Strongylocentrotus franciscanus* were reared using methods modified from Leahy (1986) and Strathmann (1987). Larvae were reared in two liter cultures at a density of 1.0 ml^{-1}. Jars were gently stirred and 75% of the water in each culture jar was replaced with filtered (0.45 μm) seawater at four day intervals. Larvae were fed every other day, using a mixture of *Chaetocerous gracilis* and *Rhodomonas lens* at a density of $2.5 - 3 \times 10^4$ cells ml^{-1}. Cultures were reared at ambient seawater temperature (11 - 14°C) and were competent to metamorphose in 28 to 40 days.

Experiment 1: Effectiveness of Astroturf™ Substratum to Induce Settlement

Four treatments were set up, with five replicates (1 L beakers) per treatment, as follows:

Treatment A: Astroturf™ panels (100cm^2) seasoned for two weeks in the field at 4 m water depth. Immediately prior to use, panels were soaked in 7.5 % MgCl (isotonic with seawater) for one hour to anesthetize and facilitate removal of epifauna on substratum, then rinsed in seawater.

Treatment B: Astroturf™ panels seasoned for two weeks in the lab, in coarse-filtered flowing seawater.

Treatment C: Natural rock removed from tidepools and encrusted with coralline algae. Rocks were soaked in MgCl as in Treatment A.

Treatment D: Control (seawater only)

Thirty larvae 50 days old (judged to be competent to metamorphose at day 40) were pipetted into each beaker. At 24 hour intervals, the substratum was removed from each beaker and all unmetamorphosed larvae were counted. The number of settled juveniles in each beaker was assumed to be the difference between number introduced and number counted that had not metamorphosed. Percent metamorphosis at 48 hours was expressed as number of assumed settled juveniles divided by thirty.

Experiment 2: Relative Effectiveness of Astroturf™ Seasoned at Two Depths

Four treatments were set up, with five replicates (1 L beakers) per treatment, as follows:

Treatment A: Astroturf™ panels (100 cm2) seasoned for six days at 4 m depth, adjacent to settlement collectors at Gregory Point. Immediately prior to use, panels were soaked in 7.5% MgCl for one hour to anesthetize and facilitate removal of epifauna, then rinsed in seawater.

Treatment B: Astroturf™ panels seasoned for six days at 22 m depth, adjacent to settlement collectors at Gregory Point. Panels were soaked in MgCl as in Treatment A.

Treatment C: Natural rock from tidepools, encrusted with coralline algae. Rocks were soaked in MgCl as in Treatment A.

Treatment D: Control (seawater only)

Larvae 28 days old were pooled from culture jars and 30 larvae judged competent to metamorphose were placed into each beaker. After 48 hours, the substratum in each beaker was removed and vigorously shaken in a freshwater bath to kill and dislodge settled juveniles. Water in the control beakers was filtered to count number of unmetamorphosed larvae. All beakers were also inspected for settled juveniles. Percent metamorphosis was expressed as number of juveniles recovered divided by thirty.

Results

Field Studies

Sea Temperature

Sea temperature patterns differed between years but were synchronous between sites in each year ([illegible]). These patterns were characterized by episodic changes in temperature beginning in March or April and continuing through the study period. Changes in water temperature corresponded to changes in wind-forcing, with colder water associated with wind from the north and warmer water [illegible] periods of calm or winds from the south. This suggests that temperature patterns at both sites reflect intermittent wind-forced upwelling and relaxation events.

In 1994, low amplitude cycles of upwelling and relaxation, as indicated by changes in surface temperature, occurred in March at both sites. The temperature signal in subsequent upwelling events increased in intensity with stronger upwelling events dominating 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, upwelling did not begin until late April. Unlike 1994, prolonged upwelling was not observed in June and July; instead, shorter upwelling events occurred through the sampling period. In general, water temperature during upwelling events was [illegible] colder at Port Orford than at Gregory Point. The duration of events [illegible] 2 to 20 days. Periods of north wind and upwelling alternated [illegible] of relaxation or reversed winds and warmer water.

The water column was stratified for longer periods and displayed a stronger thermal signal at Gregory Point than at Port Orford (Figures 3i, 3j, 4i, 4j). 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 would increase. The strongest stratification occurred during relaxation events, resulting from increased temperature of the surface layer, but increased 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 (Figures 3g, 3h; also see Figures 12 and 13 in Discussion).

Water Flux at Study Sites

There was no significant difference between dissolution rates measured on upper and lower settlement collectors (Table 1), indicating a similar flux of water moving past the collectors at different depths (paired t-test; upper and lower gypsum blocks on each mooring paired, all trials at Port Orford and August trial at Gregory Point combined; $p > 0.5$, $df = 7$). However, the collectors at Gregory Point appeared to be exposed to greater water flux than those at Port Orford. All of the gypsum blocks had dissolved at Gregory Point in the first two trials, but length of deployment was only similar to the deployment interval at Port Orford in the second trial. In the third trial, dissolution rates were significantly higher at the Gregory Point site (t-test, $0.01 < p < 0.05$, df = 3, upper and lower blocks combined at each site).

TABLE 1. Dissolution Rates of Gypsum Blocks Deployed on Settlement Collectors at Gregory Point and Port Orford

Trial	Site	Days	Strata	Weight Loss (%) (Mean of 2)	Percent Loss Day^{-1} (Mean of 2)
1 (May)	Gregory Pt.	19	Upper	100.0	> 8.7
			Lower	100.0	> 9.4
	Port Orford	13	Upper	84.4	6.5
			Lower	88.9	6.8
2 (July)	Gregory Pt.	14	Upper	100.0	> 12.1
			Lower	100.0	> 12.5
	Port Orford	13	Upper	64.8	5.0
			Lower	69.4	5.3
3 (Aug.)	Gregory Point	7	Upper	55.4	7.9
			Lower	50.6	7.2
	Port Orford	8	Upper	43.0	5.4
			Lower	44.3	5.5

Spatial and Temporal Abundance of Sea Urchin Larvae

Fewer sea urchin larvae were found in nearshore plankton in 1994 than in 1995. At Gregory Point, larvae of *Strongylocentrotus franciscanus* and *S. purpuratus* were found on 27.5% and 24.6% of dates sampled in 1995, respectively, compared to 11.8% for each 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 12.5% and 7.7% of dates sampled in 1994 and 1995, respectively (Figures 3, 4,

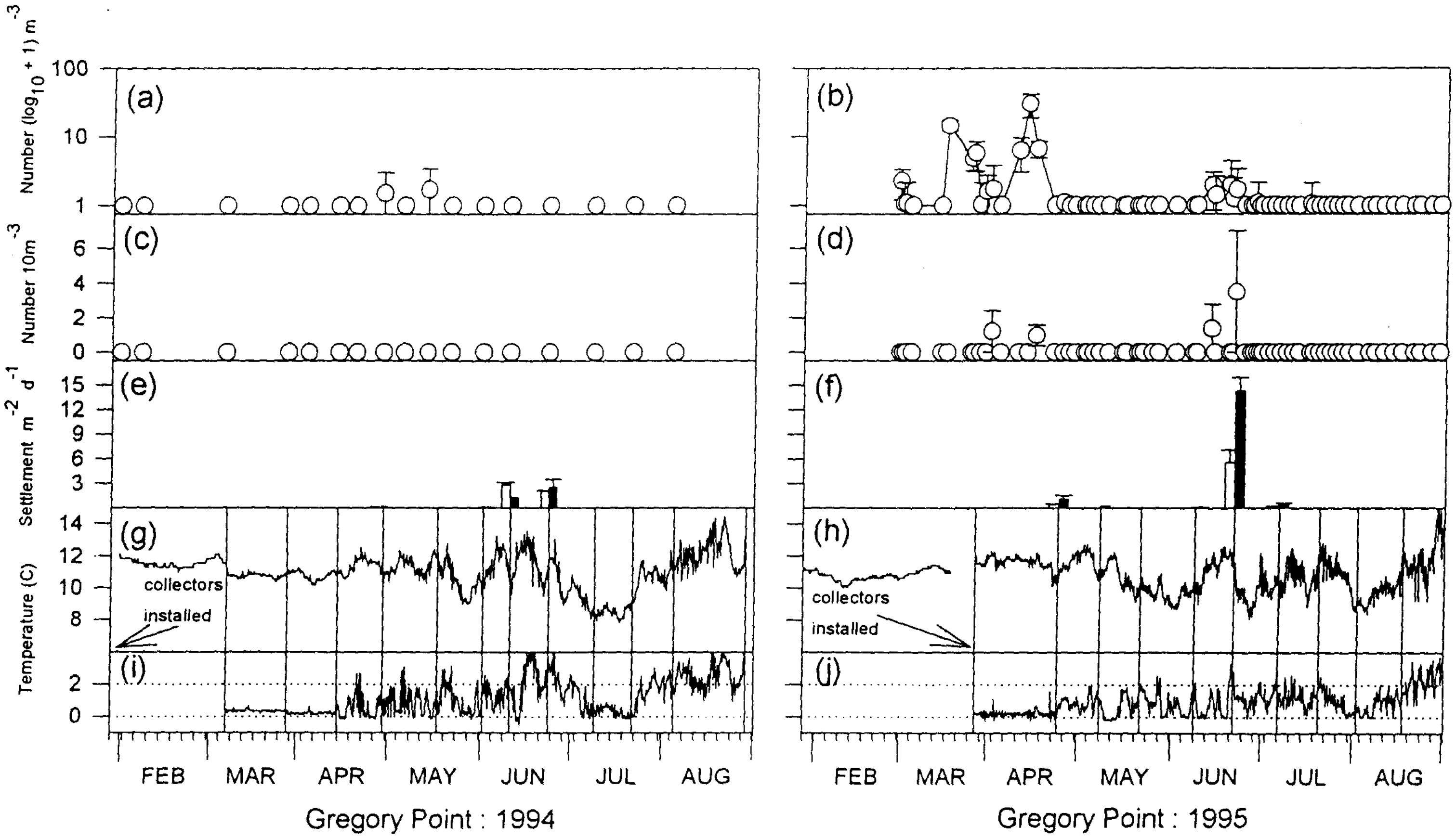

FIGURE 3. Mean larval abundance and settlement rates (± standard error) for *Strongylocentrotus franciscanus*, and sea temperature at Gregory Point; 3a and 3b, density of *S. franciscanus* larvae in plankton; 3c and 3d, density of competent *S. franciscanus* larvae in plankton; 3e and 3f, cumulative settlement (normalized for sample interval) on upper (clear bars) and lower (black bars) collectors for each sample period, and plotted on date of sample; 3g and 3h, sea surface temperature (4m depth). Vertical bars on temperature plots delineate settlement sampling periods; 3i and 3j, difference between surface and bottom (22m depth) temperature.

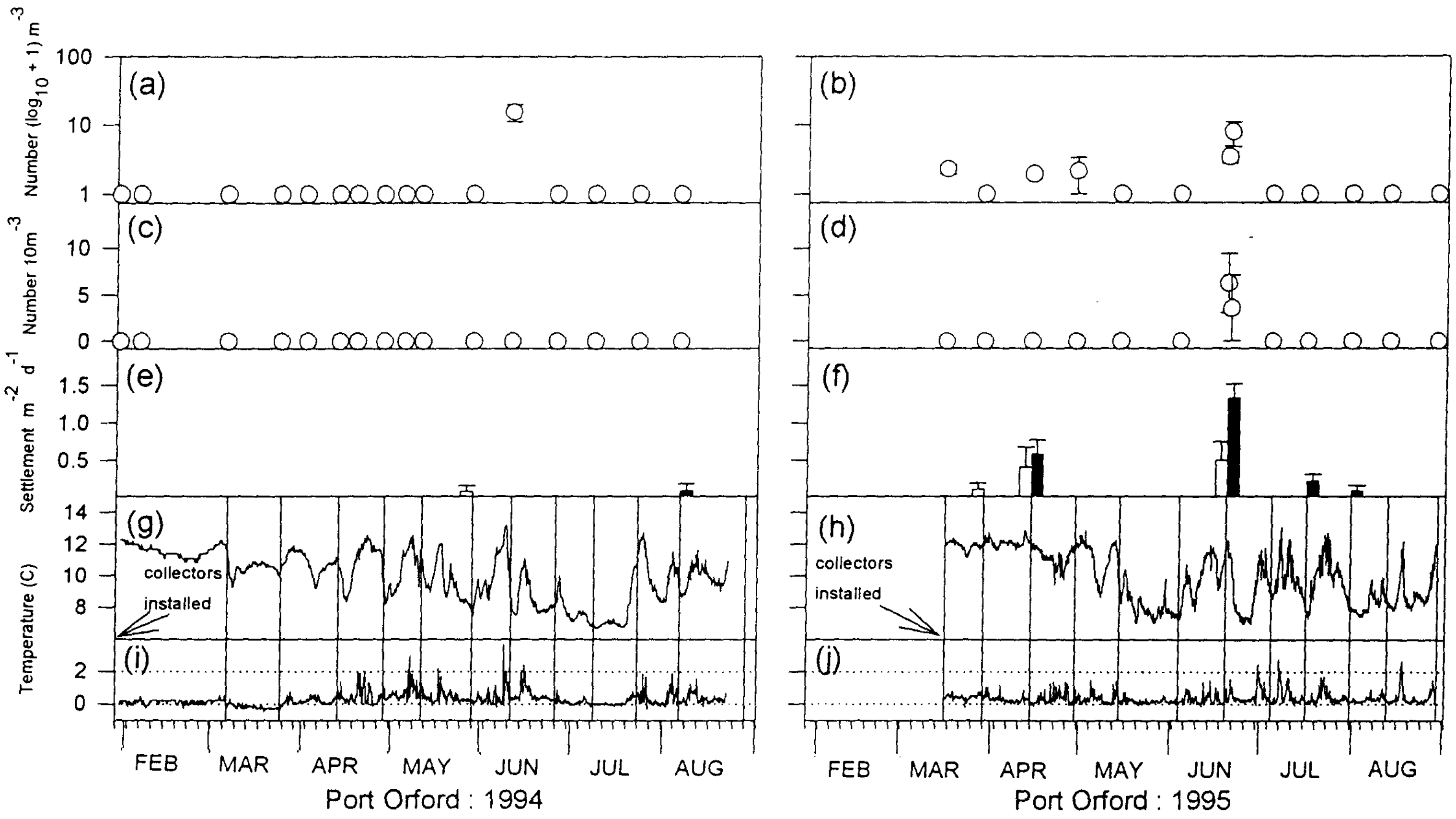

FIGURE 4. Mean larval abundance and settlement rates (± standard error) for *Strongylocentrotus franciscanus*, and sea temperature at Port Orford; 4a and 4b, density of *S. franciscanus* larvae in plankton; 4c and 4d, density of competent *S. franciscanus* larvae in plankton; 4e and 4f, cumulative settlement (normalized for sample interval) on upper (clear bars) and lower (black bars) collectors for each sample period, and plotted on date of sample; 4g and 4h, sea surface temperature (4m depth). Vertical bars on temperature plots delineate settlement sampling periods; 4i and 4j, difference between surface and bottom (18m depth) temperature.

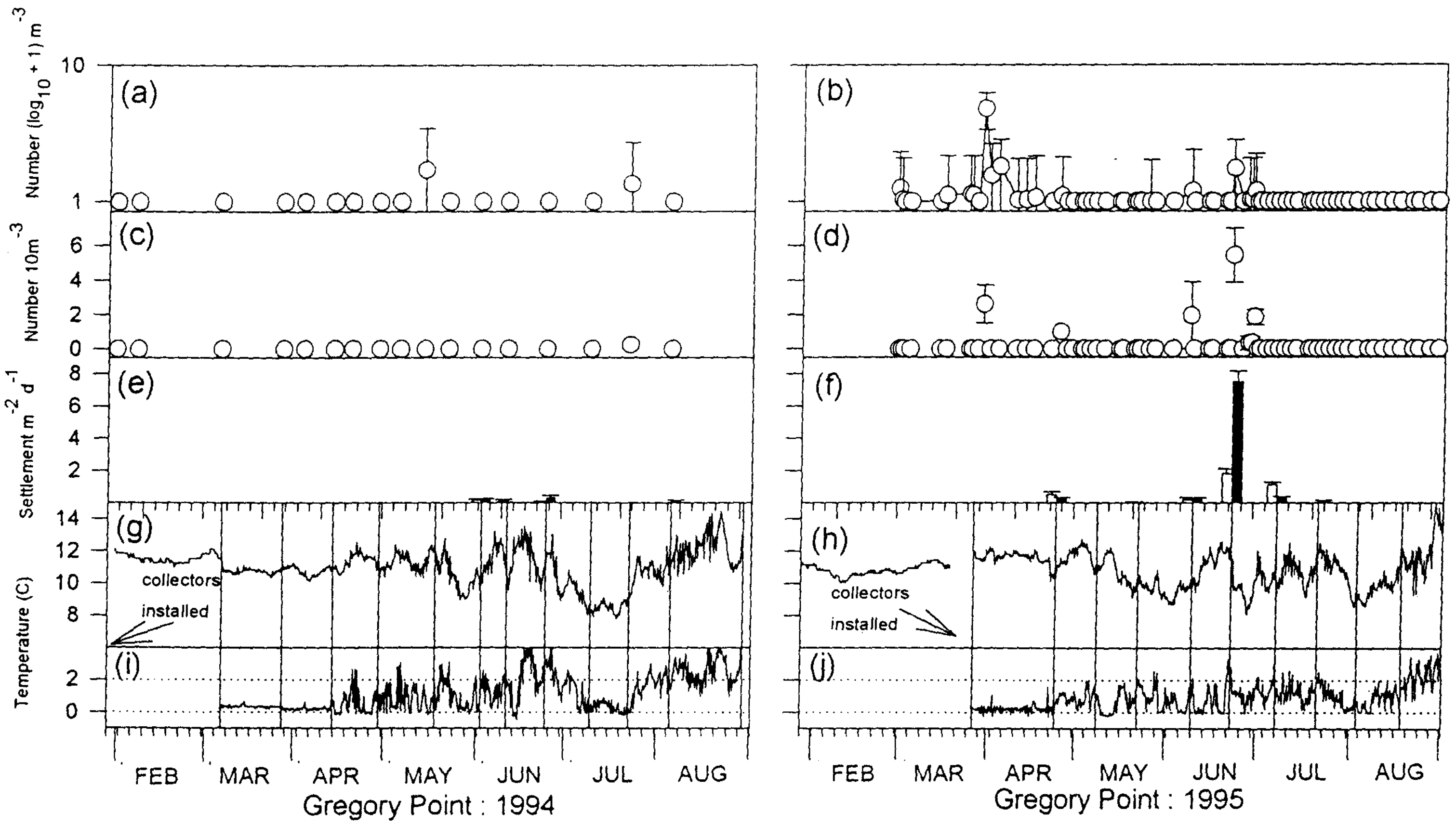

FIGURE 5. Mean larval abundance and settlement rates (± standard error) for *Strongylocentrotus purpuratus*, and sea temperature at Gregory Point; 5a and 5b, density of *S. purpuratus* larvae in plankton; 5c and 5d, density of competent *S. purpuratus* larvae in plankton; 5e and 5f, cumulative settlement (normalized for sample interval) on upper (clear bars) and lower (black bars) collectors for each sample period, and plotted on date of sample; 5g and 5h, sea surface temperature (4m depth). Vertical bars on temperature plots delineate settlement sampling periods; 5i and 5j, difference between surface and bottom (22m depth) temperature.

