

REPRODUCTIVE RESPONSES OF PURPLE SEA URCHIN (*STRONGYLOCENTROTUS PURPURATUS*) POPULATIONS TO ENVIRONMENTAL CONDITIONS ACROSS A COASTAL DEPTH GRADIENT

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ABSTRACT

Ecological influences on reproduction in sea urchins, particularly photoperiod, have been studied extensively. Effects of proximate environmental factors (temperature, water motion, food) on reproduction of purple urchins, *Strongylocentrotus purpuratus* (Stimpson, 1857), were sampled monthly for 2 yrs for intertidal, and subtidal populations at the same latitude in the Point Loma kelp forest, San Diego, California, USA. Gonad index (GI) was highest at 8 m, intermediate in the intertidal, and lowest at 18 m. GI increased across sites from spring through autumn and decreased sharply from late autumn through early winter. Stomach index (SI) peaked in summer and in autumn-winter. Increases in SI followed temporal peaks in drift plant abundance, but preceded increases in GI. Temperatures ranged from 11–22 °C, varying inversely with depth. Water movements were highest at deeper sites. Spawning coincided with high wave periods. Abundance of drift macroalgal food generally increased from deep to shallow sites, with rare peaks in abundance of intertidal drift. Algal food quantity appears to regulate reproductive output, not timing. C:N ratio of drift kelp was generally higher, and nitrogen correspondingly lower, at warmer temperatures or shallower depths; nitrogen was lower in drift than in live kelp. Gonadal growth, development, and spawning occurred earlier at deeper subtidal sites with faster flows, lower temperatures, and higher food quality, despite low drift abundance. Gonad production was highest intertidally despite high population density, prolonged high temperatures > 17 °C limiting gametogenesis, and only sporadic availability of drift. Naturally co-occurring abiotic and biotic factors combine to affect reproduction in *S. purpuratus*.

Populations of many species of marine benthic invertebrates reproduce in contrasting habitats which encompass substantial physical and biological variation in environmental conditions over small and large spatial scales. The purple sea urchin, *Strongylocentrotus purpuratus* (Stimpson, 1857), is abundant and ecologically important along the west coast of North America from Alaska to Isla Cedros, Baja California, Mexico (Pearse, 2006; Rogers-Bennett, 2007). Often considered a rocky intertidal species, populations of *S. purpuratus* occur at all depths throughout subtidal kelp forest habitats and deeper to 90 m (Harrold and Pearse, 1987; Pearse and Mooi, 2007; Rogers-Bennett, 2007). Here we contrast purple urchin reproduction at the offshore and inshore edges of a large forest with the nearby rocky intertidal habitat. These habitats span depth ranges of 0 to > 18 m, wide temperature ranges, persistent differences in algal standing stocks, drift production, and food quality; each of these habitat conditions alone affects urchin reproduction. Differences in alongshore flow, wave-induced flow, and turbulent breaking waves further diversify these habitats. Denny et al. (1985), for example, suggested that turbulence may strongly limit reproductive success in intertidal purple urchins. Hence populations of *S. purpuratus* experience considerable contrasts in depth, temperature, light, food, and water movement along a short across-habitat gradient. Although reproductive synchrony

in this urchin has been reported over large and local spatial scales, Pearse and Cameron (1991) suggested that spatial and temporal differences in reproduction probably reflect local differences in environmental conditions that influence gametogenesis.

Here we explore the effects of natural variability in environmental conditions experienced by *S. purpuratus* populations on a large spatial scale and, across a local depth gradient of tens of meters, and examine how this environmental variability affects reproduction. Although Pearse and coworkers (Pearse and Eernisse, 1982; Pearse et al., 1986; Bay-Schmith and Pearse, 1987) have experimentally demonstrated the influence of photoperiod on gametogenesis, and others have studied effects of one or two different environmental factors on reproduction in *S. purpuratus* (e.g., Cochran and Englemann, 1975; Leahy et al., 1978, 1981; Pearse, 1981), no study has looked at how multiple, naturally changing environmental factors together influence the reproduction of *S. purpuratus* in the field. We build on extensive ecological and oceanographic research in the vicinity of the Point Loma Kelp Forest (PLKF), San Diego, California, USA, to study urchin reproduction at the same latitude, at three depths with contrasting physical and biotic conditions: a rocky intertidal habitat (Ricketts et al., 1985) and two subtidal kelp forest sites (e.g., Dayton et al., 1992). Change in photoperiod is similar across sites although light levels decrease with increasing depth. Temperatures vary widely but consistently among sites, are highest at the intertidal site and lowest at 18 m (Dayton et al., 1992). Flow speeds are generally highest subtidally at 18 m and slower at shallower depths (Jackson and Winant, 1983; Denny et al., 1985; Seymour et al., 1989). There is a strong seasonal cycle in the abundance of drift kelp (the main food of *S. purpuratus*), and a significant increase in subtidal drift with decreasing depth (Tegner and Dayton, 1991). Although the nutritional value of various marine plants for *S. purpuratus* (and other urchins) is well studied (reviewed by Lawrence, 1975), the nutritive value of drift algae is not well known. Since both food amount and quality are likely to affect reproduction in urchins, we measured Stomach Index (SI) and C:N ratio of drift, respectively.