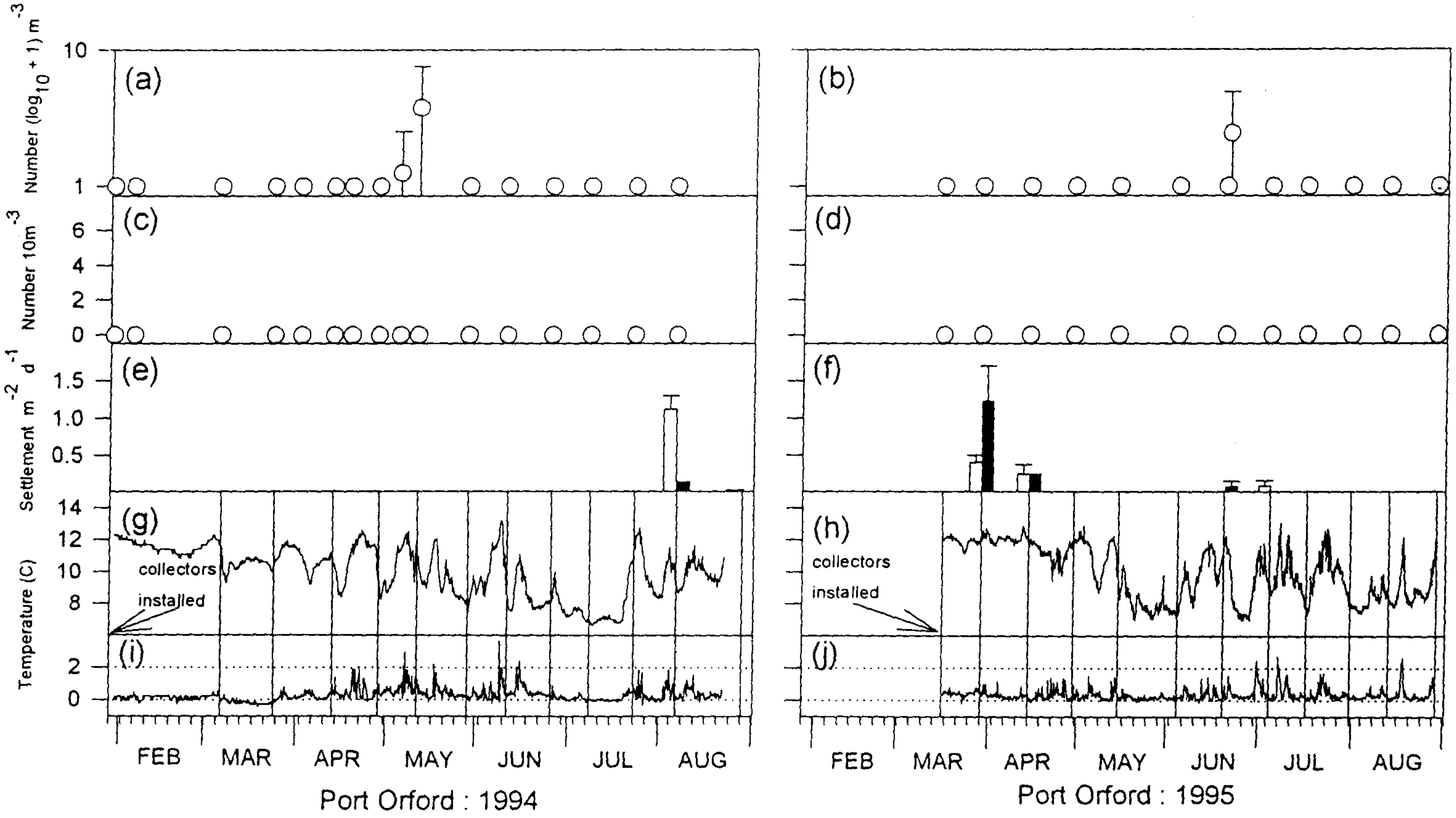

FIGURE 6. Mean larval abundance and settlement rates (± standard error) for *Strongylocentrotus purpuratus*, and sea temperature at Port Orford; 6a and 6b, density of *S. purpuratus* larvae in plankton; 6c and 6d, density of competent *S. purpuratus* larvae in plankton; 6e and 6f, cumulative settlement (normalized for sample interval) on upper (clear bars) and lower (black bars) collectors for each sample period, and plotted on date of sample; 6g and 6h, sea surface temperature (4m depth). Vertical bars on temperature plots delineate settlement sampling periods; 6i and 6j, difference between surface and bottom (18m depth) temperature.

5 and 6).

In 1994, all larvae found were precompetent four to eight arm stages except for a single competent larva of *Strongylocentrotus purpuratus* found on July 22. A density of 14 larvae m^{-3} for *S. franciscanus* in mid-June was the highest density observed.

In 1995, larvae of both species were found earlier in the year and at higher densities than in 1994. Both species were found at four and six arm stages in the first week of March. Four and six arm larvae are aproximately four to ten days old at 11-12°C (Strathmann 1987, B. Miller, unpubl. data), suggesting that spawning had occurred in late February. At Gregory Point, highest abundance of both species occurred from late March to mid-April and during June. At Port Orford, the occurrence of larvae of *Strongylocentrotus franciscanus* was synchronous with the temporal pattern found at Gregory Point. Only five larvae of *S. purpuratus* (all four arm) were found at Port Orford, on June 20. Most competent larvae (Figures 3d, 4d, 5d, 6d) were found in June when highest settlement rates were found, but competent larvae of both species were also found in April at Gregory Point.

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, Figure 7).

Vertical Distribution of Larvae

Larvae of *Strongylocentrotus franciscanus* were found at all depths sampled but were most abundant at 10-15 m depth in water depths of 20 and 30 m. This same distribution was also observed for larvae of *S. purpuratus* on two dates, but on one date most larvae were found at 1 m depth (Figure 8). All stages of larvae were found in samples from each strata, with no apparent relationship of stage to depth distribution. The water column was mixed on March 26 and 30, with <0.2°C difference between surface and bottom temperature. The water column was weakly stratified on June 20, with a 0.6°C difference between the surface and bottom temperature. The vertical distribution of larvae was constrained by bottom depth on all sample dates. The distribution of larvae relative to a pycnocline in stratified water or in mixed but deeper water was not determined.

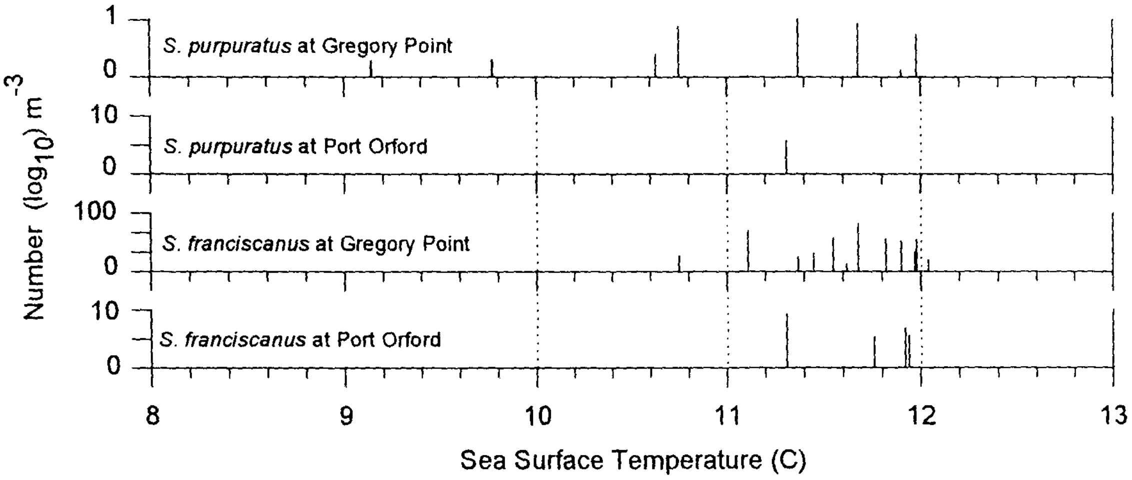

FIGURE 7. Surface temperature (4 m depth) of water mass in which larvae of *Strongylocentrotus franciscanus* and *S. purpuratus* were found in plankton samples from Gregory Point and Port Orford in 1994 and 1995. Relative densities for each species at each site are plotted on log scale.

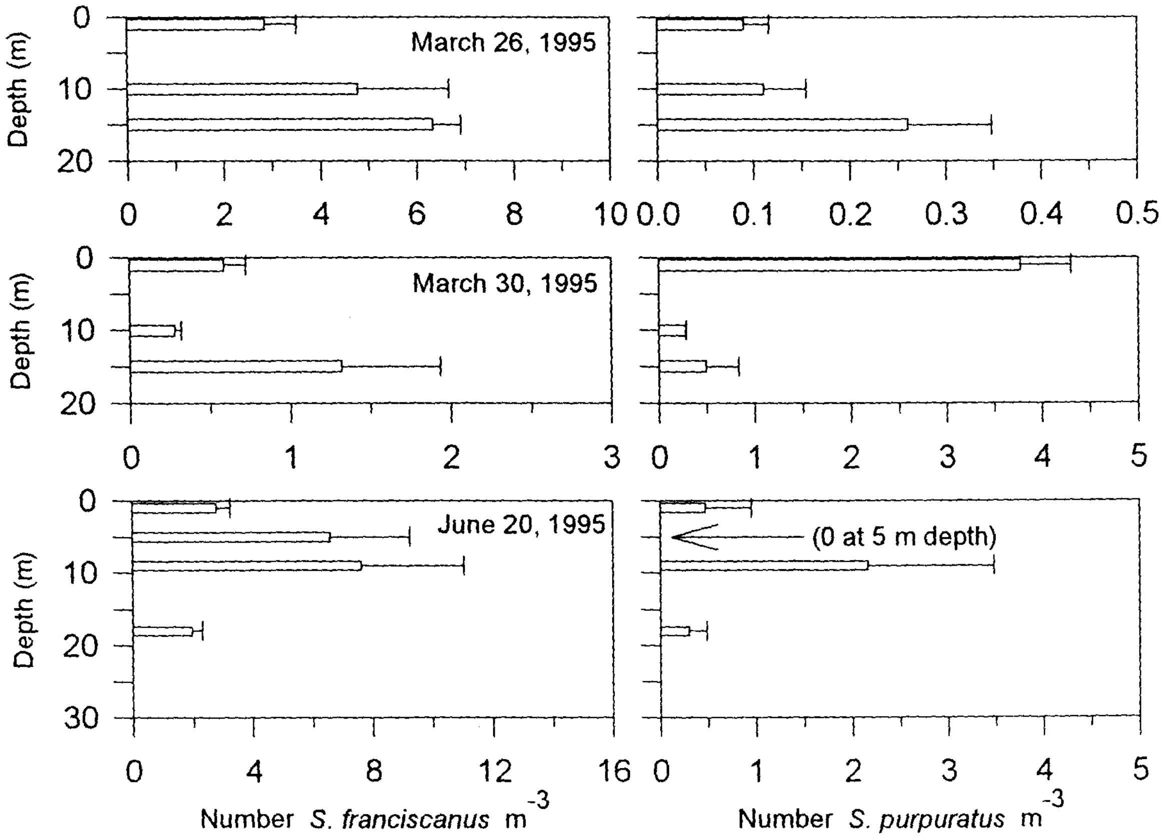

FIGURE 8. Vertical distribution of larvae of *Strongylocentrotus franciscanus* and *S. purpuratus* (mean ± standard error, n = 3 tows per strata) at Gregory Point (March 26 and 30) and Port Orford (June 20), 1995. Depth of water column was 18-22 m at Gregory Point and 30 m at Port Orford.

Spatial and Temporal Patterns of Settlement

Patterns of settlement were similar between species and between sites. Some patterns were also synchronous between years (Figures 3, 4, 5 and 6). At Gregory Point, almost all settlement of *Strongylocentrotus franciscanus* in 1994 occurred in mid-June. In 1995, peak settlement of *S. franciscanus* was also found in mid-June, but settlement also occurred in April and early May. Very few *S. franciscanus* settled at Port Orford in 1994 and 1995. Athough settlement was low in 1995, the timing of settlement at Port Orford was consistent with that observed at Gregory Point.

Settlement of *Strongylocentrotus purpuratus* at Gregory Point was consistent with patterns observed for *S. franciscanus*. In 1994, settlement densities of *S. purpuratus* were very low and settlement occurred almost entirely in June. In 1995, settlement was found as early as April, but also peaked in June. The settlement pattern of *S. purpuratus* at Port Orford 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 % CI = 66.0 - 91.6 %) after seven days, compared to 46.7 % (95 % CI = 22.63 - 67.6 %) after 14 days (Figure 9). The group means for each recovery date were significantly different (t-test on arc-sin transformed data; $p<0.001$, df=10). 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. These included several potential predators of juvenile sea urchins, including juvenile crabs, sculpins, and polychaetes.

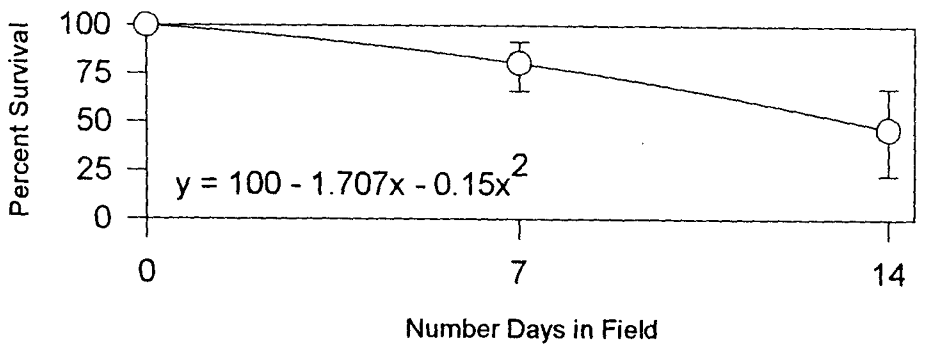

FIGURE 9. Percent recovery (± 95% confidence interval) of juvenile *Strongylocentrotus franciscanus* outplanted at age one-day on subtidal (4m depth) artificial substratum. Test for significance performed on arc-sin transformed data (Sokal & Rohlf 1981); plotted means and confidence intervals were back-transformed to percent. The regression equation represents the survival curve for 1 - 14 days.

Laboratory Studies

Evaluation of Artificial Substrate

Artificial substratum seasoned two weeks in the field induced 82 % metamorphosis in competent larvae after 48 hours in the lab, compared to 95 % metamorphosis induced by coralline algae encrusted rock (Figure 10). No settlement occurred in five control jars with seawater only. Substratum seasoned in seawater flowing through the laboratory induced only 45 % metamorphosis after 48 hours, suggesting that newly deployed panels may not be as effective at inducing settlement as those that have been in the field for several days. All group means were significantly different at $p = 0.05$ (ANOVA, F=28.3; df= 2,11; $p<0.001$: Tukeys (multiple comparisons) Test; q=0.05, 11,3: data arc-sin transformed).

Artificial substratum seasoned 6 days at 4 and 22 m depth induced 64 % and 45 % metamorphosis, respectively, after 48 hours in the lab (Figure 11). Rock encrusted with

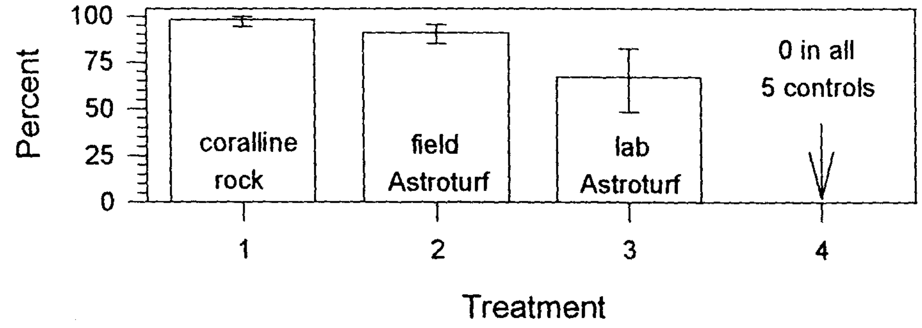

FIGURE 10. Percent metamorphosis (± 95% confidence interval) of *Strongylocentrotus franciscanus* larvae after 48 hours. Treatment 1, coralline algae encrusted rock; Treatment 2, artificial substrate seasoned seven days in field at 4m depth; Treatment 3, artificial substrate seasoned in lab for 14 days; Treatment 4, seawater only. Test for significance was performed on arc-sin transformed data (Sokal & Rohlf 1981); plotted means and confidence intervals were back-transformed to percent. All treatments were significantly different at p= 0.05.

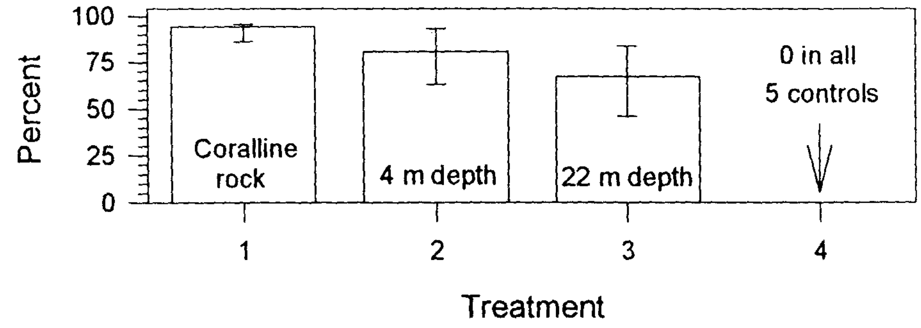

FIGURE 11. Percent metamorphosis (± 95% confidence interval) of *Strongylocentrotus franciscanus* larvae after 48 hours. Treatment 1, coralline algae encrusted rock; Treatment 2, artificial substrate seasoned six days at 4 m depth; Treatment 3, artificial substrate seasoned six days at 22 m depth; Treatment 4, seawater only. Test for significance was performed on arc-sin transformed data (Sokal & Rohlf 1981); plotted means and confidence intervals were back-transformed to percent. Treatments 2 and 3 were not significantly different at p=0.05; other treatments were significantly different.

coralline algae induced 94 % metamorphosis. No settlement occurred in five control jars with seawater only. Metamorphosis was significantly higher on natural substratum, but the two artificial substratum treatments were not significantly different at $p = 0.05$ (ANOVA, $F=12.9$; $df=2,12$; $p<0.001$: Tukeys (multiple comparisons) Test; $q=0.05$, 12,3: data arc-sine transformed).

Discussion

Spatial and Temporal Larval Abundance

Temporal patterns of larval abundance were consistent with reported spawning periods. *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 four-arm 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 (< 10 m $^{-3}$ on all but two dates) were generally an order of magnitude less than densities found in Barkley Sound, British Columbia. Rumrill (1987) found larvae of *Strongylocentrotus franciscanus* at ~100 - 300 m $^{-3}$ from mid-March through April, and larvae of *S. purpuratus* at ~ 50 - 250 m $^{-3}$ from late February to early April in Barkley Sound.

The occurrence of competent larvae in 1995 was synchronous with periods of settlement. Highest larval abundance was found in March and early April when settlement was low, but most of these larvae were precompetent. Larvae of all stages were also found during the period of peak settlement in mid-June, but competent larvae were most abundant during this period (Figures 3d, 4d, 5d). Different stages of larvae concurrent in the same water mass could result from at least two processes, including 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.

At Gregory Point, larvae of *Strongylocentrotus franciscanus* were found on all five dates sampled during the period June 9 - 22, 1995, when most settlement occurred. Larvae of *S. purpuratus* were found on five of 17 dates sampled during the period when most settlement occurred, June 9 - July 7, 1995. This suggests that settlement during June and early July was associated with a water mass containing larvae that was present over a period of several days.

Settlement Patterns

Further evidence that sea urchin larvae were present for several days during settlement events comes from the dates of settlement inferred from the estimated age of juveniles on the day settlement collectors were sampled. An ageing method described by Miller (Chapter II) is based on the time of expression of a suite of juvenile traits observed at three temperatures (8, 11, 14°C), which corresponds with the field temperature range. By adjusting developmental rates of juvenile traits for the thermal history recorded over a sample interval, day of settlement was estimated by back-calculating from stages of juveniles in the sample (see Chapter II). Figures 12 and 13 show calculated dates of settlement for six sample periods that represent the majority of settlement measured in 1994 and 1995. The relative proportion of settlers shown for each sample period was also

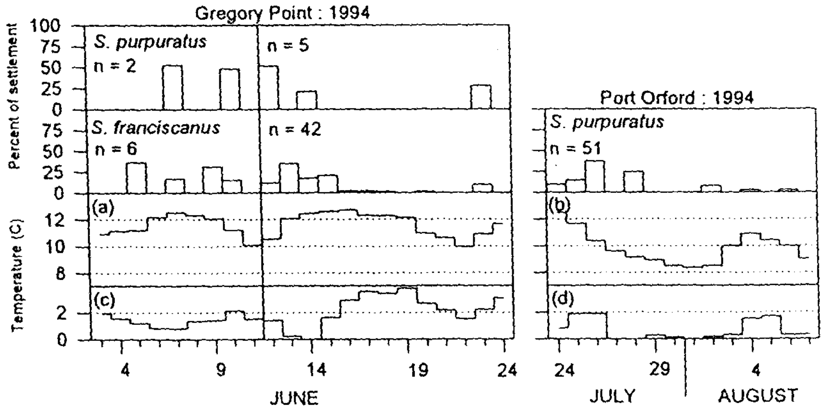

FIGURE 12. Settlement events for three sample periods at Gregory Point and Port Orford in 1994. Day and magnitude of settlement calculated from estimated age on sampling day and the survival function y = 100 - 1.707x -0.15x^2, where x = estimated age on sampling day (n = sample size) ; 12a and 12b, daily mean water temperature at upper settlement collectors (4m depth) at Gregory Point and Port Orford, respectively ; 12c and 12d, temperature difference between upper and lower settlement collectors at Gregory Point and Port Orford, respectively.

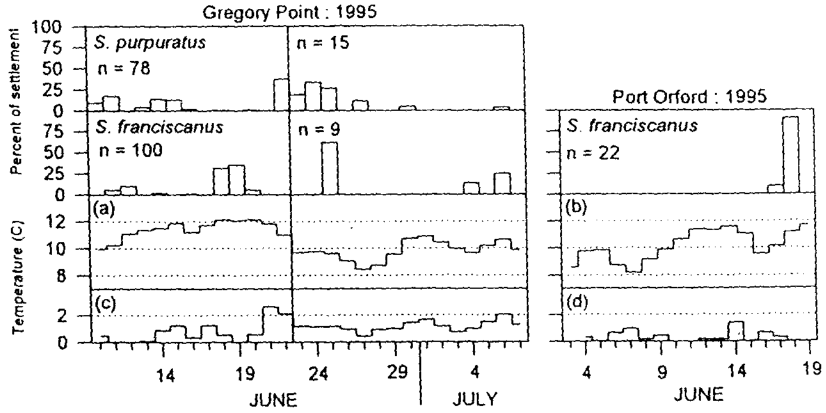

FIGURE 13. Settlement events for three sample periods at Gregory Point and Port Orford in 1995. Day and magnitude of settlement calculated from estimated age on sampling day and the survival function y = 100 - 1.707x -0.15x^2, where x = estimated age on sampling day (n = sample size) ; 13a and 13b, daily mean water temperature at upper settlement collectors (4m depth) at Gregory Point and Port Orford, respectively ; 13c and 13d, temperature difference between upper and lower settlement collectors at Gregory Point and Port Orford, respectively.

adjusted using the survival curve calculated from the juvenile *Strongylocentrotus fransicanus* outplant experiment shown in Figure 9. The survival curve for age 1 - 14 day *S. purpuratus* was assumed to be the same as that for *S. franciscanus*. The number of juveniles estimated to have settled on each date was divided by the survival function (y):

$y = 100 - 1.707x - 0.15x^2$, where x = estimated age on sampling date

Figures 12 and 13 show several modes, or "events", of settlement in each year. Although the precision of age estimation is lower for juveniles that settled early in a two week period, due to variation in developmental rates, it appears many of the settlement events occurred over a 3 to 5 day period. This 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 survival rates. An additional factor influencing settlement rates in this study may be the rate at which artificial substratum seasons in the field and becomes attractive for settlement. Newly deployed substratum induces fewer larvae to metamorphose than field-seasoned substratum (Figure 10). This factor may cause an underestimate of settlement that occurred early in a sample period, relative to that which occurred later in the period.

Recruitment was higher on collectors near the bottom in most sample periods. Dissolution of gypsum blocks attached to the collectors indicated that water flux past upper and lower collectors was not significantly different (Table 1). Although substrata seasoned near the surface induced slightly more lab-reared larvae to metamorphose in lab experiment 2 (Figure 11), this rate was not significantly different from rates measured on substrata seasoned near the bottom. Thus, differential water flux or seasoning of substrata deployed at different depths did not account for observed recruitment patterns. Stratified plankton sampling showed that larvae of both species were generally more abundant at 10 - 15 m depth under conditions of weak thermal stratification, but were found throughout the water column in relatively shallow (<20m) depths (Figure 8). Recruitment of both species was higher on the upper collectors when the bottom temperature was 1-2°C colder than the surface, and higher on the lower collectors when the water column was mixed or weakly stratified (<1°C difference). The recruitment patterns and vertical distribution of larvae suggest depth of settlement is influenced by the thermal structure of the water column, with lower rates below the thermocline in stratified water. It is also possible that differential mortality between strata may have contributed to the observed patterns, but this possibility was not investigated.

Timing of settlement and recruitment levels varied between years in this study. Inter-annual variation in sea urchin recruitment was also found in northern California. Ebert *et al.* (1994) used scrub brushes to measure sea urchin settlement over a four year period (1990-1993) in California. Little or no settlement of *Strongylocentrotus franciscansus* or *S. purpuratus* was found at the Westport and Arena Cove sites in northern California. Total settlement of *S. franciscanus* was low at a third northern site at Point Cabrillo, but settlement of *S. purpuratus* was moderate to high in three of four years at this site. Most settlement occurred during summer months from June to August, but both species settled at moderate to high densities in March 1993 at Point Cabrillo. Wing *et al.* (1995) also used scrub brushes to measure sea urchin settlement during one year (1992) at two sites between Point Reyes and Point Arena, in northern California. Settlement was found from early April through August, but peaked in July at both sites. Recruitment densities reported by Wing *et al.* were for combined species, but were within the range measured by Ebert *et al.*. Recruitment densities measured by Ebert *et al.* and Wing *et al.* are not directly comparable to densities measured in this study because of the different sample intervals and substratum used to measure recruitment. However, on the basis of area of collector substratum, the peak density of ~ 300 *S. franciscanus* per m^2 (three per brush) found by Ebert *et al.* is similar to the peak density of ~ 200 per m^2 (35 - 56 per collector) measured in this study. The peak density of 53 *S. purpuratus* per brush (~ 1×10^4 m^{-2}) found by Ebert *et al.* was much higher than recruitment densities observed in this study.

Settlement at Gregory Point and Port Orford only occurred when surface water temperature was ≥ 10°C. Most settlement for both species in both years occurred in water between 11 and 12°C surface temperature (Figures 3,4,5,6,12,13). This is consistent with larval occurrence in water between 11 and 12°C (Figure 7).

Nearshore Hydrodynamic Processes off the Oregon Coast

The association of sea urchin larvae with relatively warm water and the temporal pattern of larval abundance found in 1995 suggest that both alongshore and cross-shelf advection may be critical determinants of sea urchin larval supply to the Oregon coast. Water masses that may carry sea urchin larvae are influenced by hydrodynamic processes that fall within distinct winter and summer regimes of wind and current patterns.

During the winter regime, nearshore currents off northern California and Oregon are from the south (Hickey 1979). These currents, forced by cyclonic winter winds, are an extension of the Davidson Current found all year south of Cape Mendocino. Northward flow extends at least 265 km offshore from Oregon, but is concentrated within 160 km of the coast and is 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). The onset of southward surface currents, sloped isopycnals (shallower nearshore), and a drop in sea level may occur over a day or two during a single event of north wind stress and upwelling (Allen 1983). The rapid spring transition is partly due to local wind stress, large-scale winds along the coast, and to the alongshore pressure gradient.

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). The reversal of alongshore flow to the north corresponds to the decay or reversal of upwelling-favorable winds from the north. After May, predominant winds from the north force a southward flow from June to September. The most prominant feature off Oregon during summer is a coastal jet that has a maximum southward velocity of 0.2 to 0.4 m sec^{-1} at a distance of 5 to 25 km from the coast (Stevenson *et al.* 1974, Huyer *et al.* 1975, Smith 1981). Huyer *et al.* (1975) found the coastal jet is stronger and centered closer to shore in spring than summer (10 vs 15 km). The largest variance in flow occurs inshore of the axis of the jet, but the mean flow velocities are less nearshore, generally < 0.1 m sec^{-1}.

Influence of Nearshore Hydrodynamics on Larval Supply and Settlement

Larval Source

Some inference of sea urchin larval source in Oregon 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 drop in sea level, thus sea level records may be used to determine timing of the shift in flow regimes (Huyer *et al.* 1979). Figure 14 shows mean monthly sea level for early 1994 and 1995 at Crescent City, California (available from the National Oceanic and Atmospheric Administration archives, Sea and Lake Levels Branch). The Crescent City time series provides a good index of sea level in southern Oregon because alongshore currents are generally coherent in northern California and Oregon (Huyer *et al.* 1979). Mean monthly sea level gradually decreased between February and April in 1994. In contrast, sea level in 1995 was higher from January to March, then dropped sharply in April. The relatively high sea level and warm water temperature during March and early April in 1995 suggests strong northward and mean onshore flow.

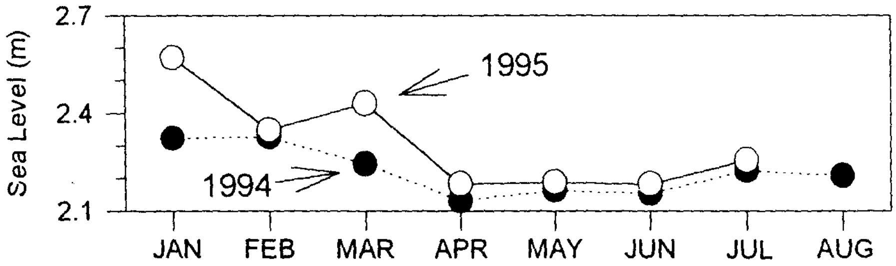

FIGURE 14. Sea level at Crescent City, California, in 1994 and 1995.

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* generally require at least 45 days at 11 to 12°C to reach competency, while larvae of *S. franciscanus* reach competency in slightly less time (B. Miller, unpubl. data). During this extended period 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.

In April and May, the mean amplitude of wind stress and alongshore current velocities along Oregon are low, but the frequency of fluctuations in these events is greatest at this time (Huyer *et al.* 1975). The relatively low alongshore current velocities and frequent decay or reversal of wind forcing in spring suggest that the distance nearshore water masses are transported alongshore is less at this time of year. If this is the true, larvae produced in early spring may be transported less distance alongshore than larvae produced earlier or later in the year, possibly contributing to recruitment near the larval source.

The summer regime after May is characterized by mean southward currents and upwelling, with intermittent periods of calm wind or northward wind stress and cessation of upwelling. Settlement during this period of generally southward flow could be from two sources, either from late spawners to the north, or from larvae transported to the north earlier in the year and able to delay metamorphosis.

Cross-Shelf Transport Mechanisms

While alongshore advection 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, leading to possible entrainment of larvae. 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 - 80m (Moores *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 (Figure 8). Rumrill (1987) found that larvae of *Strongylocentrotus droebachiensis* in Barkley Sound, British Columbia, were much more abundant at 0 - 30 m than at 30 - 60 m depth. Other echinoid larvae are also found in surface waters above the pycnocline (see 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 sea urchin 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 sea urchin larvae.

Larvae of both species settled during late March and early April in 1995. This period was characterized by relatively warm water (11-12°C), a mixed water column, relatively high sea level, and predominant wind from the south (56% of days during March 16 - 31, and 93% of days during April 1 - 15; wind information from North Bend Airport, 12 km north of Gregory Point). This suggests that wind-forced onshore Ekman transport contributed to the delivery of larvae to study sites during this period.

Following the spring transition in 1995, no settlement occurred during May. Upwelling and offshore Ekman transport, evident by progressively colder surface water (< 11 °C), 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, but the mechanism underlying these events is not clear. The dynamics of the onset, or so-called spin-up phase, of upwelling have received considerable attention and are generally understood for the California Current System. The reverse of upwelling, the so-called spin-down or relaxation phase, has received less study and the forcing mechanisms and dynamics of mass and heat transfer are poorly understood (Send 1987). The relaxation phase has great biological significance as a key process influencing onshore movement of surface waters and larval supply.

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 and Clarke 1974, Halpern 1976). Others have reported that return of higher temperatures may proceed in an entirely different manner. Send (1987) found that increased nearshore temperature did not result from onshore advection during relaxation or Ekman transport during moderate reversed winds in northern California. The source of heat during relaxation was attributed to both net solar heat flux and alongshore advection of warmer water from the south. Halpern (1976) also found that surface heating accounted for most of the warming found during a relaxation event in Oregon. Onshore advection was unlikely because near-surface current meters recorded offshore flow during the relaxation period. Huyer *et al.* (1974) measured nearshore warming along Oregon while near-surface isopycnals appeared to move offshore. The depth of the nearshore temperature signal and a flow reversal (from the south) suggested nearshore warming resulted from both surface heating and alongshore advection.

While the mechanism underlying relaxation events observed in 1994 and 1995 is not clear, the patterns of water temperature, larval abundance and settlement provide evidence that several mechanisms may contribute to nearshore warming and, in some circumstances, larval transport. Several warm water events were observed during the summer flow regime (after mid-April) at Gregory Point in 1995 (Figure 3h). Warm water events centered on May 3 and July 1, 12 and 23 occurred during periods of calm winds and generally sunny weather (B. Miller, pers. obs., wind information from North Bend Airport). Figure 3j shows the water column was stratified (1-2°C colder on bottom) during these events, suggesting the heat influx was due to either onshore flow of a thin surface layer or to surface heating. The 1-2°C daily variation in surface temperature was at a tidal frequency, due to the temperature recorder (at 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 in the plankton or settlement was found during these events.

In contrast, the water column was mixed during warm events with modes centered on May 12, and June 14 and 19. These events occurred during periods of strong southerly wind (wind SW 10-25 knots on May 9-13, and SW 10-25 knots on June 9-13 and 17-19).

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 (Figures 3f, 4f and 5f). 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.

This suggests sea urchins may recruit by a different mechanism than that proposed for barnacle cyprid larvae in California. Farrel *et al.* (1991) and Roughgarden *et al.* (1991) found that barnacle recruitment was correlated with increased temperature, decreased salinity, and decreased southward wind, signalling relaxation from upwelling. Roughgarden *et al.* (1991) hypothesized that cyprids transported offshore during upwelling become concentrated in a front between the colder inshore water and the warmer offshore water in which they reside. In this hypothesis, pulsed recruitment occurs when upwelling ceases and the upwelling front, with its accumulated load of larvae, moves onshore.

The small-scale processes that control distribution of plankton at upwelling fronts are poorly understood (Mann & Lazier 1991). However, two requirements of the hypothesis proposed by Roughgarden *et al.* (1991) are that 1) larvae must be surface-oriented, and 2) larvae must swim at sufficient speed to remain in surface waters at the convergence zone of the front, where downward flow of the offshore directed upwelled water may carry weak swimmers away from the front. Sea urchin larvae are not oriented to strata very near the surface and are distributed at least 20 m deep (Figure 8). Sea urchin larvae have swimming speeds of < 1 mm sec^{-1}, compared to 5-6 mm sec^{-1} for cyprid larvae (Mileikovsky 1973). Banse (1986) found that sea urchin larvae behaved as passive particles but remained associated with a particular water mass. Weak swimmers such as sea urchin larvae may not be able to overcome convergent and downward flow and become concentrated at an upwelling front.

If sea urchin larvae behave as passive particles, dispersal of larvae within a water mass may be inferred from dye studies. Okubo (1971) used releases of flourescent dye in the ocean to develop a diffusion diagram relating time scales to dipersal scales. Okubo found that over 1 -2 days, scale of surface dispersal was ~ 1 km, while at 1-2 weeks dispersal was ~ 10 km, and for 1 month, dispersal was ~ 100 km. Thus, larvae that are weak swimmers may be confined vertically by density discontinuity layers, but become horizontally dispersed over several weeks.

An alternative mechanism proposed here is that sea urchin larvae do not become concentrated in upwelling fronts and, consequently, do not recruit in short-period pulses if such fronts move onshore during relaxation events. Rather, sea urchin larvae are 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 rate 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 two 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 sea 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. If this is true, it may be possible to predict regional differences in recruitment success based on long-term wind, sea level, and water temperature records.

Summary of Findings and Conclusions

In summary, larval occurrence 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. Nearshore warming during low wind stress may have resulted from surface flux or onshore flow of a thin surface layer. 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.

The source of larvae to Oregon is dependent on timing of spawning, timing of the spring transition in flow regimes, and variability of alongshore flow within each flow regime. Before the spring transition in April, larvae are probably advected from the south. The highest probability for entrainment of local larvae occurs during the spring period of frequent alongshore flow reversal. Larval source may be most variable in summer when southward flow may carry larvae from northern sources as well as older larvae transported northward earlier in the year.

Recruitment variability in Oregon appears closely linked to timing of spawning, interannual variation in larval density, timing of the spring transition in flow regimes, and variablity in hydrodynamics within each flow regime.

CHAPTER II

TEMPERATURE-DEPENDENT DEVELOPMENTAL RATES AND AGE DETERMINATION OF NEWLY SETTLED RED AND PURPLE SEA URCHINS

Introduction

Populations of the red sea urchin, *Strongylocentrotus franciscanus* (A. Agassiz), and purple sea urchin, *S. purpuratus* (Stimpson), are distributed along the west coast of North America from Cedros Island, Mexico, to the Gulf of Alaska (Emlet 1995). Within the portion of this range from California to Washington, the frequency of annual recruitment of juveniles to local populations varies with latitude, in general decreasing in frequency at higher latitudes (Ebert & Russell 1988, Ebert *et al.* 1994). Variation in recruitment has been attributed to various physical processes that influence larval supply. Larval transport alongshore and across the shelf during the one to four month pelagic larval phase (Strathmann 1978), and the timing of larval production relative to winter and summer flow regimes within the California Current System have each been suggested as sources of variation in recruitment (Ebert & Russell 1988, Ebert *et al.* 1991, 1994, Wing *et al.* 1995, also see Chapter I). Within the ranges of both species, different nearshore processes control the movement of coastal water due to regional differences in winter and summer flow regimes. The relative importance of different nearshore processes to larval supply may vary within each hydrographic regime. Describing the link between nearshore hydrodynamics and larval supply and settlement is fundamental to understanding the 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 hydrographic processes, such as coastal upwelling and downwelling, 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 hydrodynamic processes and larval supply to a specific region (eg. Farrell *et al.* 1991 for barnacle recruitment).

Studies of juvenile recruitment that focused on settlement of sea urchins have been conducted at various locations along the west coast of North America (Ebert *et al.* 1991, 1994, Harrold *et al.* 1991, Wing *et al.* 1995, also see Chapter I). In each of these studies, recruitment was measured as the number of juveniles that survived out of all those that settled over sample intervals of 1 week to 1 month. These studies measured recruitment over intervals that included distinct changes in water temperature, suggesting advection of different water masses over the settlement collector sites (Wing *et al.* 1995, also see Chapter I). However, without a method for estimating age of recruits, it has not been possible to relate settlement events to specific hydrographic events which occurred during the sample period.

I have developed a method for estimating age of early (1 - 14 day) juvenile red and purple sea urchins based on development of specific juvenile traits. Because developmental rates are a function of temperature (Schmidt-Nielsen 1975), rates are described for three temperatures that span the range that juvenile sea urchins are likely to experience in the field. The morphological descriptions provide an aid for species identification at the early juvenile stage.

Methods

Larvae of *Strongylocentrotus franciscanus* and *S. purpuratus* were reared using methods modified from Leahy (1986) and Strathmann (1987). Sibling larvae were reared in two liter cultures at a density of 1.0 ml^{-1}. Jars were gently stirred to keep larvae and algal cells in suspension. Water in culture jars was replaced (75% of volume) with filtered (0.45 μm) seawater at four day intervals. Larvae were fed every other day, using a mixture of *Chaetocerous gracilis* and *Rhodomonas lens* at a density of 2.5 - 3 x 10^4 cells ml^{-1}. Cultures were reared at ambient seawater temperature (13 -15°C) and were competent to metamorphose in 29 days for *S. purpuratus* and 31 days for *S. franciscanus.*

Naturally metamorphosed juveniles of known age were obtained from competent larvae placed in one liter beakers containing small rocks encrusted with coralline algae. After eight hours, larvae that had not settled were removed by replacing the water in each beaker. Juveniles in each temperature treatment were reared in two replicate beakers. Temperature of each treatment was recorded at 24 minute intervals on submersible data loggers (Onset Computer Corp.) that were intercalibrated to a thermometer accurate to ±0.1°C. One group of juveniles was reared at 8°C (± 0.1°C). A second group was reared at 11°C (±0.1°C), and a third group was reared at ambient temperature of seawater flowing through the lab (mean = 14.4°C, range = 13.5 - 15.2°C for *Strongylocentrotus franciscanus*, and mean = 14.7°C, range = 13.6 - 16.3°C for *S. purpuratus*). Variation in ambient temperature was primarily diel and the daily mean temperature on consecutive days differed little from the two week mean.

At one day intervals, at least ten individuals from each temperature treatment were haphazardly removed and observed under a binocular dissecting microscope. Notes were made on development and a sample (6-10) from each treatment was preserved in 1.5 % buffered formaldehyde to allow comparison between preserved samples and live juveniles. Measurements were made using an ocular micrometer accurate to 10 μm.

The development, size, and functionality of specific juvenile structures were noted at each observation. These structures included adult pedicellariae, sphaeridia, adult primary spines, anal test plate, and jaws of the lantern apparatus. Based on development of juveniles reared at 14°C, a series of stages were defined according to the set of traits on a given day. Notes that described each stage included presence or absence of structures, length of structures, whether a structure was functional, and the percentage of individuals that fit the suite of characteristics for that stage.