We compare reproductive responses of this important grazer across this environmental-depth gradient over two annual breeding cycles, and ask: (1) Are there contrasting habitat- or site-related environmental attributes that lead to differences in the reproductive condition, output, or timing of purple sea urchins from nearby intertidal and subtidal populations? (2) Do between-habitat differences in availability and quality of food affect changes in urchin reproductive and nutritional condition? (3) Do contrasting temperatures, or (4) water movements at these sites influence reproductive patterns? We discuss how small scale environmental variability leads to reproductive differences among local populations which may influence their relative contribution to successive generations. Local differences in reproduction among populations may confer ecological or evolutionary benefits to *S. purpuratus*, or may reflect differential susceptibility to environmental change among populations.

METHODS

STUDY SITES

Sites at each depth were not replicated due to numbers of adult urchins present, and a desire to not deplete populations. As there were no intertidal sea urchin populations directly inshore of the Point Loma Kelp Forest (PLKF), at the Cabrillo National Monument and farther north along the Point Loma Peninsula, we studied the closest intertidal population on the

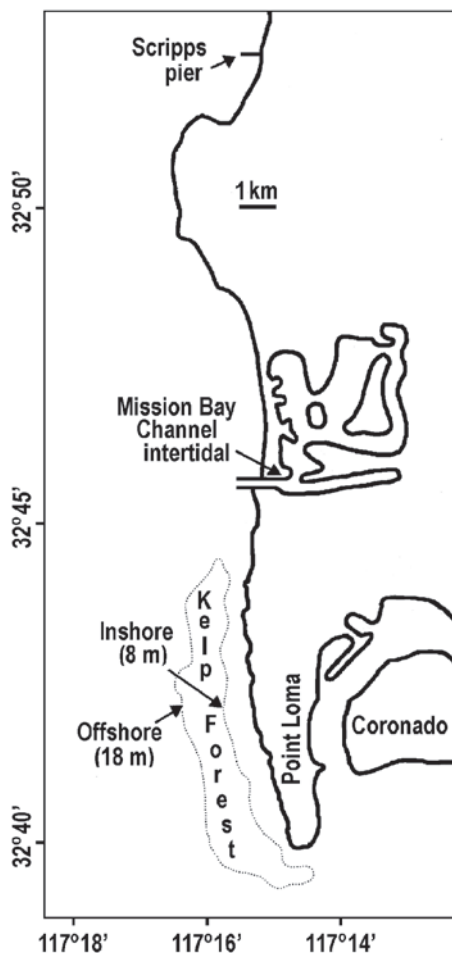


Figure 1. Map of intertidal and subtidal study sites near San Diego, California, USA. The dotted line represents a general outline of the *Macrocystis pyrifera* canopy in the Point Loma Kelp Forest; there is much interannual variability in canopy cover.

north jetty of the Mission Bay Channel, San Diego, CA, about 1 km inshore from the bay entrance, and about 8 km north of the central sites of the PLKF (Fig. 1). The intertidal substrate consists of granite boulders about 0.5–2.0 m in greatest dimension, sloping 45° to a sand plain about 5 m below Mean Lower Low Water (Ebert, 1977). Boulders were mainly covered with a turf of geniculate coralline algae (primarily *Corallina* spp.), sessile invertebrates, and encrusting corallines. Rare attached foliose algae included (in order of decreasing abundance): *Sargassum muticum* (Yendo) Fensholt, 1955, *Cystoseira osmundacea* (Turner) C. Agardh, 1820, *Dictyopteris undulata* Holmes, 1896, *Egregia menziesii* (Turner) J. E. Areschoug, 1876, and *Codium fragile* (Suringar) Hariot, 1889.