Results

Juvenile Morphology

Numbering of ambulacral and interambulacral radii follows the Lovenian system of

Roman numerals I through V for ambulcra and numbers 1 through 5 for interambulacra (Hyman 1955). Abbreviations for ambulacra (A) and interambulacra (IA) are used in conjunction with the numbering system throughout the morphological descriptions for each species. Terminology of structures follows that of Hyman (1955). The juvenile spines termed "tetraradiate spines" by Gordon (1926) and "juvenile spines" by Emlet (1988) are transitory structures only found in the early juvenile stage. The term juvenile spine is used in this report.

Strongylocentrotus franciscanus

The earliest stage of juvenile *Strongylocentrotus franciscanus* had four primary spines per interambulacrum, two tetraradiate juvenile spines and one oral podia per ambulacrum, seven to nine additional tetraradiate juvenile spines located aborally, and three aboral pedicellariae (Figure 15a). These aboral pedicellariae were a distinctive feature of juvenile *S. franciscanus*, distinguishing them from juvenile *S. purpuratus*, which lack aboral pedicellariae entirely. These pedicellariae develop on the pluteus larva (Mortenson 1937). In *S. franciscanus*, two pedicellariae form at the bases of the postoral and posterodorsal arms on the right side of the larva and are associated with calcareous ossicles that are precursors to genital plates 3 (from the posterodorsal arm) and 5 (from the postoral arm) on the juvenile test. The third pedicellaria is located medially at the posterior end of the larva. These pedicellariae are fully functional in the larval stage. Development of pedicellariae in larvae of *S. franciscanus* appears to follow a sequence similar to that described for larvae of *Lytechinus pictus* (Burke 1980).

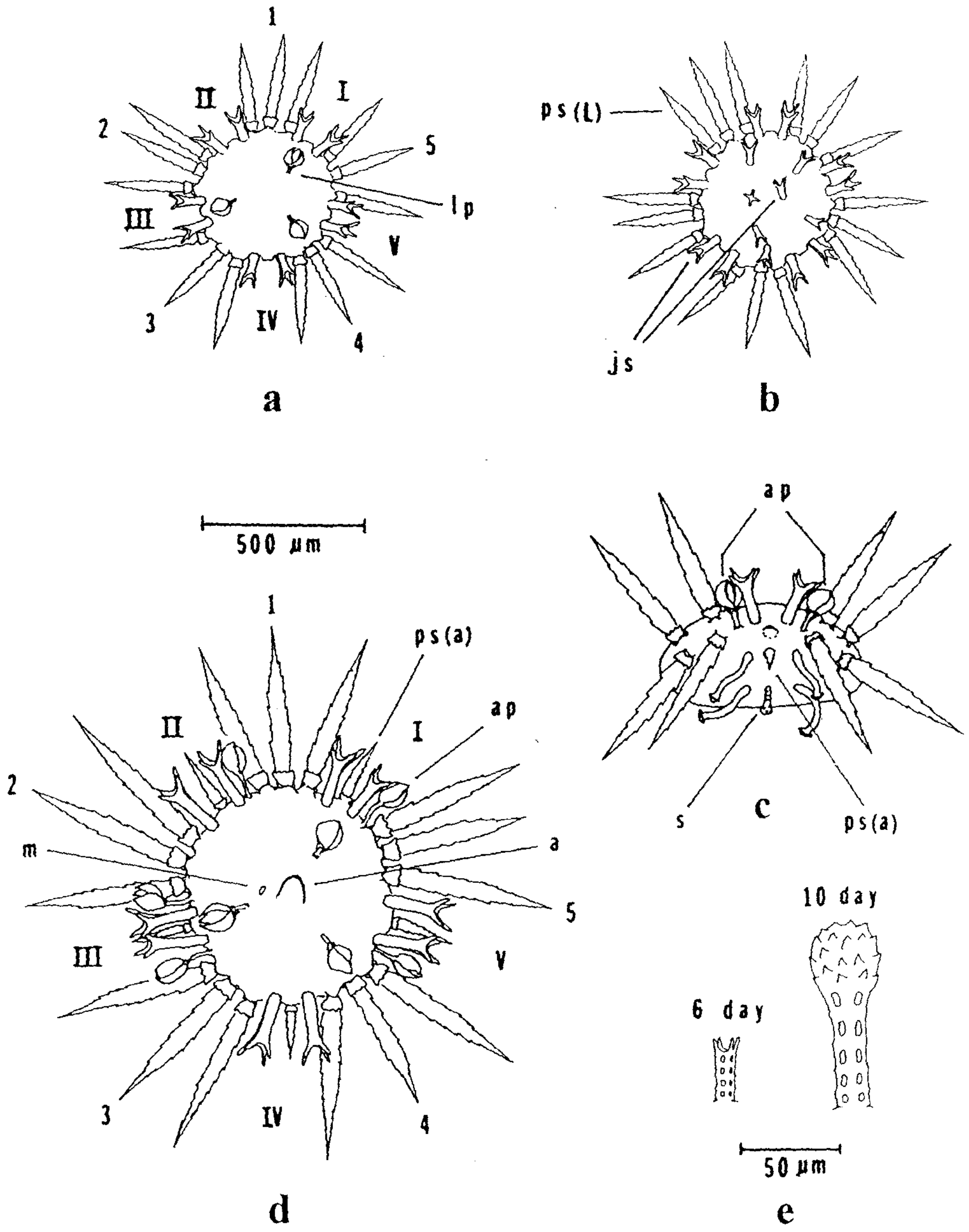

FIGURE 15. Morphology of early juvenile *Strongylocentrotus franciscanus* and *S. purpuratus*; 15a, pattern of larval pedicellariae on *S. franciscanus*, age 2 day (aboral juvenile spines, podia, oral primary spines not shown); 15b, aboral view of *S. purpuratus*, age 2 day (podia, oral primary spines not shown); 15c, lateral view of ambulacrum on *S. purpuratus*, showing origin of adult pedicellariae, first adult primary spine, and sphaeridium, age 14 day ; 15d, pattern of larval and adult pedicellariae, first adult primary spines, anal plate and madreporite on *S. franciscanus*, age 14 day; 15e, sphaeridia at 6 and 10 days. a, anal plate; ap, adult pedicellaria; js, juvenile spines; lp, larval pedicellaria; m, madreporite; ps(L), larval primary spine; ps(a), first adult primary spine; s, sphaeridium. Figs. a-d scale to 500μm bar, fig. e scales to 50μm bar. Numbering of ambulacra and interambulacra follows the Lovenian system (Hyman 1955).

Following metamorphosis, the larval pedicellariae were found on the aboral surface in apparent bilateral symmetry (plane of symmetry from AII to IA4) imposed on the pentamerous symmetry of the juvenile test. The pedicellaria that was posterior and medial on the larva became centered on IA4. The pedicellariae on genital plates 3 and 5 were located on IA3 and IA5, respectively. The stalks of these latter pedicellariae were located at the edges of the genital plates 3 and 5, making the pedicellariae appear to be centered over AI and AIII, respectively (Figure 15a). This provides a convenient means of orienting the different radii of the juvenile, with one pedicellaria centered aboral to the primary spines on IA4 and two pedicellariae appearing to be aboral to the ambulacral juvenile spines on AI and AIII (Figure 15a).

Tissue buds of new adult pedicellariae were visible on day three between the ambulacral juvenile spines and the lateral primary spines (all age references are to juveniles reared at 14°C). These new coronal pedicellariae formed in a pattern characteristic of *Strongylocentrotus franciscanus*. Viewed aborally and adradially, a single pedicellaria formed to the right of the ambulacral juvenile spines on AI, AII and AV. Two pedicellariae formed on AIII, lateral to each ambulacral juvenile spine, while no pedicellariae formed on AIV (Figure 15b, also 15c for origin of pedicellaria relative to spines). This arrangement of coronal pedicellariae was consistent on cohorts from two different sets of parents in the lab and on early juveniles collected from natural settlement (Chapter 1). This arrangement was different from the pattern of pedicellariae on *S. purpuratus* (described below) and provides another distinguishing character, in addition to presence of aboral pedicellariae, for species identification.

Calcification of the adult pedicellariae valves began at the distal end as three small spicules. By day six the three presumptive valves were separated by a triradiate cleft at the distal end (eg. Burke 1980). The adult pedicellariae were functional at 110-120 μm (base of stalk to distal tip of valves) and were 150 μm when fully developed. Functionality was tested by mechanical stimulation of pedicellariae in live juveniles, and the valves of functional pedicellariae were separated open in preserved material.

Sphaeridium formation was initiated on the center of each ambulacrum at day four, adoral to the single larval podia (Figure 15c). Calcification of the sphaeridia was apparent within one day after formation of the tissue bud and by day nine sphaeridia appeared fully calcified with a bulbous distal end (Figure 15e).

Additional podia began to form on day four, adoral to each ambulacral juvenile spine (one pair of podia per ambulacrum). A second pair of podia had formed adoral to the first pair by day eight. Between days ten and eleven, the single larval podia on the center of each ambulacrum was lost, by resorption. An ossicle that extended radially over the proximal end of the larval podia was apparent for several days after loss of this podia. Between this ossicle and the sphaeridium, a primary spine bud appeared on the center of each ambulacrum on day 12 (Figure 15d, also 15c for origin of new spines relative to other structures).

The plate covering the anus was open in some individuals by day six and was open in all individuals by day eight. The jaws of the lantern apparatus increased in length as they developed. By day eight, the distal ends of the lantern teeth were able to contact opposing teeth and the lantern apparatus became very active prior to the eruption of the teeth through the peristome. Teeth erupted in some individuals on day nine and by day ten 90% of individuals observed had jaws open through the peristome. Fecal pellets were excreted the first day that jaws opened, indicating the gut was complete at this time.

The madreporite is difficult to see in early juveniles, but is located on IA2, just counter-clockwise to and near the hinge of the anal plate (Figure 15d).

Strongylocentrotus purpuratus

The earliest stage of juvenile *Strongylocentrotus purpuratus* had four primary spines per interambulacrum, two tetraradiate juvenile spines and one oral podia per ambulacrum, and five to eight additional tetraradiate juvenile spines, located aborally (Figure 15b). There were no aboral pedicellariae, distinguishing this species from juvenile *S. franciscanus.*

Tissue buds of new adult pedicellariae were visible on day two between the ambulacral juvenile spines and lateral primary spines. These coronal pedicellariae formed in a symmetric pattern of two per ambulacrum, in contrast to the asymmetric pattern found in *S. franciscanus* (Figures 15c and 15d). The adult pedicellariae were functional at 110-120 μm and were 150 μm when fully developed.

Development of sphaeridia and the first ambulacral primary spines was similar to that found in *S. franciscanus* (Figures 15c and 15e).

By day seven, the anal plate was open in 90% of individuals observed, opposing lantern teeth first made contact, and the lantern apparatus was active. The lantern teeth first erupted through the peristome at day nine. Fecal pellets were excreted the first day lantern teeth emerged, indicating a complete gut.

Temperature Dependence of Juvenile Development

Juveniles reared at 14°C were initially classified into new stages each day because traits developed quickly. By ten days after metamorphosis, trait development slowed and new stages were assigned at two day intervals. Juveniles reared at 8°C and 11°C advanced through stages more slowly, but specific suites of traits (ie. stages) recognized at 14°C were still associated for juveniles raised at lower temperatures (Tables 2 and 3). The relationships between developmental stage and age for each temperature treatment were approximately linear (Figures 16a and 16b). Because of their linearity, ordinary least square regression equations for each correlation were calculated to determine the slope which represents the developmental rate as stage per day (Table 4).

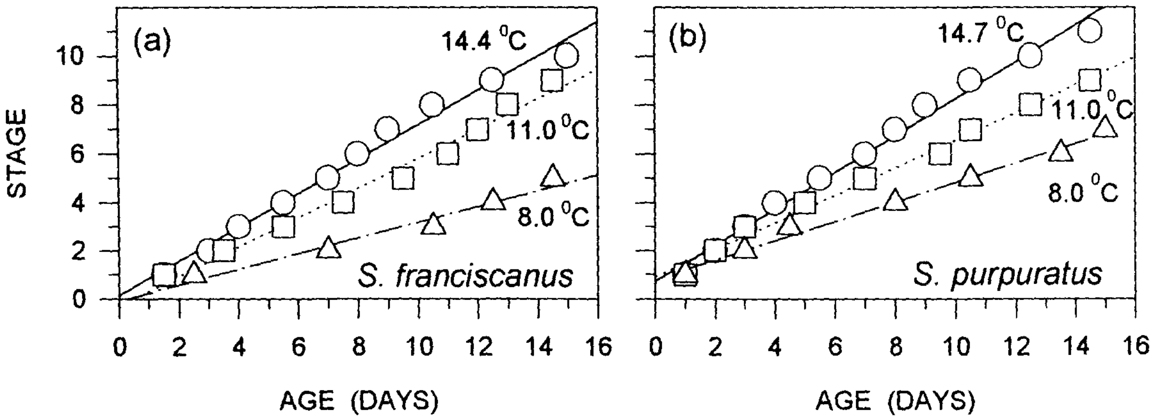

FIGURE 16. Relationship of developmental stage and age at three temperatures for *Strongylocentrotus franciscanus* (a) and *S. purpuratus* (b). For stages assigned to a range of days, an intermediate day (age) was used in the regression.

TABLE 2. Development Schedule of Juvenile *Strongylocentrotus franciscanus* at Three Temperatures.

STAGE	PEDICELLARIAE	SPHAERIDIAE	PRIMARY SPINES	ANAL PLATE	LANTERN / GUT	AGE (DAYS) AT 14.1°C	11°C	8°C
1	No tissue buds					1 - 2	1 - 2	1 - 4
2	Tissue buds 10-30μm, no calcification					3	3 - 4	5 - 9
3	Buds 20-40μm, >75% are <30μm, valve spicules in 30-40μm buds	Tissue buds 10-20μm, no calcification				4	5 - 6	10 - 11
4	Buds 20-70μm, <50% are >40μm, valves calcifying in buds >30μm, triradiate distal cleft in buds >40μm	Buds 10-50μm, >75% are <40μm, calcification in buds 20-50μm		Open in 25%		5 - 6	7 - 8	12 - 13
5	Buds 30-70μm, 50% at 50-70μm with partially calcified valves	40-60 μm		Open in 75 %		7	9 - 10	14+
6	Buds 40-100μm, >75% are >60μm, valves separated in > 75%	50-70 μm, distal end slightly bulbous		Open in > 90%	Teeth contact, lantern active in > 90%	8	11	
7	Buds 50-100μm, >75% are >70μm	60-80μm, distal end bulbous		Open in 100%	Jaws open thru peristome in 75%, excreting	9	12	
8	Buds 70-120μm, 25% are >110μm, functional at 110-120μm				Jaws open thru peristome in 90%	10 - 11	13	
9	Functional (>110μm) in 75% of individuals		Tissue buds 10-30μm		Jaws open in 100%	12 - 13	14+	
10	Functional in 100% (110-150μm)		Spines 30-100μm, 75% are <60μm			14+		

TABLE 3. Development Schedule of Juvenile *Strongylocentrotus purpuratus* at Three Temperatures.

STAGE	PEDICELLARIAE	SPHAERIDIAE	PRIMARY SPINES	ANAL PLATE	LANTERN/GUT	AGE (DAYS) AT		
						14.7°C	11°C	8°C
1	No tissue buds					1	1	1
2	Buds 10-50μm, 75% are <30μm, distal valve spicules in buds >30μm					2	2	2 - 4
3	Buds 20-50μm, 75% are >30μm, partially calcified valves in buds >30μm					3	3	3 - 6
4	Buds 30-50μm, 50% are >40μm, triradiate distal cleft in 40-50μm buds	Buds 10μm				4	4 - 6	7 - 9
5	Buds 30-70μm, 50% are >60μm, valves appear fully formed, calcified in buds > 60μm.	Buds 20-40μm, early calcification		Open in < 50%		5 - 6	6 - 8	9 - 12
6	Buds 60-120μm, 25% are > 100μm, functional at 110-120μm	Buds 20-60μm		Open in > 90%	Teeth contact, lantern active in 25%	7	9 - 10	13 - 14
7	Functional (>110μm) in 50% of individuals	Buds 40-70μm, 50% are >50um		Open in 100%	Teeth contact in 75%	8	10 - 11	14+
8	Functional in > 90%	Buds 50-70μm, 90% are > 60μm	Buds 10-20μm on ambulacra		Jaws open thru peristome in 25%	9	12 - 13	
9	Functional in > 95%, 140-150 μm at full size	60-80μm, distal end bulbous	Buds 20-80μm on ambulacra		Open thru peristome in > 90%, excreting	10 - 11	14+	
10	Functional in 100%		Spines 20-130μm, 75% are >60μm		Open in 100%	12 - 13		
11			75% are 100-250μm			14+		

TABLE 4. Regression equations for the relationship of developmental stage to age in juvenile *Strongylocentrotus franciscanus* and *S. purpuratus* reared at three temperatures. The coefficient of x represents the developmental rate expressed as stage day^{-1}.

Temperature (°C)	Regression Equation	
S. franciscanus		
14.4	$y = 0.7013x + 0.1699$	$r = 0.993$
11.0	$y = 0.6082x - 0.2706$	$r = 0.992$
8.0	$y = 0.3271x - 0.0743$	$r = 0.982$
S. purpuratus		
14.7	$y = 0.7867x + 0.6002$	$r = 0.995$
11.0	$y = 0.5659x + 0.9132$	$r = 0.995$
8.0	$y = 0.4018x + 0.8141$	$r = 0.995$

The sensitivity of developmental rate to temperature can be described with Q10 (the rate increase caused by a 10°C increase in temperature) and this value can then be used to predict a developmental rate at a temperature between those measured (Schmidt-Nielson 1975). Values for Q_{10} were calculated for the temperature ranges 8 - 11°C and 11 - 14.4°C for *Strongylocentrotus franciscanus*, and 8 - 11°C and 11 - 14.7°C for *S. purpuratus*, by the equation:

$Q_{10} = (R_2/R_1)^{10/(T2-T1)}$, where R = developmental rate (stage day^{-1}) at temperature (T)

The Q_{10} values were used to calculate developmental rates at 0.5°C intervals between 8 and 15°C (Table 5), by the equation:

$R_2 = R_1 * Q_{10}^{(T2-T1)/10}$, where $R_1 = 0.3271$, $Q_{10} = 7.9057$ at 8 - 11°C, and
$R_1 = 0.6082$, $Q_{10} = 1.5204$ at 11 - 14.4°C for
S. franciscanus
and
$R_1 = 0.4018$, $Q_{10} = 3.1315$ at 8 - 11°C, and
$R_1 = 0.5659$, $Q_{10} = 2.4361$ at 11 - 14.7°C for
S. purpuratus

Rates for each temperature interval (R_2) were calculated at the mid-point for each interval (eg. at 8.25°C for the interval 8.0 to 8.5°C).

TABLE 5. Developmental rates (stage day^{-1}) for age 1- 14 day *Strongylocentrotus franciscanus* and *S. purpuratus*.

Temperature Range (°C)	Developmental Rate (Stage Day $^{-1}$)	
	S. franciscanus	*S. purpuratus*
8.0 - 8.5	0.3444	0.4134
8.5 - 9.0	0.3822	0.4377
9.0 - 9.5	0.4236	0.4634
9.5 - 10.0	0.4697	0.4906
10.0 - 10.5	0.5208	0.5195
10.5 - 11.0	0.5776	0.5500
11.0 - 11.5	0.6146	0.5786
11.5 - 12.0	0.6276	0.6050
12.0 - 12.5	0.6409	0.6325
12.5 - 13.0	0.6545	0.6613
13.0 - 13.5	0.6683	0.6914
13.5 - 14.5	0.6825	0.7229
14.0 - 14.5	0.6969	0.7558
14.5 - 15.0	0.7117	0.7902

Age Determination for Field Sampled Juveniles

The estimated age of field-sampled juveniles was calculated from the sum of daily developmental rates (R) that correspond to the thermal history of the rearing environment. In practice, a juvenile of unknown age was assigned a stage number that best corresponded to the suite of juvenile traits in Tables 2 and 3. A table was prepared for the sample interval, with days of the interval in ascending order in one column and the mean water temperature of each day in a second column. In a third column, the daily developmental rates (from Table 5) that correspond to the mean temperature of each day were summed (each day added to the sum of previous days), starting with the most recent day of the sample interval. When the cumulative sum of developmental rates from the table was equal to the stage number assigned to the juvenile, the corresponding day from the table was the estimated age, or number of days since settlement.