Subtidal sites are offshore of the Mia J. Tegner State Marine Conservation Area, near the inshore (8 m depth) and seaward (18 m depth) edges of the PLKF (Fig. 1, stippled boundary), a community that has been studied intensively, almost continuously since 1956 (e.g., Pearse et al., 1970; North, 1971; Tegner and Dayton, 1981, 1991; Dayton et al., 1984, 1992; Tegner et al., 1996). The giant kelp [*Macrocystis pyrifera* (Linnaeus) C. Agardh, 1820] forest extends for 8–10 km along the coast and is about 1 km wide. The substrate is generally a broad, low sloping mud- and sand-stone terrace with patches of high-relief rock reef, boulders, and sand

channels. Subtidal rocks are covered by diverse assemblages of encrusting red corallines, turf-forming algae, and sessile invertebrates, *Macrocystis*, understory kelps, and other plants (see Dayton et al., 1984; Foster and Schiel, 1985).

ENVIRONMENTAL FACTORS

Bottom temperatures were measured every 3 hrs at 8 (or 12) and 18 m depths (Tegner and Dayton, 1991; as detailed in Dayton et al., 1992) by recording thermistors (TempMentors, Ryan Instruments, Inc., Redmond WA, or Stowaways, Onset Computer Corp., Pocasset, MA), and averaged by month. Gaps in bottom temperature records resulted from occasional instrument failures. Bottom temperatures from an intermediate site at 12 m depth are plotted to provide as continuous a temperature record as possible. Intertidal temperatures were estimated from surface measurements taken daily at the Scripps Institution of Oceanography (SIO) pier, about 12 km north of the intertidal site; these were very similar to those taken during monthly sampling. Spawning of various invertebrates occurs across a wide range of tidal heights and flows, lunar phases, and times of day or night (e.g., Hendler and Meyer, 1982; Giese and Kanatani, 1987; Pearse et al., 1988; Babcock et al., 1992). The few field observations of echinoid spawning also show no consistent pattern: urchins, including *S. purpuratus*, spawned in still water, surge, or current conditions, and as scattered individuals or in aggregations (Pennington, 1985, Table 1; Levitan, 1995). Flow patterns in and around the PLKF have been well characterized for typical and storm periods (Jackson and Winant, 1983; Seymour et al., 1989). Daily maximum significant wave height data are available from 1 May 1994 to 1 July 1995 from the oceanographic data buoy moored at about 150 m depth, 8 km west of Mission Bay Channel, via the Coastal Data Information Program, SIO. Maximum significant wave height, H_s , is defined as the average of the 1/3 highest waves (Seymour et al., 1989).

Drift plant matter available as food for urchins was sampled monthly at each site from four 1 m² quadrats haphazardly placed in urchin habitats. Drift samples were sorted, identified, and the total sample wet weight measured (nearest g). These data were used to estimate drift abundance and rank order composition by percent frequency of occurrence.

C:N ratio, an indicator of the nutritional value of algae, was analyzed from drift samples taken in the spring-summer (April, June, July 1995) period of cold temperatures subtidally, and autumn (September 1995, 1996) periods of warmer temperatures. At these times among-site differences in nutrient availability for plants (and their presumed nutritional quality for urchins) are predicted to be high, due to average annual differences in temperature (Jackson, 1977; Gerard, 1982; Zimmerman and Kremer, 1984). Replicate samples ($n = 3-10$) of lamina (blades) from drift (and in September 1996, live, attached lamina [not sporophylls] taken 2 m above the holdfast of) giant kelp, *Macrocystis* (the main component of drift), were oven-dried to constant weight for 24–60 hrs at 60–65 °C. Dried samples were weighed to the nearest 0.1 µg with a precision electronic microbalance, and placed in a C, H, N elemental analyzer (Perkin-Elmer model 2400) to determine carbon and nitrogen levels. Analytical accuracy was verified with acetanilide, a compound of known C, H, and N content.

SAMPLING OF SEA URCHINS

We counted adult (> 25 mm test diameter) *S. purpuratus* within four 1 m² quadrats placed haphazardly in urchin patches at each site every month. Approximately 30–90 urchins were sampled from each population from May 1994 through April 1996. Animals were transported in ice chests to a chilled (10 °C), flow-through seawater holding tank for 1–2 d to minimize spawning prior to dissection. Animals that were observed spawning were not used.

Urchin reproduction and nutrition were assessed in parallel with variation in environmental conditions. Test diameter at the ambitus was measured with vernier calipers. Wet body weight was measured to the nearest 0.1 g. The reproductive cycle and condition of 20 adults of similar, large size from each site was assessed monthly by the gonad index method and histological examination of ovaries; size range was minimized to avoid possible effects of

urchin size on GI (Gonor, 1972). Nutritional condition was assessed by stomach index and gut content (see below).

Gonads were weighed to the nearest 0.1 g and the most intact and representative of the five gonads per urchin was preserved in Bouin's fixative for histological analysis (Humason, 1979). Ripeness was subjectively assessed by the presence (if any) and relative volume of gametes spontaneously spawned, or extruded from gonads during dissection. Gonad Index (GI) was calculated as wet weight of gonads \times 100% / total wet body weight.

Twenty preserved gonads in samples from June 1994 to May 1995 had 3–5 mm³ cubes cut from their central portion, which were fixed in Bouin's fluid for at least one month. Cubes were dehydrated through an ethanol-xylene series, embedded in paraffin, sectioned at 10 μ m, mounted on microscope slides using standard histological techniques (Humason, 1979), and stained with toluidine blue. Initial observation of sections through entire gonads showed that the gametogenic condition seen in the center cube was representative of the whole gonad. Sex, stages of germinal growth, and size frequency distribution of ovarian cells were determined by examining stained sections at 10 \times magnification with a compound microscope.

Female reproductive condition was categorized according to the presence and relative abundance of ovarian cells seen throughout the oogenic cycle, using a scale of I to IV, modified from the staging schemes of Fuji (1960), Pearse (1969), and Byrne (1990). Stage I: Recovery stage. Ovaries in Stage I contain small oocytes, mainly along the acinal wall. Nutritive phagocytes, non-germinal cells, appear uniform, and fill most of the ascinus. These cells contain dark granular droplets resulting from phagocytosis of relict oocytes and ova (Byrne, 1990, N. Holland, Scripps Institution of Oceanography, pers. comm.). Stage I ovaries may also contain unspawned, deteriorating ova and relict oocytes. Stage II: Growth stage. Primary oocytes increase in diameter with the start of vitellogenesis. They either remain attached to the ascinal wall, or begin to detach from it and move inward through the nutritive phagocytes to the ascinal lumen. Large primary oocytes may occur in the center of the ascinus. With growth to maximum size, oocytes quickly mature into ova that collect in the lumen of the ovary. Stage III: Mature stage. Ovaries prior to spawning are densely-packed with many large, round ova. Few (no more than one cell layer) small oocytes may line the ascinal wall; these may be closely associated with a thin layer of nutritive phagocytes. Stage IV: Spent stage. The lumen of many spent stage ovaries are still packed with mature ova, but not as densely as in the mature stage (III), due to spawning of ova. Or the lumen may appear empty except for a few oocytes. The nutritive phagocyte layer is thin, and contains few or no dark-staining droplets. The appearance at this stage can be highly variable, particularly in partly spawned ovaries. Oocytes at all stages may be present; unspawned ova are not round, they appear to be collapsing, and are presumably being broken-down by nutritive phagocytes in order to accumulate reserves toward the next oogenic cycle. These stages were used to describe the annual cycle of oogenesis for the three populations. When sections of an ovary contained two or even three distinct reproductive stages, reproductive condition was classified by the most predominant stage present. Testes were not analyzed.

Size frequencies of oocytes and ova were determined by measuring the diameter of the first 50 seen in each ovary with an ocular micrometer. Measurable germ cells were defined as primary oocytes (minimum size \sim 20 μ m) sectioned through the nucleolus and ova sectioned through the nucleus. The diameter of non-spherical oocytes was taken as the average length of the shortest and longest axes. Relict oocytes showing clear signs of degeneration or resorption were not measured. Data from ten females per site and time were pooled to determine ovarian cell size-frequency distributions.

In many sea urchins food is retained in the stomach for much less time than in the intestine (Lawrence and Hughes-Games, 1972), hence we used the modified Stomach index (SI) to integrate nutritional condition over long periods. SI was calculated as wet weight stomach, intestine, and contents \times 100% / total wet body weight. Food items from the entire gut tract were identified to the lowest taxon possible, and ranked in order of decreasing abundance.

The spawning potential of individuals collected from October 1994 to April 1996 was determined by injection of about 1 ml of 0.5 M KCL per 100 ml body volume (Strathmann, 1987). Animals were scored either as spawning (gametes seen on aboral body surface), spawning copiously (estimated ≥ 1 ml of gametes covering aboral surface), or non-spawning; sex of spawning individuals was noted.