Discussion

The feeding structures became functional in both species on a similar schedule, requiring at least nine days at 14.4 - 14.7°C and 12 days at 11°C. Juveniles underwent several morphological changes prior to feeding, including development of pedicellariae, adult podia, sphaeridia, feeding structures (lantern apparatus and gut system), and calcification of test plates. Because these traits appeared before feeding, the rate of development was not effected by juvenile feeding.

Development of these early juvenile traits was fueled by the energetic reserves acquired by the larva. Thus, developmental rate of early juveniles may be influenced by energetic reserves of settling larvae and by temperature. An assumption of the ageing method described here is that the energetic reserves in lab-reared larvae are similar to reserves in wild larvae, and early post-metamorphic development proceeds at a similar rate in juveniles from either source.

In addition to potential differences in energetic reserves between wild and lab-reared larvae, a second factor that may influence developmental rates is delay of metamorphosis. Highsmith and Emlet (1986) found that delayed metamorphosis in two echinoid species (the sand dollars *Dendraster excentricus* and *Echinarachnius parma*) reduced growth rate in juveniles. The rudiment in both species, including the lantern apparatus, continued to develop during extended competence. Development of the gut system in juvenile *Dendraster excentricus* requires at least seven days following settlement (Chia & Rice 1978). Thus, while some structures may continue to develop during extended competence, development of the gut system following metamorphosis determines the timing of juvenile feeding. Delay of metamorphosis may reduce lipid energy reserves and influence developmental rates in juveniles prior to feeding.

Because development of traits occurs prior to feeding by juveniles, sea urchins provide an opportunity to study early juvenile performance independent of effects from feeding following metamorphosis. Measures of juvenile performance, such as growth and survival, may be effected by pre-feeding developmental rates, which may in turn be effected by larval nutritional history and the energetic reserves at settlement.

Two factors that influenced the precision of age estimation by this method were variation in developmental rate and temperature. For a given species reared at a given temperature, individuals varied in their developmental rate, resulting in a longer time period (more than one day) for most individuals of a cohort to pass through some stages. Juveniles reared at colder temperatures proceeded through successive sets of traits (stages) more slowly, at greater than one day intervals. Thus, precision of age estimation by this method decreases as water temperature decreases and as juvenile age increases. The best age estimate of juvenile sea urchins sampled in the field requires temperature records that provide a thermal history of the immediate rearing environment.

With modification, this method could be applied to other taxa for which development occurs prior to juvenile feeding. When applied to sea urchins, this method may provide an additional tool for studies describing the link between physical oceanographic processes and recruitment dynamics (see Chapter I).

CHAPTER III

LARVAL ABUNDANCE AND EARLY JUVENILE RECRUITMENT OF ASTEROIDS AND HOLOTHUROIDS ON THE OREGON COAST

Introduction

Asteroids and holothuroids are conspicuous and ecologically important members of subtidal communities in the northeast Pacific and elsewhere. Asteroids are major predators within these communities (Menge 1982), while holothuroids primarily function as either filter feeders (eg. most dendrochirotes) or as deposit feeders (eg. aspidochirotes)(Massen 1982). Deposit feeding holothuroids turn over sediments, disturbing stratification and modifying the stability of sediments. Some burrowing, filter-feeding holothuroids (eg. some *Cucumaria* spp.) may transfer particles obtained from the water or water-sediment interface to the sediment. In subtidal communities of the northeast Pacific, holothuroids also serve as prey for asteroids (Mauzey *et al.* 1968).

Spawning seasons have been reported for many northeast Pacific asteroids and holothuroids, based on patterns of gametogenesis and observations of spawning in the laboratory and field. Peak spawning for most shallow (less than ~ 100 m depth) species with pelagic development occurs from March to August for asteroids (Strathmann 1987) and from March to July for holothuroids (McEuen 1986).

Larvae and early juvenile stages have been described for most of the shallow water taxa of holothuroids found from California to the Gulf of Alaska (Inaba 1930, Cameron 1985, McEuen 1986, McEuen & Chia 1991; geographic range of taxa from Morris *et al.* 1980, Lambert 1984). Larval feeding mode and development times for most shallow asteroid taxa from this same geographic range have been reported (Strathmann 1987), but detailed descriptions that permit identification of field-caught larvae are lacking for many species. Newly settled juveniles of many asteroids are also poorly described.

A limited number ecological studies on larval and early juvenile stages have been conducted for asteroids in the northeast Pacific (Greer 1962; Birkeland *et al.* 1971; Cameron 1983; Rumrill 1987, 1989; Sewell and Watson 1993) or in other temperate regions (Loosanoff 1964; Barker 1977, 1979; Barker & Nichols 1983). Very little work has been conducted on the ecology of larval and early juvenile stages of holothuroids with pelagic development (Young and Chia 1982). Recruitment of asteroids and holothuroids has been reviewed by Chia *et al.* (1984), Ebert (1983), and Young and McEuen (1984).

During 1994 and 1995, asteroid and holothuroid larval abundance in nearshore plankton and early juvenile recruitment was measured at two sites along the Oregon coast. These data were collected in conjunction with a study on larvae and recruitment of red and purple sea urchins (Chapter 1). Spatial and temporal patterns of larval abundance and recruitment of asteroids and holothuroids are described and compared with findings from sea urchins. Patterns of asteroid larval abundance and recruitment are used to support the hypothesis that brachiolariae of some species of asteroids are associated with cold water below the pycnocline and may be transported onshore during wind-forced upwelling.

Methods

Detailed descriptions of study sites, settlement collector design, and methods of plankton sampling and recruitment monitoring have been described previously (Chapter I). In summary, larval abundance in nearshore plankton and juvenile recruitment were measured at sites near Gregory Point and Port Orford along the southern Oregon coast. Sampling was conducted from late January to August in 1994, and from March to August in 1995. Plankton was sampled at approximately one week intervals in 1994. In 1995, plankton was sample at two week intervals at Port Orford and at two day intervals at Gregory Point. On each sample date, three replicate oblique tows were made from 0 to 5 m depth. Between 8 and 15 m^3 were sampled per tow. Abundance of asteroid brachiolariae larvae was measured in both years. Asteroid bipinnariae were not counted as the focus of the study was on late larval stages and their relationship to settlement. Holothuroid doliolariae (non-feeding) larvae were only counted in 1995. Vertical distribution of larvae was measured on two dates in March and one date in June, 1995. Plankton was sampled using a close-open-close mechanism to sample from discrete depths. Three replicate tows, sampling between 12 and 30 m^3 per tow, were made at each depth sampled. Settlement collectors were sampled at approximately two week intervals at both sites in both years. Water temperature was recorded on submersible data loggers at the same depths as the settlement collectors at each site.

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.

Because sample intervals varied, all juvenile data was adjusted to a "settlement rate" (number m^{-2} day^{-1}) and plotted on the day of sample.

Results

Larval Abundance

Occurrence of brachiolariae was generally synchronous between sites and between years (Figures 17a, 17b, 18a, 18b). All brachiolariae found were those of planktotrophic species (Table 1) and almost all were found from early June through July in both years. At Gregory Point in 1995, brachiolariae were also found in low abundance on three dates in late March and April.

In 1995, doliolariae of combined holothuroid species were found from March to late June at Gregory Point, and from May to early July at Port Orford (Figures 19 and 20). This group includes the doliolaria stage larvae of *Parastichopus* sp., which has feeding larvae (auricularia) that metamorphose into non-feeding doliolariae prior to settlement. All other taxa in this group have only non-feeding doliolaria larvae.

Orange-red larvae of *P. chitonoides* were found in June just prior to settlement of this species on collectors at Gregory Point (Figures 19 and 20). In addition to color, these larvae were identified by presence of three ciliated bands (McEuen & Chia 1991) and confirmed by metamorphosis of field-caught larvae in the lab (see Appendix).

Orange doliolariae were also found on March 25 and May 7, 1995, (two on each date) at Gregory Point. These larvae were not identified based on number of ciliated bands, but

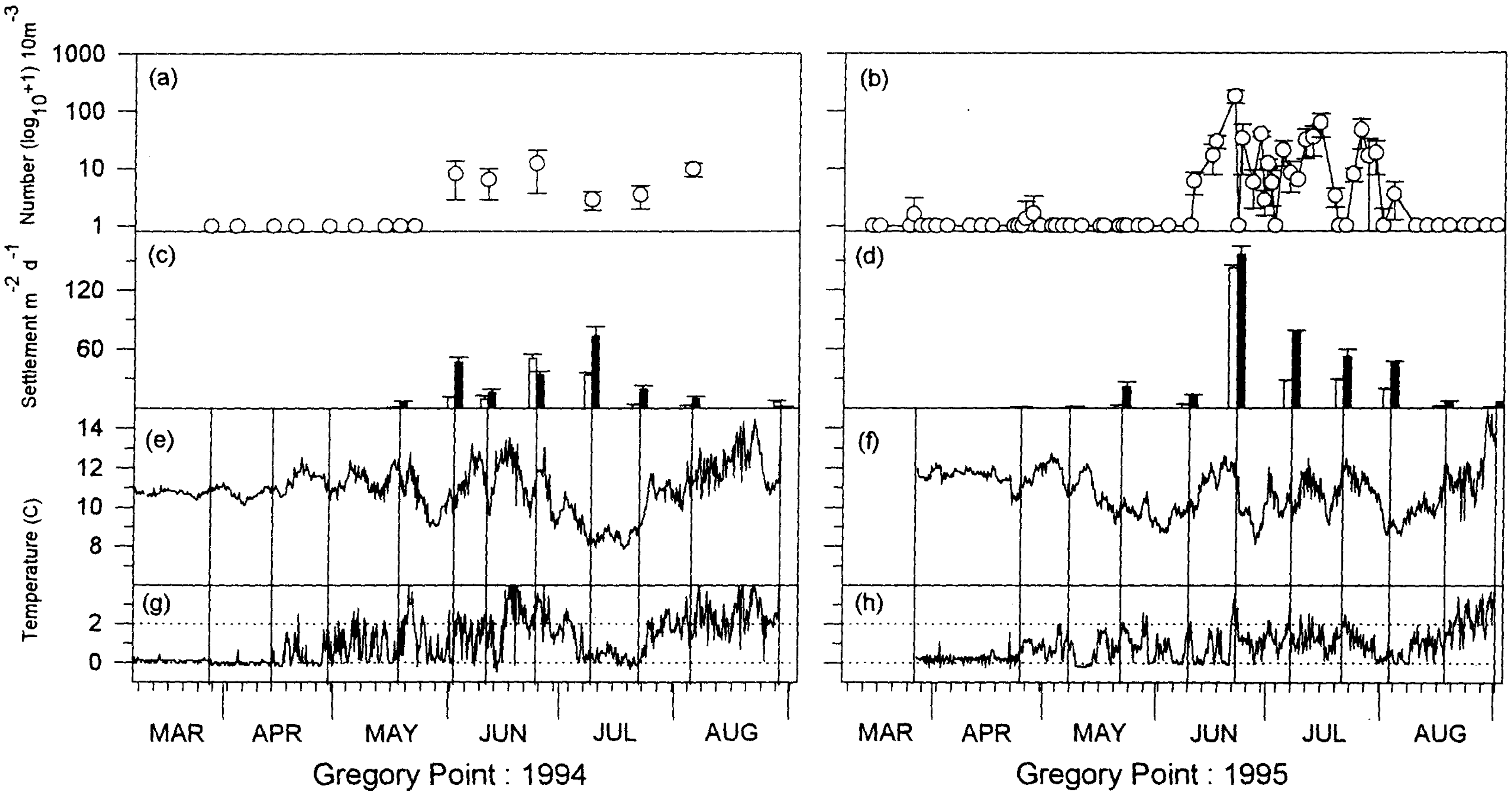

FIGURE 17. Mean larval abundance and settlement rates (± standard error) of brachiolariae, and sea temperature at Gregory Point in 1994 and 1995; 17a and 17b, larval abundance of brachiolariae in plankton; 17c and 17d, cumulative settlement (normalized for sample interval) on upper (clear bars) and lower (black bars) collectors for each sample period, and plotted on date of sample; 17e and 17f, sea surface temperature (4m depth). Vertical bars on temperature plots delineate settlement sampling periods; 17g and 17h, difference between surface and bottom (22m depth) temperature.

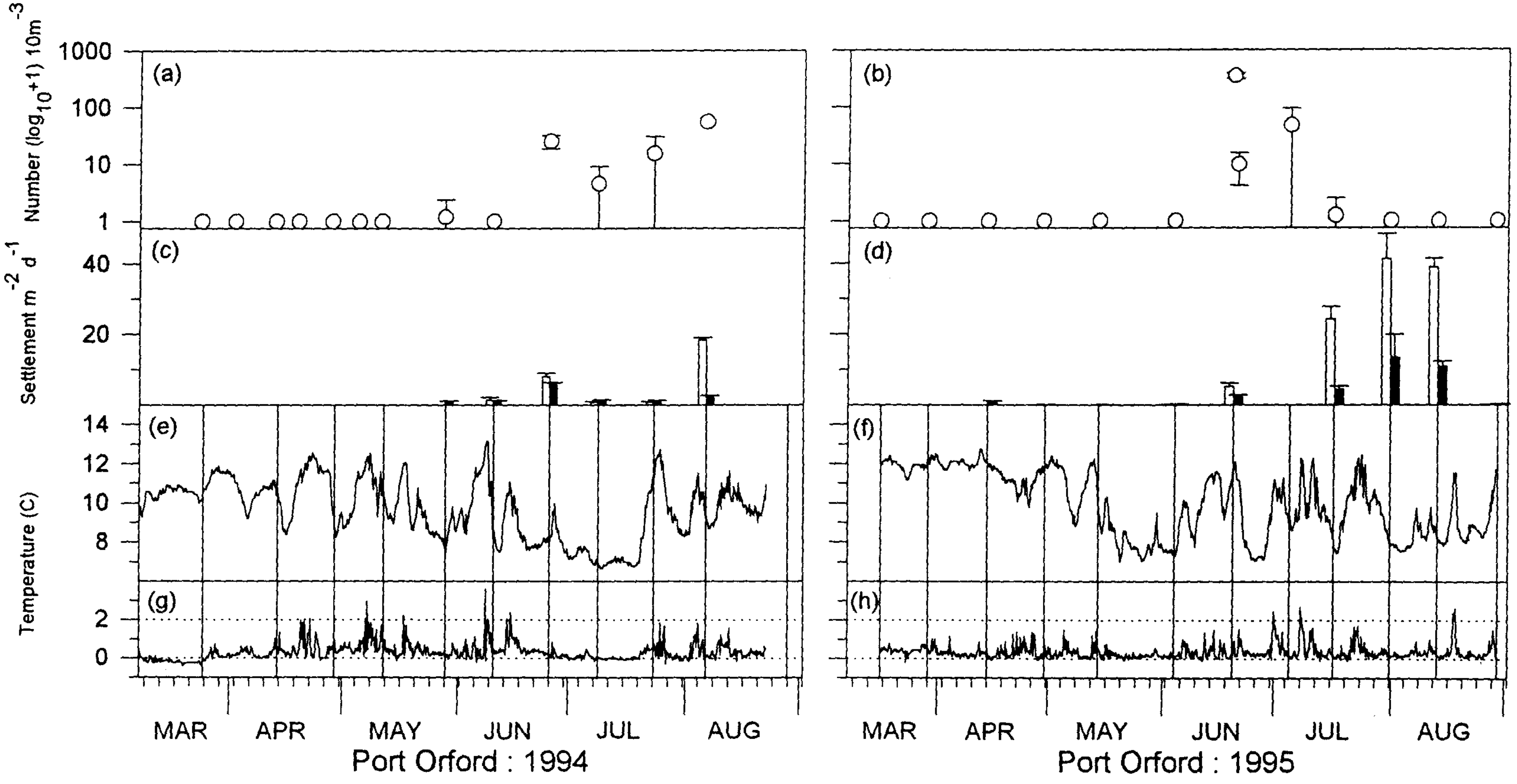

FIGURE 18. Mean larval abundance and settlement rates (± standard error) of brachiolariae, and sea temperature at Port Orford in 1994 and 1995; 18a and 18b, larval abundance of brachiolariae in plankton; 18c and 18d, cumulative settlement (normalized for sample interval) on upper (clear bars) and lower (black bars) collectors for each sample period, and plotted on date of sample; 18e and 18f, sea surface temperature (4m depth). Vertical bars on temperature plots delineate settlement sampling periods; 18g and 18h, difference between surface and bottom (18m depth) temperature.

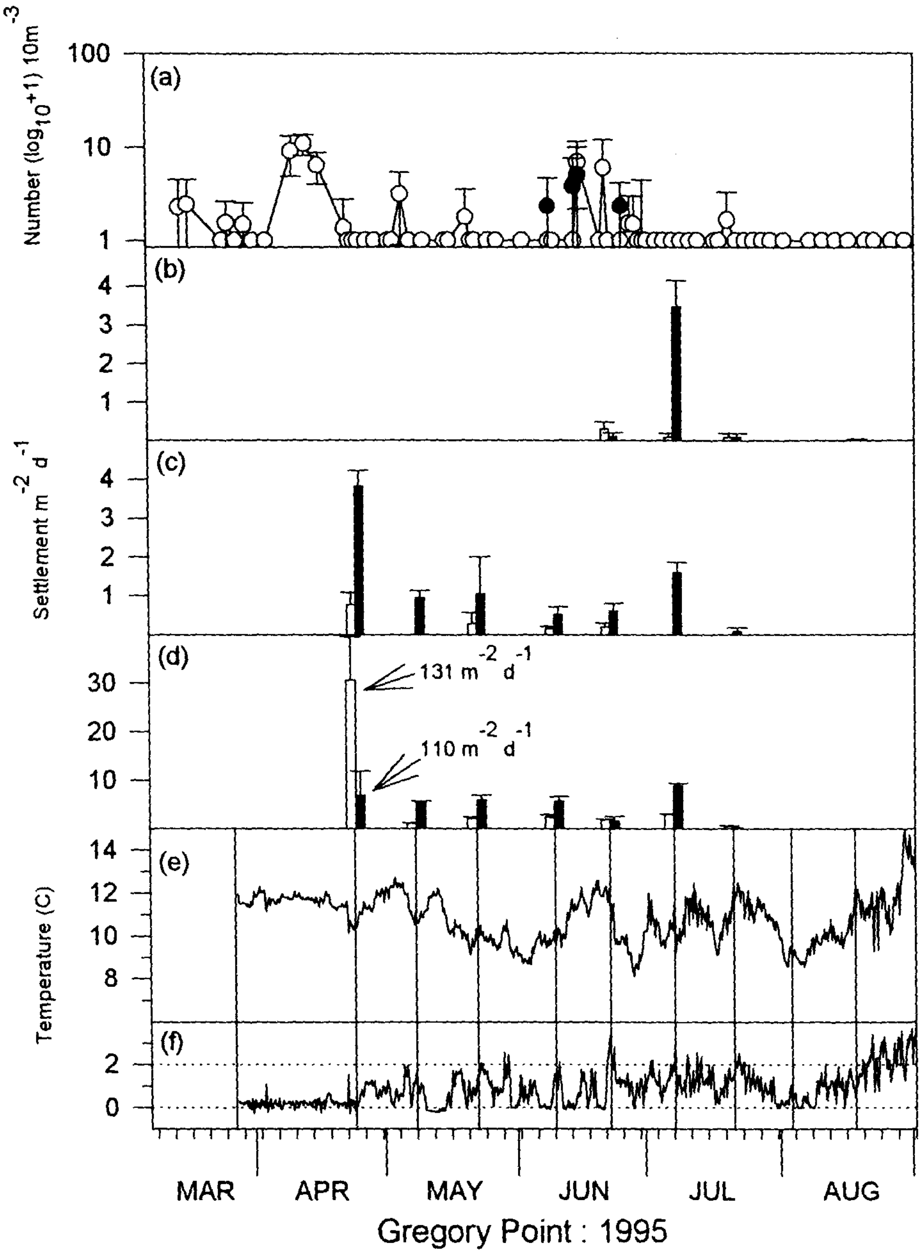

FIGURE 19. Mean larval abundance and settlement rates (± standard error) of holothuroids at Gregory Point in 1995; 19a, larval abundance of all species except *Psolus chitonoides* (clear circles) and *P. chitonoides* (black circles); 19b, cumulative settlement of *P. chitonoides*; 19c, cumulative settlement of *Parastichopus* sp; 19d, cumulative settlement of combined species. Cumulative settlement on upper (clear bars) and lower (black bars) collectors is normalized for each sample period and plotted on date of sample; 19e, sea surface temperature (4m depth). Vertical bars on temperature plots delineate settlement sampling periods; 19f, difference between surface and bottom (22 m depth) temperature.

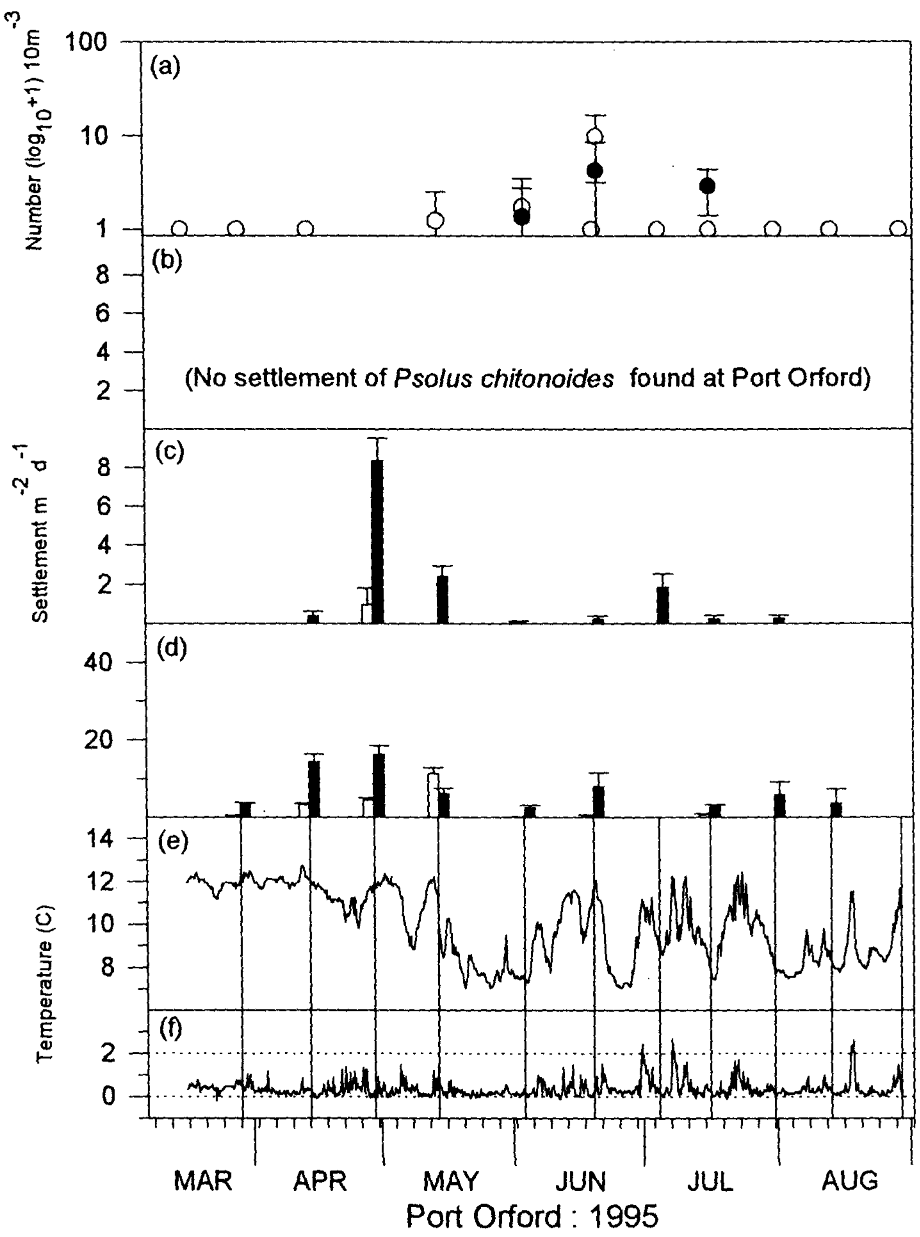

FIGURE 20. Mean larval abundance and settlement rates (± standard error) of holothuroids at Port Orford in 1995; 20a, larval abundance of all species except *Psolus chitonoides* (clear circles) and *P. chitonoides* (black circles); 20b, cumulative settlement of *Psolus chitonoides*; 20c, cumulative settlement of *Parastichopus* sp; 20d, cumulative settlement of combined species. Cumulative settlement on upper (clear bars) and lower (black bars) collectors is normalized for each sample period and plotted on date of sample; 20e, sea surface temperature (4m depth). Vertical bars on temperature plots delineate settlement sampling periods; 20f, difference between surface and bottom (18 m depth) temperature.

the occurrence of orange doliolariae in spring is consistent with the reported spawning period of February through May for *P. chitonoides* in Puget Sound (McEuen & Chia 1991). The auricularia stage larva of *Parastichopus californicus* was found on March 17 and 26, 1995, but this small, transparent larval stage was possibly overlooked in samples on other dates.

Table 6. Partial List of Asteroid Species with Pelagic Larval Development Found off Oregon

Species (Order)	Reported range	Source
Species with Feeding Larvae:		
Asterina miniata (Valvatida)	Sitka, Ak. to Baja California	1, 4
Dermasterias imbricata (Valvatida)	Prince William Sound, Ak. to Point Loma, Ca.	1, 4
Evasterias troschelii (Forcipulata)	Bering Sea, Ak. to Monterey Bay, Ca.	3, 4
Luidia foliolata (Platyasterida)	Southeast Alaska to San Diego, Ca.	1
Orthasterias koehleri (Forcipulata)	Yakutat Bay, Ak. to Channel Islands, Ca.	2, 4
Pisaster brevispinus (Forcipulata)	Sitka, Ak. to San Diego, Ca.	3, 4
Pisaster giganteus (Forcipulata)	Vancouver Island, B.C. to Baja California	3, 4
Pisaster ochraceus (Forcipulata)	Prince William Sound, Ak. to Santa Barbara, Ca.	3, 4
Pycnopodia helianthoides (Forcipulata)	Aluetian Islands, Ak. to San Diego, Ca.	3, 4
Stylasterias forreri (Forcipulata)	Southern Alaska to San Diego, Ca.	2
Species with Non-feeding Larvae:		
Crossaster papposus (Spinulosida)	Bering Sea, Ak. to Washington, (Oregon ?)	1
Henricia leviuscula (Spinulosida)	Aluetian Islands, Ak. to Baja California	1, 4
Hippasteria spinosa (Valvatida)	Kodiak Island, Ak. to southern California	1
Mediaster aequalis (Valvatida)	Alaskan Peninsula to Baja California	1
Solaster dawsoni (Spinulosida)	Aluetian Islands, Ak. to Monterey Bay, Ca.	1, 4
Solaster stimpsoni (Spinulosida)	Bering Sea, Ak. to Trinidad Head, Ca.	1, 4
Pteraster tesselatus (Spinulosida)	Bering Sea, Ak. to Oregon	1

Source: 1 - Fisher (1911), 2 - Fisher (1928), 3 - Fisher (1930), 4 - Morris *et al.* (1980)

Vertical Distribution

On March 26, brachiolariae were found at all depths samped (1, 10 and 15 m) in an 18 to 22 m depth water column, but were most abundant at 15 m (Figure 21). The water column was mixed on this date, with < 0.2°C difference between surface and bottom temperature. No brachiolariae were found in stratified samples collected on March 30. On June 20, brachiolariae were also found at all depths sampled (1, 5, 9 and 18 m) in a 30 m depth water column, but were slightly more abundant near the surface. The water column was weakly stratified, with 0.6°C colder water on the bottom. In addition to temperature, high densities of phytoplankton in strata near the surface on this date may have influenced distribution of these feeding larvae.

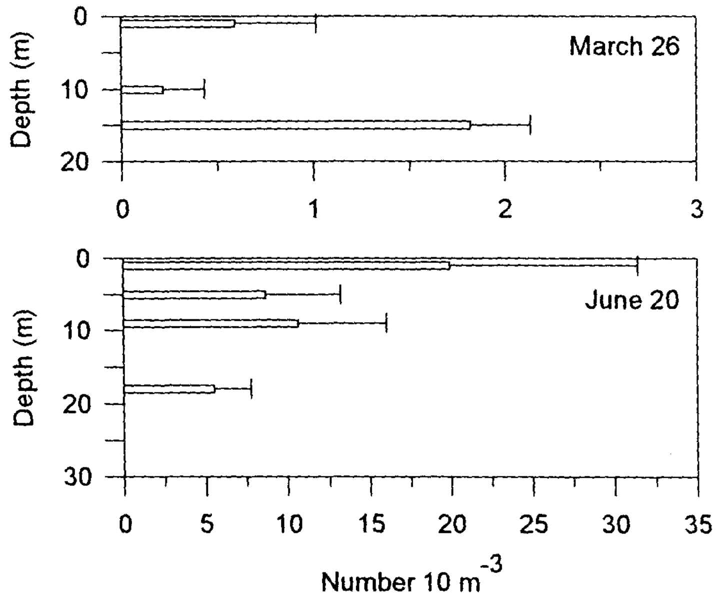

FIGURE 21. Vertical distribution (mean density ± standard error) of brachiolariae at Gregory Point (March 26) and Port Orford (June 20) in 1995. Depth of water column at Gregory Point was 18-22m, depth at Port Orford was 30m.

Doliolariae were distinctly stratified on both sample dates in March, with almost all larvae found at 15 m depth (Figure 22). The water column was mixed on both dates (< 0.2°C colder on bottom). On June 20, when the water column was slightly stratified, doliolariae were approximately three times more abundant at 10 m depth than at other depths sampled (1, 5, and 18 m) in a 30 m water column. All doliolariae found in stratified samples were shades of green, thus did not include red-orange larvae of *Psolus chitonoides* or brown-red larvae of *Paracaudina chilensis* (Inaba 1930).

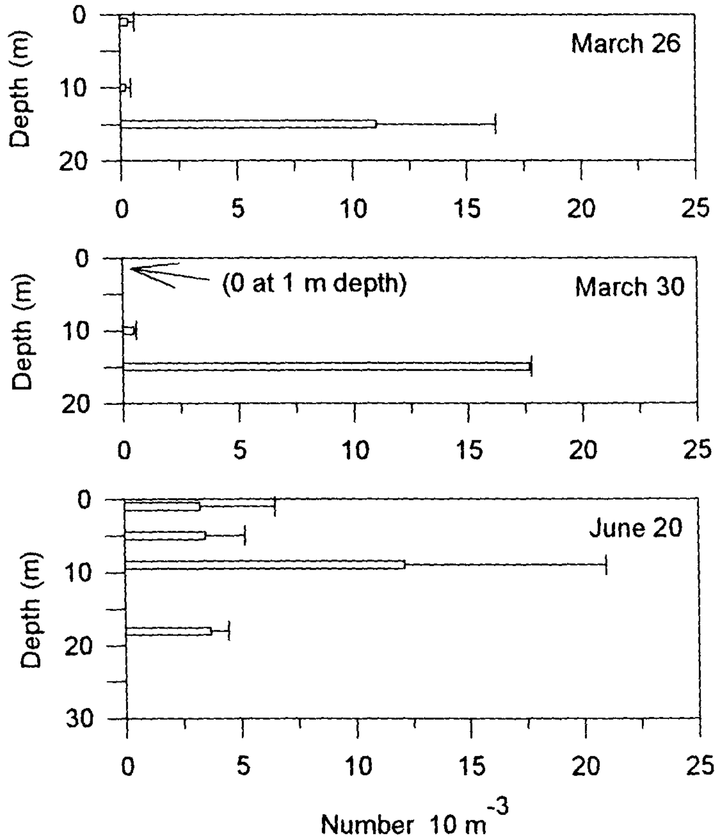

FIGURE 22. Vertical distribution (mean density ± standard error) of doliolariae at Gregory Point (March 26 and 30) and Port Orford (June 20) in 1995. Depth of water column at Gregory Point was 18-22m, depth at Port Orford was 30m

Patterns of Recruitment

Asteroids

Asteroid settlement generally coincided with occurrence of brachiolariae in both years, with most settlement occurring from late May to early August (Figures 17c, 17d, 18c, 18d). Temporal patterns of recruitment were similar at both sites, but the within-site patterns of recruitment between upper and lower collectors differed between sites. At Gregory Point, recruitment was higher on the collectors near the bottom on 75% and 100% of sample periods with asteroid settlement in 1994 and 1995, respectively. At Port Orford, recruitment was always higher on the upper collectors during periods of moderate to high recruitment (relative to other periods). The majority of juvenile recruits were of species with planktotrophic larvae. Juveniles from all species with non-feeding larvae (Table 6) were only found on the lower collectors at both sites in both years, but the numbers of settlers from these species were low and thus did not account for the higher recruitment on lower collectors at Gregory Point.

Almost all the juveniles from planktotrophic species found on settlement collectors formed a group that were morphologically similar, differing only in color of the internal pyloric caecum. One of these species was determined to be the forcipulate *Pycnopodia helianthoides* (see Appendix). Early post-metamorphic juveniles of forcipulate asteroids appear morphologically similar (B. Steele, Univ. of California (Santa Cruz), and M. Strathmann, Univ. of Washington (Friday Harbor), pers. comm.), thus it is likely most of the juveniles found on settlement collectors were from species within this Order.

Morphology and color of early post-metamorphic juveniles from this group were similar to juvenile rudiments found on several forms of brachiolariae in plankton samples. The three most common juvenile asteroids had red-orange, pale green, and pale orange pyloric caeca, respectively. Most brachiolariae also matched these same colors, with one form having transparent, red-orange tipped bipinnarial arms and a red-orange rudiment, a second form having pale green bipinnarial arms and rudiment, and a third form having pale orange bipinnarial arms and rudiment. It is likely some of these juveniles and larvae of the same color are the same species.

Juveniles and metamorphosing larvae of lecithrotrophic species were also found, including *Pteraster tesselatus*, *Henricia* sp., and *Solaster* sp. (R. Emlet, University of Oregon (OIMB, Charleston), pers. comm., also McEdward 1992). *P. tesselatus* settled on collectors in mid-June in both years, and orange-colored juveniles of *Henricia* sp. were found from June through August in 1994 and from May to mid-July in 1995 (Table 7). Pale green-colored juveniles of *Solaster* sp. were found in June and August in 1994 and in June and July in 1995. Early juveniles of *S. dawsoni* and *S. stimpsoni* are shades of green (R. Stathmann, Univ. of Washington (Friday Harbor), pers. comm.), while juveniles of *S. endeca* are orange at settlement (R. Emlet, pers. comm.). *S. endeca* is not reported south of Washington, thus the green juveniles of *Solaster* are likely *S. dawsoni* or *S. stimpsoni*. Adults of both species of *Solaster* are locally common (B. Miller, pers. obs.).

Holothuroids

Combined species of holothuroids settled primarily from early April to late June in

1994 (Figures 23 and 24), and from March to August in 1995 (Figures 19 and 20). At least four species settled on collectors, including *Cucumaria* sp. (probably *C. miniata*), *Eupentacta quinquesemita*, *Parastichopus* sp., and *Psolus chitonoides* (see Appendix 1). Juvenile *Psolus chitonoides* and *Parastichopus* sp. were distinguished from other holothuroid species in 1995. *P. chitonoides* settled from mid June to mid July at Gregory Point, but none were found at Port Orford (Figure 19b). Settlement of *Parastichopus* sp. coincided with settlement of other holothuroid species at each site (Figures 19 and 20). Recruitment on most sample dates was higher on the collectors near the bottom at both sites. During peak recruitment events (for combined species) at Port Orford in 1994 and Gregory Point in 1995, recruitment was similar on both upper and lower collectors.

Table 7. Dates and Number of Recruits of Asteroid Species with Non-feeding Larvae on Settlement Collectors at Gregory Point and Port Orford in 1994 and 1995.

	Date (Number) Found			
Species	Gregory Point		Port Orford	
	1994	1995	1994	1995
Henricia sp.	June 24 (1)	May 8 (1)	June 25 (13)	July 16 (3)
	July 9 (1)	July 7 (3)	July 8 (2)	
	Aug 5 (1)	July 16 (3)	Aug 6 (3)	
	Aug 29 (5)			
Pteraster tesselatus	June 24 (1)	June 22 (2)	June 25 (13)	
Solaster sp.			June 25 (15)	June 19 (12)
			Aug 28 (2)	July 4 (4)
				July 16 (1)

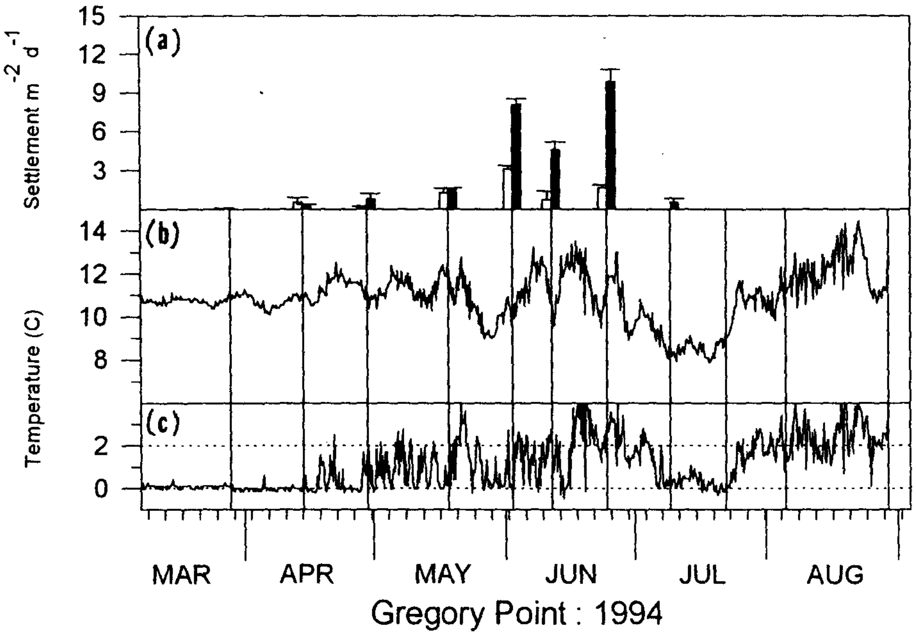

FIGURE 23. Settlement rates (± standard error) of holothuroids at Gregory Point in 1994; 23a, cumulative settlement (normalized for sample interval) on upper (clear bars) and lower (black bars) collectors for each sample period and plotted on date of sample; 23b, sea surface temperature (4m depth). Vertical bars on temperature plots delineate settlement sampling periods; 23c, difference between surface and bottom (22 m depth) temperature.

Discussion

Patterns of Larval Abundance

Asteroids

Planktotrophic larvae of northeast Pacific asteroids (see Table 6) are planktonic for extended periods, generally ranging from seven weeks to seven months (Strathmann 1978, Strathmann 1987). During this time, alongshore currents may transport larvae hundreds of kilometers from their source (Scheltema 1986). Brachiolariae occurred in nearshore

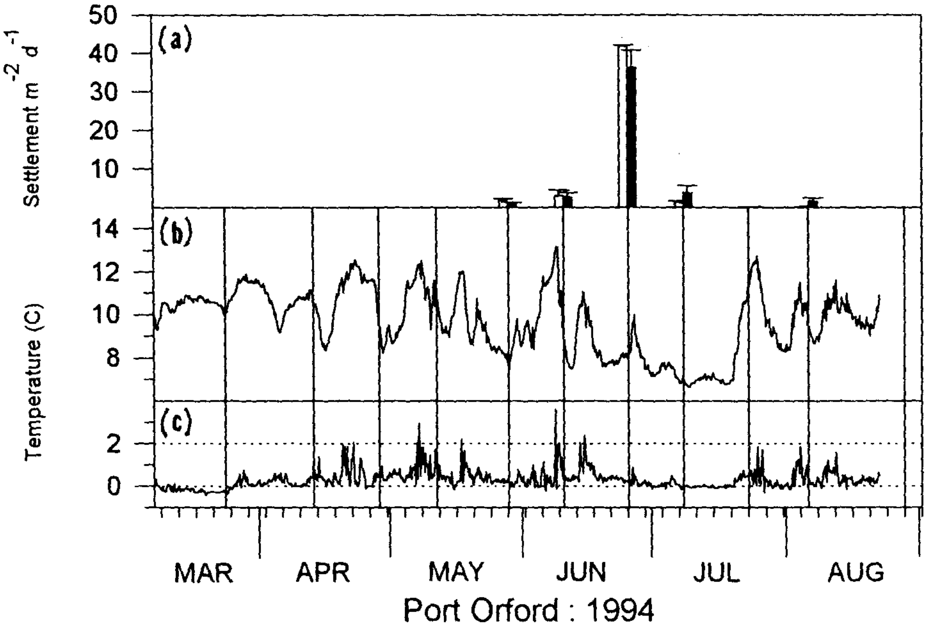

FIGURE 24. Settlement rates (± standard error) of holothuroids at Port Orford in 1994; 24a, cumulative settlement (normalized for sample interval) on upper (clear bars) and lower (black bars) collectors for each sample period and plotted on date of sample; 24b, sea surface temperature (4m depth). Vertical bars on temperature plots delineate settlement sampling periods; 24c, difference between surface and bottom (18 m depth) temperature.

plankton primarily during June and July in both 1994 and 1995. Predominant alongshore currents are from the north during summer, suggesting a larval source to the north (see discussion of nearshore hydrodynamics in Chapter 1). Because asteroid larvae are planktonic for such an extended period, and are able to delay metamorphosis (Strathmann 1987), it is also possible that currents from the north may carry larvae derived locally or from sources to the south that were transported north earlier in spring or late winter. The potentially broad range of larval source suggests that the brachiolariae sampled in plankton and settled juveniles may include species whose principal range may be north or south of Oregon.