Differences in egg and larval quality of urchins from sites differing in food availability for adults were documented by George (1996). Fertilization success of gametes produced by spawners from the three sites was determined monthly from October 1994 to April 1996 using methods of Strathmann (1987). Regardless of population or month, if animals spawned, their gametes were viable, there was 100% fertilization, and development of zygotes was normal through the 4-arm echinopluteus stage (hence these parameters are not discussed further).

STATISTICAL ANALYSES

Data were tested for homogeneity of variances using Cochran's test, and transformed (square-root or \ln), when necessary, to meet assumptions of ANOVA (Zar, 1984). Data sets were analyzed using 1- or 2-factor ANOVA, ANCOVA, or correlation ($\alpha = 0.05$). Unless otherwise noted, significant differences were all $P < 0.05$, determined using ANOVA. Ratio data were analyzed using ANCOVA (Packard and Boardman, 1988). The sign, magnitude, and significance of differences among means in a posteriori pair-wise comparisons were determined using the Bonferroni test. The P values presented for pair-wise comparisons are Bonferroni-corrected and should be compared to $\alpha = 0.05$. All statistical analyses were run using SYSTAT (Wilkinson et al., 1992).

RESULTS

Environmental variables, reproductive and nutritional responses, and population measures of *S. purpuratus* in the present study are summarized in Table 1.

ENVIRONMENTAL FACTORS

Temperature ranged from 11–22.5 °C across sites, and varied inversely with depth (Fig. 2). There were large temperature differences among depths during spring and summer; these differences were minimal when the water column overturned in autumn. Temperatures were similar between 8 m and 12 m for most periods when there were overlapping data.

Daily maximum significant wave heights ≥ 250 cm occurred in mid-October through late November 1994, late-December 1994 through late-January 1995, and again in March and April 1995 (Fig. 3). Highest waves occurred in December 1994 and January 1995. Surface waves (estimated at ~ 200 –400 cm height) cause distinct pressure changes (on scales of seconds to minutes), high surge, and turbulence sufficient to move attached macroalgae and small rocks at < 8 to 21 m bottom depths in the PLKF. These surface wave heights lead to increases in benthic flow velocity (drag and lift) and acceleration that are experienced by urchins. Denny (1995) details how surface flows translate to the bottom, and the predicted effects on the probability of surviving dislodgement for various benthic organisms, including *S. purpuratus*. Benthic flows may also create sufficient disturbance to trigger spawning of *S. purpuratus*, however, our reproductive data indicating post-spawned conditions in subtidal urchins following high wave periods are only suggestive.

Mean drift plant abundances did not vary consistently nor significantly among sites during this 2 yr study, but often tended to be higher at shallower depths (Fig. 4). Maximum mean abundances of 250–500 g drift m^{-2} occurred in intertidal samples

Table 1. Summary of long-term relative importance of environmental factors, and reproduction, nutrition, and population responses of *Strongylocentrotus purpuratus* among sites.

Site	Environmental factors			Reproductive responses			Reproductive spawning		Nutritional response	Population measures	
	Temperature	Water movement	Drift food abundance	Drift food quality	GI	Gonad production	Onset/Period	Onset/Period		Urchin size	Urchin density
Intertidal	+++	+	+	+	++	+++	Latest/++	Latest/+++	++	+	+++
8 m	++	++	++	++	+++	++	Later/++	Later/++	+	+++	+
18 m	+	+++	+	++	+	+	Early/+++	Early/+	++	++	+

GI, mean per capita gonad index; Gonad production m⁻²; SI, Stomach Index; + Low/Small/Short; ++ Intermediate; +++ High/Large/Long.

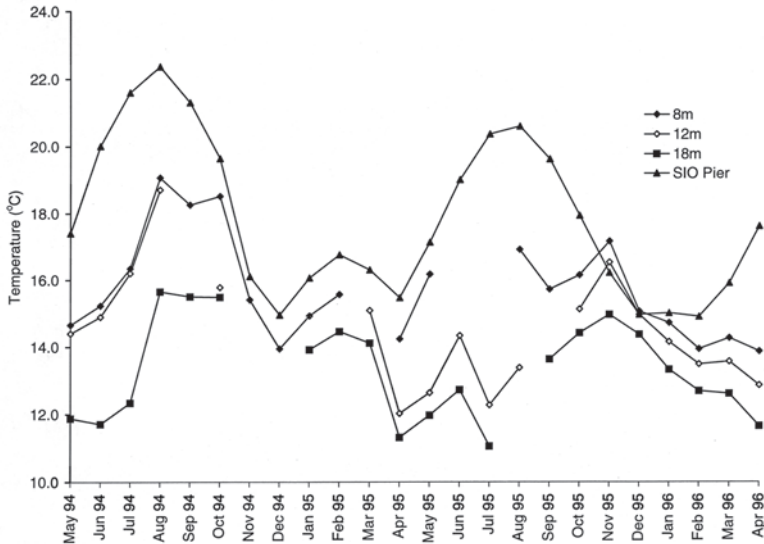


Figure 2. Mean bottom temperatures at the two subtidal sites in the Point Loma Kelp Forest, with temperatures at an intermediate site (12 m) for more complete record. Mean surface temperatures at Scripps Institution of Oceanography (SIO) pier, about 12 km north of the intertidal site, included as a proxy for temperatures at the intertidal site.

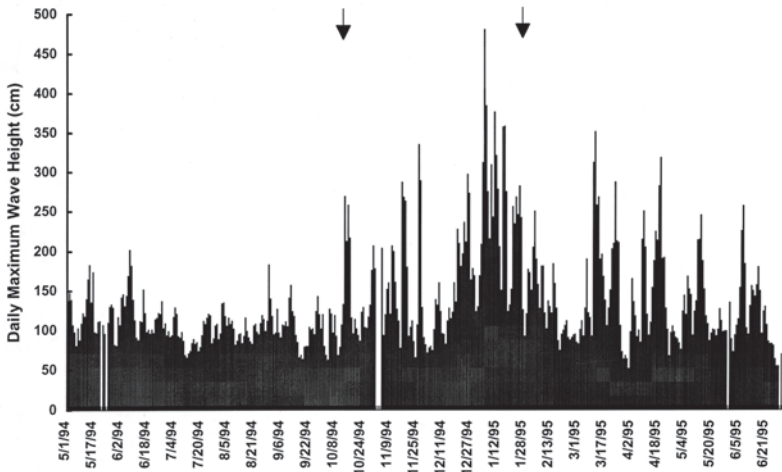


Figure 3. Daily maximum significant wave height (cm) at Mission Bay buoy, offshore from San Diego, California, from May 1994 to July 1995 (Data gaps reflect periods when buoy was in-operable during this study, including July 1995–April 1996). Source: Coastal Data Information Program, Scripps Institution of Oceanography. Significant wave heights ≥ 250 cm occurred in the period bounded by arrows (October 1994–January 1995), which coincided with sharp declines in urchin GI, indicating spawning (shown in Fig. 8).

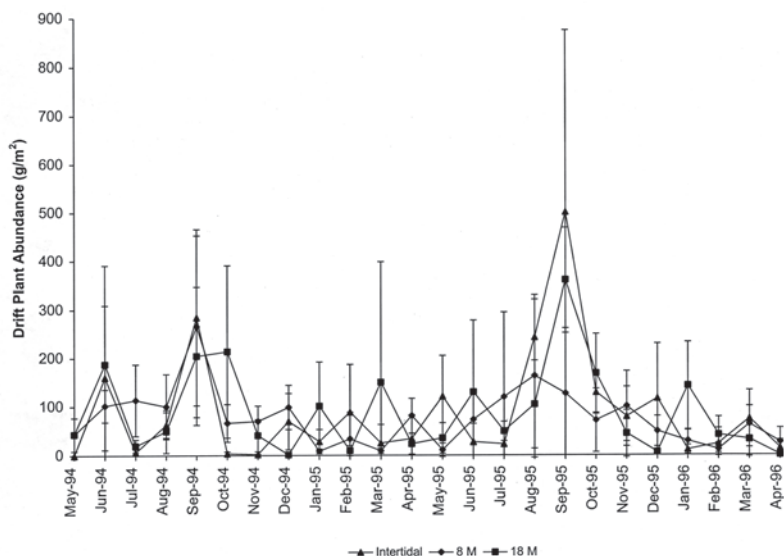


Figure 4. Mean (\pm SD) drift plant abundance (g m^{-2}) at the intertidal, 8 m, and 18 m subtidal study sites in the Point Loma Kelp Forest, San Diego, California, USA, from May 1994 to April 1996.

of September 1994 and 1995. Average drift plant abundance showed significant seasonal variability (drift levels in summer and autumn were larger than in winter or spring, but not significantly different among other seasons). High drift levels were followed by successive peaks in SI and GI (see below).