Although species with non-feeding larvae also settled on collectors, no larvae of these species were found in plankton samples. Species found included *Pteraster tesselatus*, one or more species of *Henricia*, and possibly species of *Solaster*. Larvae of *P. tesselatus* require ~ 25 days to complete metamorphosis at 10 - 13°C, *Henricia* sp. may require four to six weeks at 10°C, and *Solaster stimpsoni* requires ~ 38 days at 9 - 10°C (Strathmann 1987). However, settlement generally occurs prior to completion of metamophosis (eg. in eight to ten days for *Solaster* sp., Carson 1988). Non-feeding larvae that are planktonic for only two to three weeks will presumably not be transported alongshore as far as feeding larvae with a longer planktonic period. If this is true, species with non-feeding larvae may be more likely to contribute to recruitment closer to the parent populations than species with feeding larvae.

Holothuroids

The majority of shallow water holothuroids found off Oregon have non-feeding larvae (Inaba 1930, McEuen 1986). These taxa include four species of dendrochirotids (*Cucumaria miniata, C. piperata, Eupentacta quinquesemita*, and *Psolus chitonoides*) and the apodid *Paracaudina chilensis* (Morris *et al.* 1980). Development in the plankton is rapid, ranging from six to 13 days to settlement. Eggs and early larval stages have yolk reserves with low specific gravity at the anterior end and are positively bouyant, but older larvae may be slightly negative or neutral (McEuen 1986). Development of transverse ciliated bands or uniform ciliation permit older larvae to regulate depth. The relatively high density of doliolariae found at 15 m depth compared to shallower depths (in non-stratified water, Figure 22) suggests these ciliated swimmers are capable of stratifying in open ocean conditions.

The only local holothuroids with feeding larvae are in the aspidochirote genus *Parastichopus*. Adults of *P. californicus* are common nearshore, but *P. parvimensis* and *P. leukothele* may also be found along the Oregon coast (Lambert 1986, Morris *et al.* 1980). *P. californicus* has an early feeding auricularia stage larva but metamorphoses to a non-feeding doliolaria larva before settling at ~ 60 days (Smiley 1986, Strathmann 1987). This genus is characterized by the presense of "table ossicles" on the external surface of both juveniles and adults (Lambert 1986). Juveniles with table ossicles were found on settlement collectors from April through July in 1995. These juveniles were assumed to be of the genus *Parastichopus*.

Patterns of Recruitment

Asteroids and holothuroids settled at much higher densities than sea urchins at each study site (see Chapter I). Few urchins settled at either site in 1994. In 1995, most urchin settlement occurred during a two week sample interval in mid-June, at mean rates of 14.3 *S. franciscanus* and 7.5 *S. purpuratus* m^{-2} day^{-1}. In contrast, asteroids settled as high as 73 and 156 m^{-2} day^{-1} in 1994 and 1995, respectively. Holothuroids settled as high as 42 and 131 m^{-2} day^{-1} in 1994 and 1995, respectively.

Asteroids and holothuroids recruited regularly throughout the period of larval occurrence. During the summer upwelling season, highest recruitment in both groups generally occurred during sample intervals that included one or more periods of relaxation from upwelling, as indicated by an increase in temperature. However, some recruitment also occurred during intervals dominated by upwelling and cold water (eg. Figures 17e, 18e, and 18f for asteroids, and 19b, 20b, and 24e for holothuroids). Regular recruitment in these groups contrasts with the patterns of recruitment observed for sea urchins. Sea urchin recruitment was variable between sites and between years (Chapter I). Recruitment was linked to warm water events based on the estimated age of juveniles on the sample date and inferred settlement dates. No settlement occurred during periods dominated by upwelling or during many events of increased water temperature signalling relaxation from upwelling. Few sea urchin larvae were found in water colder than 10°C.

It was not possible to link asteroid and holothuroid settlement to specific events within sample intervals that included both upwelling and relaxation events, thus temporal and within-site vertical settlement patterns are not directly comparable to those found for sea urchins. However, the regular recruitment of asteroids and holothuroids compared to sea urchins suggest that these groups may recruit by different mechanisms.

Highest abundance of brachiolariae was found in water between 10 and 12°C, but these larvae were also abundant in water between 8 and 10°C, and were found in water as low as 6.8°C at Port Orford (Figure 25). Doliolariae were most abundant in water between 11 and 12°C, primarily due to the prevalence of these larvae in spring when water temperature was relatively warm. Samples collected later in summer indicated that holothuroid larvae were also present at low densities in water between 7 and 10°C (Figure 26). Water temperatures below 10°C during summer reflect upwelling, thus larvae of both asteroids and holothuroids were present during periods of upwelling.

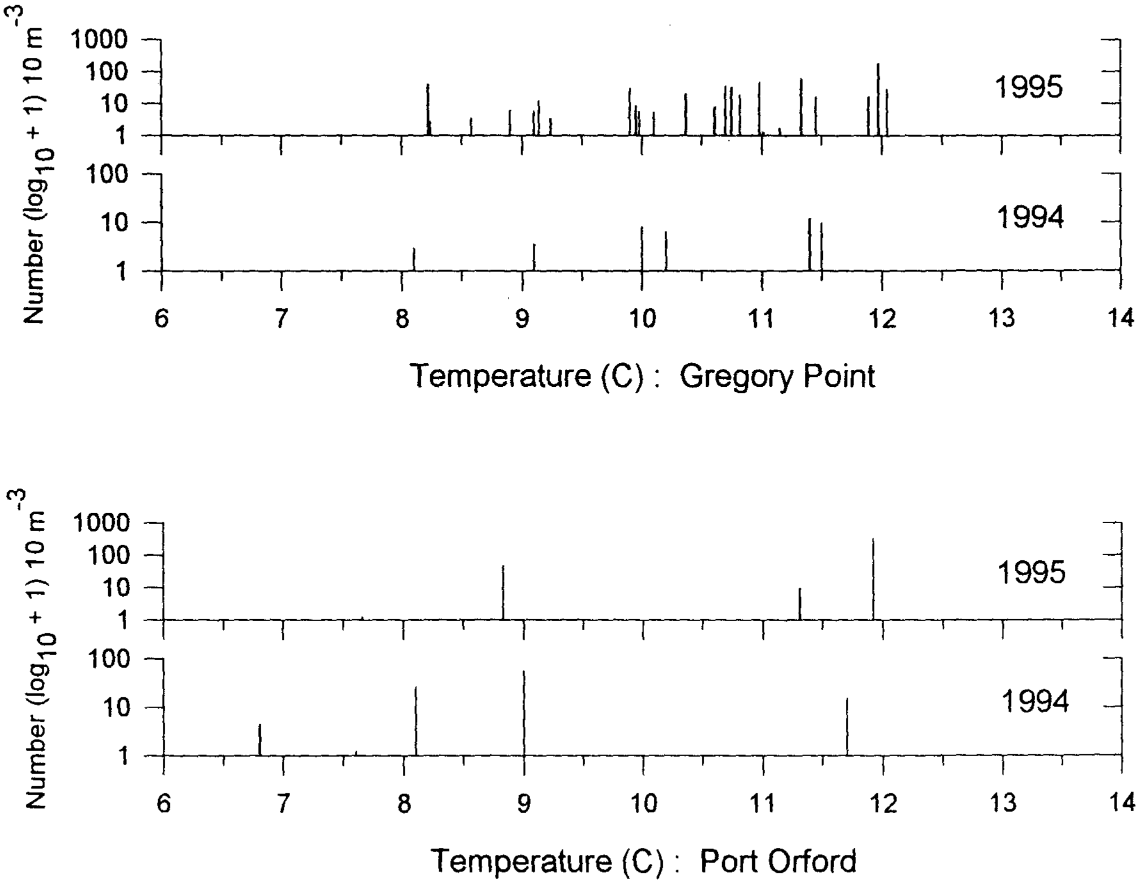

FIGURE 25. Surface temperature (4m depth) of water mass in which brachiolariae were found in nearshore plankton at Gregory Point and Port Orford in 1994 and 1995. Larval densities are plotted on log scale.

The occurrence of brachiolariae in cold water and the within-site and between-site patterns of asteroid recruitment provide limited evidence that brachiolariae of some species of asteroids may be associated with cold water and possibly recruit in association with onshore transport of upwelled water. At Gregory Point, settlement of planktotrophic species was higher on the lower collectors during most intervals, while at Port Orford, settlement was higher on the upper collectors. The major physical differences between sites were the degree of water column stratification and the influence of upwelling. At

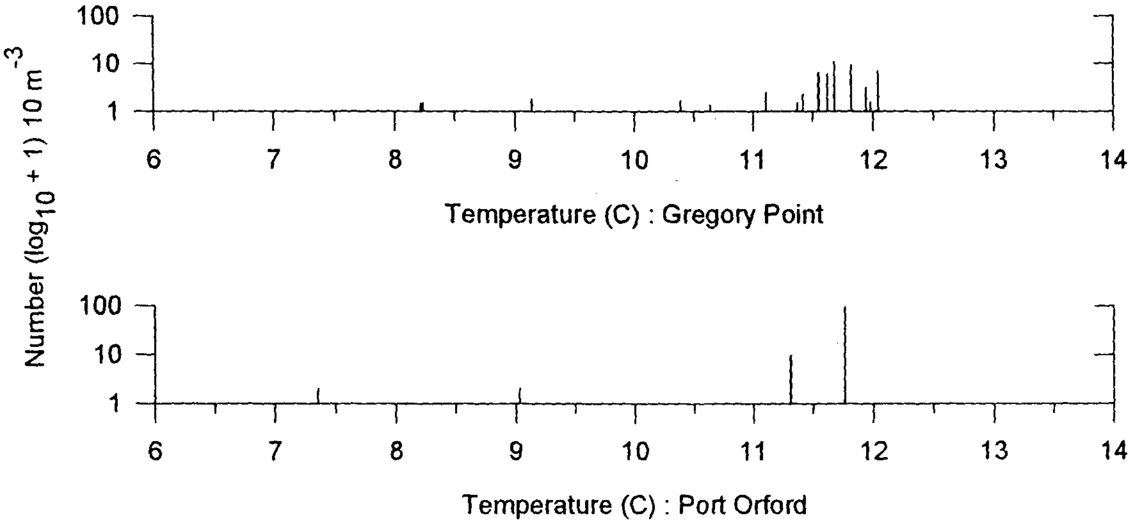

FIGURE 26. Surface temperature (4m depth) of water mass in which doliolariae were found in nearshore plankton at Gregory Point and Port Orford in 1995. Larval densities are plotted on log scale.

Gregory Point, the bottom was generally 1 - 2 °C colder than the surface during most upwelling and relaxation events. At Port Orford, the water temperature was 1 - 2°C colder than Gregory Point during upwelling and the water column was weakly stratified, with colder water at all depths during upwelling (Figures 1g, 1h, 2g, 2h). The higher recruitment on the lower collectors at Gregory Point may be due to the strong stratification and not due to larvae preferentially settling in deeper water, evident by the consistently higher recruitment on upper collectors within a weakly stratified water column at Port Orford. These patterns suggest some species may be associated with colder water and settle within the colder water mass.

Asteroid species with non-feeding larvae were never found in plankton samples (0- 5 m depth) or on the upper collectors at either site. The low number of recruits of these species on settlement collectors may reflect their relative rarity in the plankton, explaining their absence in plankton samples. An alternative explanation, consistent with the observed settlement patterns, is that larvae of these species were associated with deeper, colder water and thus not sampled in near-surface plankton tows.

At least three mechanisms may explain the occurrence of brachiolariae and settlement during the active phase of upwelling, including 1) larvae of some asteroid species are associated with colder water and are transported onshore during upwelling, 2) larvae within parcels of warm nearshore surface water become trapped against the coast during onset of upwelling and subsequently mixed into colder upwelled water, and 3) larvae are able to persist nearshore during the transition from a warm water phase to upwelling, perhaps by a behavioral response.

If brachiolariae of some asteroids (both feeding and non-feeding) are associated with colder water, this suggests a possible mechanism for onshore transport of larvae. During the spring and summer period of mean southward wind stress, 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 water off Oregon is less than 20 m deep and upwelled water comes from mid-depths of 20 - 80 m (Moores et al. 1976, Smith 1981). Peterson *et al.* (1979) proposed a two-cell model of nearshore circulation to explain the nearshore persistence of some copepod and cladoceran species during upwelling. Peterson *et al.* hypothesized that the offshore directed layer of surface water during upwelling is shallow, no more than 5 m depth. The seaward surface flow is balanced by onshore flow from the upwelling divergence at about 10 m depth. Plankton populations within this nearshore cell are maintained inshore of the upwelling front by maintaining maximum abundance below 5 m depth, within the deeper, colder layer. While some physical studies support this model of nearshore upwelling circulation (Stevenson *et al.* 1974, Huyer 1976, Moores *et al.* 1976), the evidence for this model is equivocal (Halpern 1976, Brink 1983).

Although nearshore upwelling circulation is not clearly understood, the predictable onshore movement of cold water during upwelling provides a possible mechanism for onshore movement of larvae. The larval period for asteroids falls within the upwelling season in the northern portion of the California Current System. Stratification of asteroid larvae in colder water below the pycnocline, or a behavioral response by competent brachiolariae to move into slightly deeper, colder water could both facilitate onshore transport during upwelling. However, there is no empirical data to support an ontogenetic migration of asteroid larvae from warmer surface water to deeper layers, and there is little data on vertical distribution of asteroid larvae. Brachiolariae were distributed throughout the upper 15 to 18 m on both dates these larvae were found in stratified plankton samples from Gregory Point and Port Orford, but distribution below 18 m or below a distinct pycnocline was not determined. In Barkley Sound, British Columbia, Rumrill (1987) found brachiolariae were most abundant between 0 and 30 m depth, compared to 30 to 60 m, or 60 to 90 m depth, but distribution relative to a pycnocline was also not determined.

The hypotheses that brachiolariae of some species of asteroids are associated with colder water below the pycnocline could be tested by measuring vertical distribution of larvae within a stratified water column. Stratified sampling in relation to an upwelling front may also test whether larvae reside within the upwelled water on the shoreward side of the front, as well as colder water beneath surface water on the offshore side of the front.

Several species of asteroid larvae and settled juveniles were found at each study site. It is likely that vertical distribution of competent larvae and settlement behavior varies between species according to the habitat requirements of juveniles or adults. The observed patterns of recruitment reflect the range of larval behaviors for these species and the interaction of those behavioral traits with a range of physical transport processes. In order to link transport processes to distribution and recruitment of individual species, descriptive studies are also needed to permit identification of field caught larvae and juveniles.

Summary of Findings and Conclusions

Occurrence of brachiolariae and doliolariae coincided with settlement in both years and both study sites. Brachiolariae were found over a broad range of water temperatures, from 7 to 12°C, but were most abundant between 10 and 12°C. Doliolariae were most abundant between 11 and 12°C, but were also found at low abundance in colder water.

Spatial and temporal recruitment patterns of brachiolariae were synchronous between sites and years. Recruitment of asteroids was higher on collectors near the bottom at Gregory Point, where the water column was more stratified than at Port Orford. Recruitment was higher on the upper collectors at Port Orford, where water was 1-2°C colder during upwelling and was weakly stratified.

In 1995, holothuroid larvae settled over a longer period than in 1994. Settlement was higher on collectors near the bottom during most intervals, but was similar in both strata during peak settlement events.

Recruitment of both asteroids and holothuroids occurred regularly throughout the period of larval occurence, including sample intervals dominated by upwelling. This suggests that some species of asteroid and holothuroid larvae may recruit by different mechansims than those controlling sea urchin recruitment. Larval and settlement patterns provide limited evidence for the hypothesis that larvae of some species are associated with colder water below the pycnocline and may be transported onshore in deeper strata during upwelling.

APPENDIX

NATURAL HISTORY NOTES ON LAB-REARED JUVENILE ASTEROIDS AND HOLOTHUROIDS

General Introduction

In 1995, live larvae and juveniles of asteroids and holothuroids were periodically removed from plankton samples and settlement collectors at Gregory Point and Port Orford (see sampling methods in Chapter 1). An attempt was made to rear these larvae and juveniles in the lab to facilitate species identification, measure growth, and observe behavior. These notes provide a summary of natural history observations complementary to results presented in Chapters 1 and 3. These efforts were incidental to the primary focus of field and other laboratory studies, therefore many of the notes in this section are based on intermittent and short-term observations.

Methods and Results

Asteroid Brachiolariae and Juveniles

One of the more common forms of brachiolariae found in plankton at both sites had long, transparent bipinnarial arms with red-orange tips, and a juvenile rudiment that varied from orange to red-orange in color (Figure 27a). One larva of this form with a red-orange rudiment was removed from Gregory Point plankton on June 21 and placed in a glass beaker. This larva had metamorphosed by the following day. At one day post-metamorphosis, arm length (AL) was 440 μm (arm length was measured as distance from arm-tip to the center of the disc). The pyloric caecum was the same red-orange color as found in the juvenile rudiment of the larva . This juvenile had four terminal spines on each arm, a single, round porous ossicle associated with six spines located aborally on each arm, a single, round ossicle with three spines located aborally on each interradius, and a single round aboral ossicle with one spine in the center of the disc (Figure 27b). This juvenile was offered prey (see below for methods) but did not survive beyond two weeks.

On June 29, three forms of brachiolariae were removed from plankton at Gregory Point. These included six individuals of the form with red-orange tipped arms described above, nine individuals with pale green bipinnarial arms and a pale green rudiment, and three individuals with pale orange bipinnarial arms and an orange rudiment (Figure 27). All of these larvae were precompetent. Each larval form was reared in separate one liter beakers and fed a mixture of *Rhodomonas lens* and *Chaetocerous gracilis* at a cell density of ~ 5 x 10^3 ml^{-1}. Larvae were pippeted to clean beakers and water at four day intervals. After five weeks, most larvae had settled on small rocks encrusted with coralline algae that had been placed in each beaker. Although larvae had settled and the bipinnarial arms were lost, metamorphosis was not complete by six weeks (one week after settling) and all larvae gradually perished.

Several attempts were made to rear juvenile asteroids sampled from settlement collectors at each site. Most of the juveniles that settled on collectors were morphologically similar, varying only in the color of the pyloric caeca. The pattern of ossicles on these juveniles was the same as that described above for the single juvenile metamorphosed in the lab. The three most common juveniles had red-orange, pale orange, and pale green pyloric caeca, respectively. Combined juveniles in this group collected June 25 at Gregory Point had a mean size of 410 μm AL (n = 20, range = 315 - 450 μm; maximum age 14 days). Fifteen juveniles of each color (pale green, pale orange, and red-orange) were collected July 7 at Gregory Point and sorted, by color, into flow-thru containers with small samples of macroalgae (primarily *Neorhodomela larix*, *Odonthalia floccosa*, and *Plocamium* sp.) collected from tidepools. Epiphytes on the algae were offered as potential prey for juvenile asteroids and included juvenile snails, bivalves, barnacles, hydroids, and bryozoans. All pale green or pale orange juveniles perished within three weeks after sampling. Eleven red-orange juveniles survived during the first two weeks after sampling (Figure 27c). These juveniles were observed to feed on partially crushed juvenile snails (*Lacuna* sp.,) and mussels (< 1 mm prey size) placed in the containers. By the third week after sampling, these juveniles captured and preyed upon juvenile snails and mussels. By 46 days after the sample date (age 47 - 61 days post-settlement), all eleven juveniles had developed a sixth arm bud, indicating this species was *Pycnopodia helianthoides*. Juveniles were 2.10 mm mean AL (range = 1.53 - 2.55 mm) when the sixth arm formed. In all 11 juveniles the sixth arm formed on the interradius of the madreporite. At 63 days after sampling, juveniles were 3.65 mm mean AL (n=6). The three largest (3.85 - 4.62 mm AL) had buds for arms 7 and 8 on the interradii adjacent to the sixth arm. By 99 days after sampling (5 - 6 mm AL), arms 9 and 10 were forming adjacent to arms 7 and 8, on the interradii between arms 7 and 8 and the primary juvenile arms (not adjacent to arm 6).

At three months (5 - 6 mm AL), *Pycnopodia helianthoides* also fed on lab-reared juvenile sea urchins (*Strongylocentrotus purpuratus* and *S. franciscanus*) at 1 - 3 mm test diameter. One juvenile *P. helianthoides* (age 70 day after sampling, 5.4 mm AL) was placed in a separate bowl to observe feeding behavior on sea urchins. In a 24 hour period, two of three sea urchins placed in the bowl were preyed upon (*S. franciscanus* at 1.4 and 0.8 mm test diameter), while the third sea urchin (*S. purpuratus* at 1.2 mm) had crawled out of the water to escape and dessicated. Three *S. purpuratus* (2.4, 2.1, and 2.0 mm) and two *S. franciscanus* (0.9 and 0.8 mm) were then placed in the bowl. The juvenile *S. purpuratus* appeared to have an escape response at this size, fleeing rapidly (relatively) upon contact with the juvenile *P. helianthoides*. The behavioral response *S. franciscanus* to contact with *P. helianthoides* was not observed. During the next 24 hours, all five sea urchins were preyed upon. Five *S. purpuratus* (2.0 - 2.9 mm) were then placed in the bowl. Predation on two of these sea urchins was observed. One individual was attacked, consumed and the empty test released in six hours. The second individual was consumed in five hours. All five were consumed within 48 hours of introduction to the bowl. The discarded sea urchin tests were unbroken, but the apical plates were free from the test and mixed with the lantern parts and spines around the discarded test.

Two juvenile *Henricia* sp. were sampled from settlement collectors on July 16, 1995. Both orange-colored juveniles still had brachiolar arms when sampled, but seven days later the brachiolar arms were resorbed. Seven days after sampling, arm length of individuals was 590 and 725μm, and by 23 days after sampling, arm length was 820 and 920 μm. A single juvenile *Pteraster tesselatus* was sampled on June 22. At seven weeks after sampling, this juvenile *P. tesselatus* was 1.22 mm AL and had a partially formed nidamental chamber (see McEdward 1992).

Holothuroid Larvae and Juveniles

Psolus chitonoides were cultured from juveniles sampled from settlement collectors and from doliolariae collected in plankton samples. Two orange doliolaria were collected from 0 -5 m oblique plankton tows on June 14 (Figure 29a). Five days later, both larvae settled on rock encrusted with coralline algae in the culture container, and within three days both had metamorphosed to a pentacula with ossicle spicules on the body surface. Two weeks after metamorphosis, one surviving pentacula (920μ m body length) was sessile with the ventral ambulacra forming a flattened sole (the trivium) against the rock substratum, and was completely armored dorsally with external ossicles (the bivium). This is consistent with the reported time of 16 days post-settlement for sole formation in *P. chitonoides* (McEuen & Chia 1991). At seven weeks post-metamorphosis, this individual was 1.4 mm body length (excluding feeding tentacles). Four *P. chitonoides* pentacula sampled from settlement collectors were also reared in the lab on encrusted rock in flow-thru containers. These pentacula also became sessile within two weeks of sampling. Mean length was 1.12 mm four weeks after sampling, but had increased to only 1.18 mm eight weeks after sampling (Figure 29b).

Two other forms of holothuroid juveniles were sampled from settlement collectors and reared in the lab. One form had a spiny appearance, resulting from protruding "table ossicles" on the surface of the pentacula (Figure 30a). At three months, juveniles of this form were 2.2 - 2.5 mm body length, had four or five pairs of long podia on the ventral ambulacra, shorter podia along other ambulacra, and branched feeding tentacles. The anus was elevated posterodorsaly and the entire body surface, including podia, was covered with protruding table ossicles (Figure 30b). Table ossicles are characteristic of the genus *Parastichopus* (Lambert 1986), but juveniles with table ossicles were not identified to the species level.

A second form of juvenile varied in color from pale green to tan or golden, and had smooth, porous, oval-shaped ossicles on the body surface (Figure 31). The ossicles varied between individuals, with green juveniles generally having large ossicles with large pores, while tan or gold-colored juveniles, generally smaller on the sample day, had smaller ossicles (relative to body size) with smaller pores. Juveniles of this group were initially assumed to be a single species of different ages and samples were collected to rear in the lab. At approximately two months in age, juveniles in this group had developed two distinct morphologies. One form, at ~ 2 mm length, was characterized by 12-14 podia on the ventral ambulacra, several short papillae on the dorsal surface, slightly upturned (anteriorly) smooth ossicles covering the body surface, an elevated anus located posterodorsally, and branched feeding tentacles.. A second form, also ~ 2 mm length at two months, had more numerous and longer podia along the ambulacra, and the anus was not elevated dorsally. Development was not followed beyond two months, but juveniles in this group were distinctly two different species. Morphology of the former of these species (with upturned ossicles and elevated anus) most resembled the adult characteristics of *Cucumaria* sp., while the morphology of the latter (with numerous long podia) most resembled *Eupentacta quinquesemita*. Adults of *C. miniata* and *E. quinquesemita* are locally abundant, thus it is likely the green and gold-colored juveniles on settlement collectors include these species.

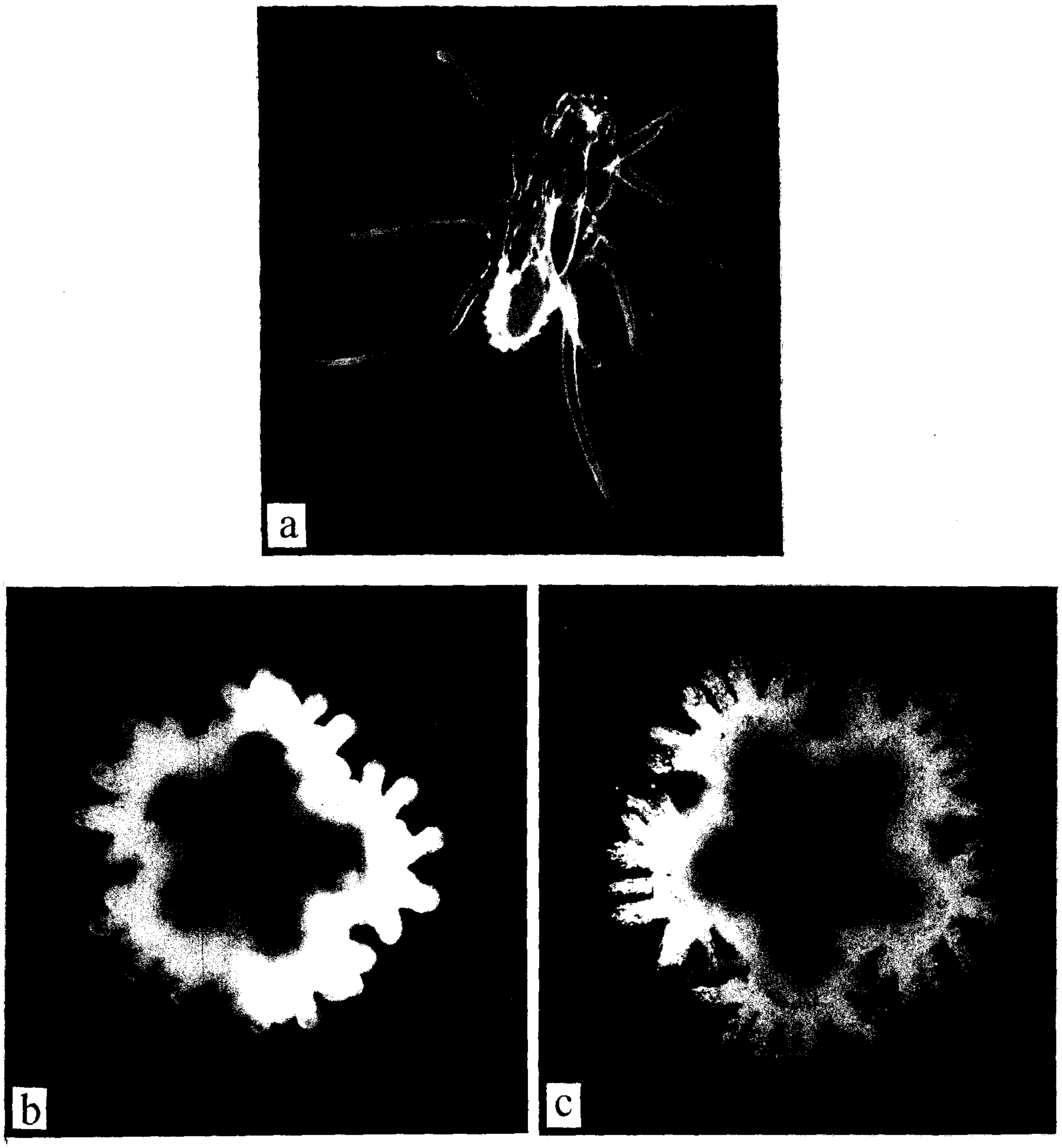

FIGURE 27. Asteroid brachiolaria and early juveniles from plankton and settlement collectors at Gregory Point; 27a, precompetent brachiolaria with red-orange bipannarial arm tips and red-orange rudiment, collected July 7, 1995, (body length ~ 1.8 mm); 27b, one-day old juvenile asteroid metamorphosed in lab from same form of brachiolaria shown in 27a, 440μm arm length (distal arm tip to center of disc); 27c, juvenile *Pycnopodia helianthoides* from settlement collectors (450μm arm length, age < 2 week).

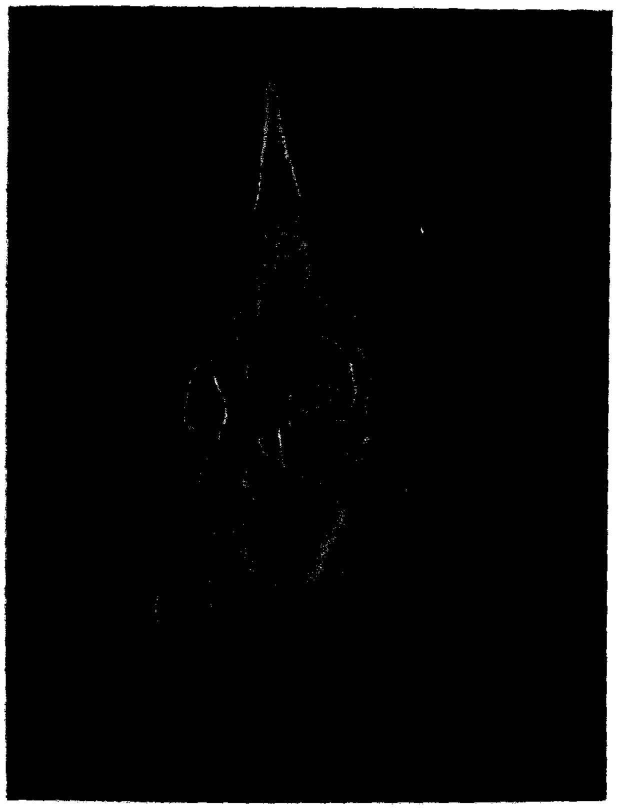

FIGURE 28. Precompetent brachiolaria from plankton at Gregory Point, collected July 7, 1995, (body length ~ 1.8 mm). Bipinnarial arms and pyloric caecum of juvenile rudiment are pale orange.

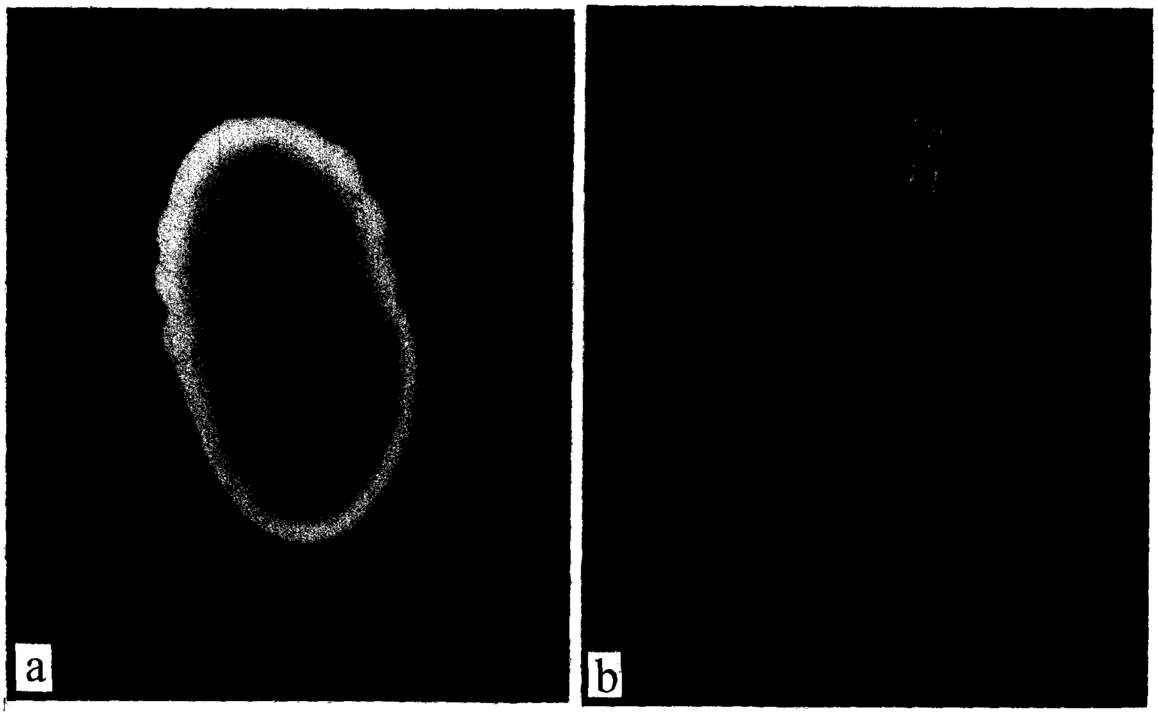

FIGURE 29. Doliolaria and early juvenile of *Psolus chitonoides* from plankton and settlement collectors at Gregory Point; 29a, ventral view of doliolaria collected in plankton June 14, 1995 (900μm); 29b, dorsal view of juvenile reared from pentacula collected July 7, 1995, age < 4 weeks (1.12 mm). Feeding tentacles are directed toward top of page.

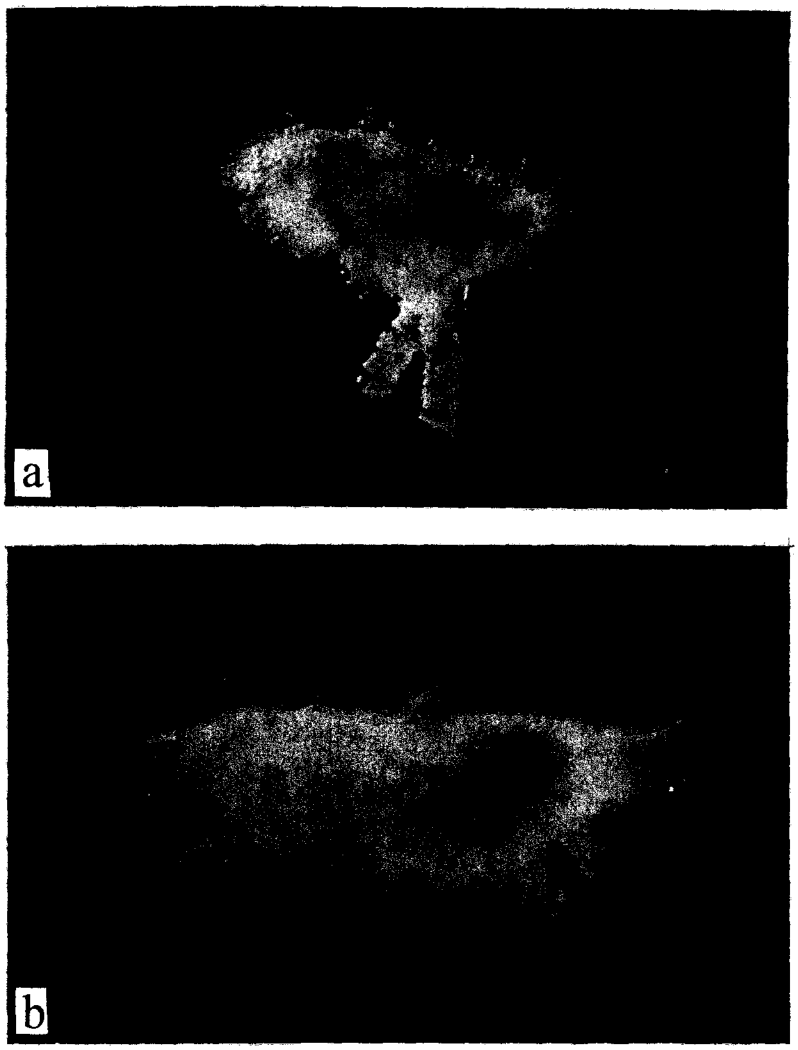

FIGURE 30. Juvenile *Parastichopus* sp. reared from pentacula collected from settlement collectors at Gregory Point, June 22, 1995; 30a, lateral view of juvenile at < 2 week age, body length 1.1 mm. Anterior end is facing left. Protruding ossicles on body surface are table ossicles; 30b, juvenile at ~ 3 months in age, body length 2.4 mm. Anterior end is facing left.

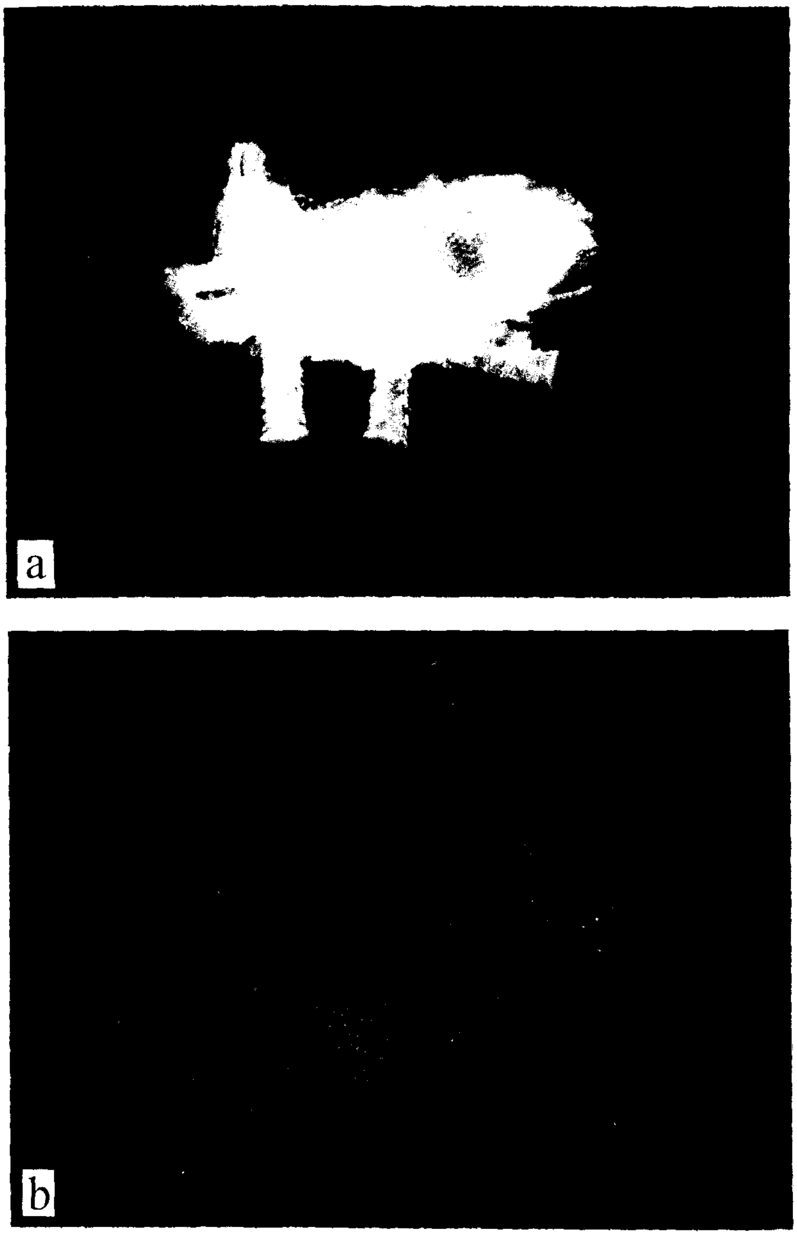

FIGURE 31. Juvenile holothuroids from settlement collectors at Gregory Point; 31a, juvenile at < 3 weeks age, body length 1.1 mm. Anterior end is facing right; 31b, juvenile *Cucumaria* sp. at ~ 6 weeks age, body length 1.8 mm. Anterior end is facing right.

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