Macrocystis occurred in > 90% of drift plant collections at all sites; the balance consisted of other brown algae (*Laminaria farlowii* Setchell, 1893, *E. menziesii*, *Eisenia arborea* J. E. Areschoug, 1876, small amounts of *C. osmundacea* and *S. muticum*), foliose red algae [*Pterocladia capillacea* (S. G. Gmelin) Bornet, 1876, *Rhodomenia* sp. Greville, 1830, etc.], coralline algae (*Corallina* sp.), and sea grasses (*Phyllospadix* spp. W. J. Hooker, 1838, and a small quantity of *Zostera marina* Linnaeus, 1753) (Fig. 5). Drift *Laminaria*, foliose brown, red, and coralline algae, and sea grass were more abundant at kelp forest sites than in the intertidal, where *Macrocystis* was proportionately more abundant.

Although not all carbon is digestible (McClintock, 1986), C:N ratio, a potential indicator of the nutritional value of kelps for grazers, often varied significantly among sites, and over time. C:N was generally higher (and N lower) at shallower, higher temperature sites during the generally cold-water spring-summer months. In contrast C:N was lower (and N higher) at warmer, shallower sites than colder, deeper sites during warmer conditions in September 1995. Comparisons between months at each site indicate similar patterns. Overall seasonal and site patterns in drift kelp C:N levels conform to the predicted inverse relationship between temperature and nitrogen levels in sea water and in live kelp tissue (Figs. 2, 6).

We compared C:N in live and drift kelp in September 1996. During this period there were marked among-site differences in mean water temperature (SIO pier 19 $^{\circ}\text{C}$, 8 m 17°C , 18 m 14°C) predicted to result in among-site differences in nitrogen levels in sea water and live kelp. C:N in live kelp was significantly greater at 8 m than at 18 m (ANCOVA: $P < 0.00001$), and there was one-third the amount of nitrogen in

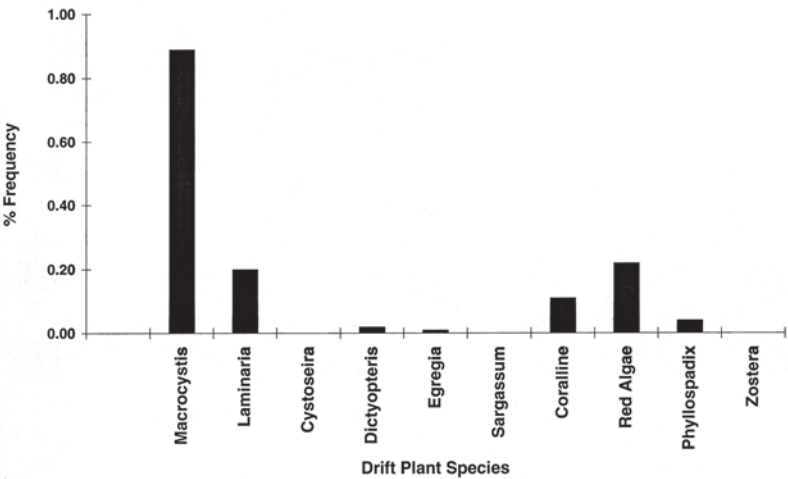


Figure 5. Mean drift plant composition from intertidal, 8 m, and 18 m subtidal study sites in the Point Loma Kelp Forest, San Diego, California, USA, May 1994–April 1996 (expressed as mean percent frequency; all sites pooled. Drift *Cystoseira osmundacea*, *Sargassum muticum*, and *Zostera marina* were rare but present).

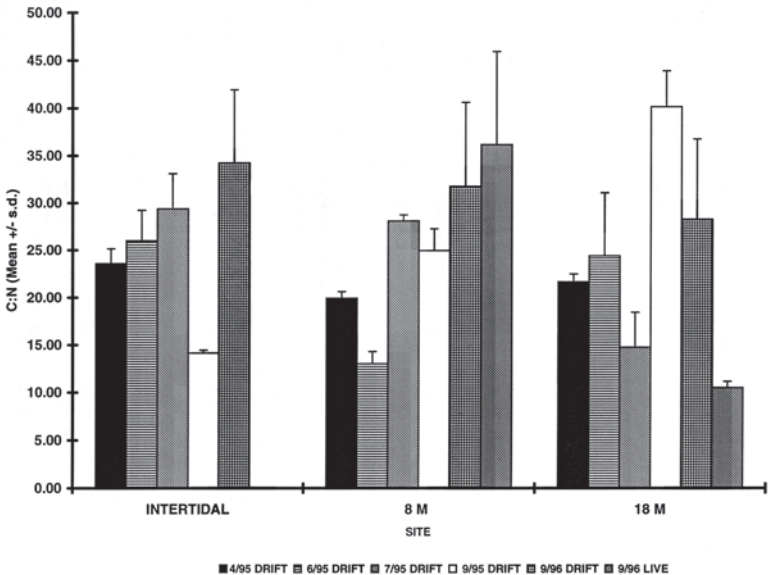


Figure 6. Mean (\pm SD) C:N ratio of drift or live giant kelp (*Macrocystis pyrifera*) lamina, at the intertidal, 8 m, and 18 m subtidal study sites in the Point Loma Kelp Forest, San Diego, California, USA, May 1994–April 1996; (n = 3–10 per sample set).

live kelp at 8 m (0.88% dry weight) relative to 18 m (2.7%). C:N in drift was greater than in live kelp at 18 m (ANCOVA: $P = 0.00007$), but not at 8 m (Fig. 6); correspondingly, nitrogen content in drift (1.2%) was one-half that in live kelp (2.7%) at 18 m, while differences between drift (1.06%) and live (0.88%) kelp N were smaller at 8 m. Note that drift kelp at 18 m had lower C:N (i.e., higher N) than live or drift kelp at 8 m. These data suggest that under relatively low nutrient, non-upwelling conditions, subtidal bottom temperature may be a useful proxy for both live and drift kelp nitrogen content. However, the relationship between live and drift C:N was not consistently significant, and drift kelp C:N data must be interpreted cautiously. Small amounts of drift lamina in many samples limited the number of CHN replicates, and hence the power of analyses for differences in C:N among sites or times. Second, the source location of plants that produced drift, along with prevailing temperature/nutrient conditions near the time and place of drift production, is unknown. Neither is it known if, among sites, fresh drift produced by disturbance is equally good in nutritive value, or senescent drift is equally poor.

POPULATION MEASURES

Urchin size, density, and dispersion varied significantly among sites. *Strongylocentrotus purpuratus* adults were uniform in size within populations, but each differed significantly from one another in diameter and weight; mean diameter (mm): 8 m (65) > 8 m (57) > intertidal (52) (ANOVA: $P < 0.001$; Fig. 7). As expected, diameter and weight were significantly correlated at each site (site, r : 8 m, 0.945; 18 m, 0.922; intertidal, 0.977; $P < 0.001$ for all sites).

Adult density varied with microhabitat availability; intertidal urchin density ($\sim 50\text{--}120\text{ m}^{-2}$) was significantly greater than 18 m ($\sim 10\text{--}35\text{ m}^{-2}$) and 8 m ($\sim 10\text{--}30\text{ m}^{-2}$; $P < 0.05$), which had similar within-patch densities (Fig. 7). At 8 m, urchins were in low-to-moderate density patches, mainly limited to the bases of large boulders, within boulder piles, in holes, or under bedrock shelves < 1 m high. At 18 m, high-relief reefs and the edges and underside of large boulders and boulder piles were common, patchy microhabitats for urchins. For several years prior to this study, subtidal densities across the PLKF decreased with decreasing depth (Tegner and Dayton, 1991). These combined data indicate that within-patch densities were at least an order of magnitude higher than overall densities, and intertidal urchin densities were up to an order of magnitude higher than subtidal ones. There was a significant inverse correlation ($P < 0.05$) between density and both weight and diameter at 8 m, where density was low and animals were largest, but not elsewhere ($P > 0.05$). There were high densities of small urchins intertidally, and medium-sized urchins at intermediate density at 18 m (Fig. 7).

REPRODUCTION

Mean gonad indices (GI; males and females were similar and were combined) in both years of this study peaked and declined earlier at greater depth: gonad production and spawning peaked first at 18 m, a month later at 8 m, and a month later still at the intertidal site (Fig. 8). Mean gonad indices did not vary consistently with depth; GIs were generally highest at 8 m, intermediate intertidally, and lowest at 18 m (Fig. 8): 8 m > 18 m (ANCOVA: $P = 0.02$), 18 m < intertidal ($P < 0.001$), 8 m not significantly different from intertidal ($P = 1.00$). In contrast, mean gonad production m^{-2} was significantly higher in the intertidal population due to higher urchin biomass, and de-

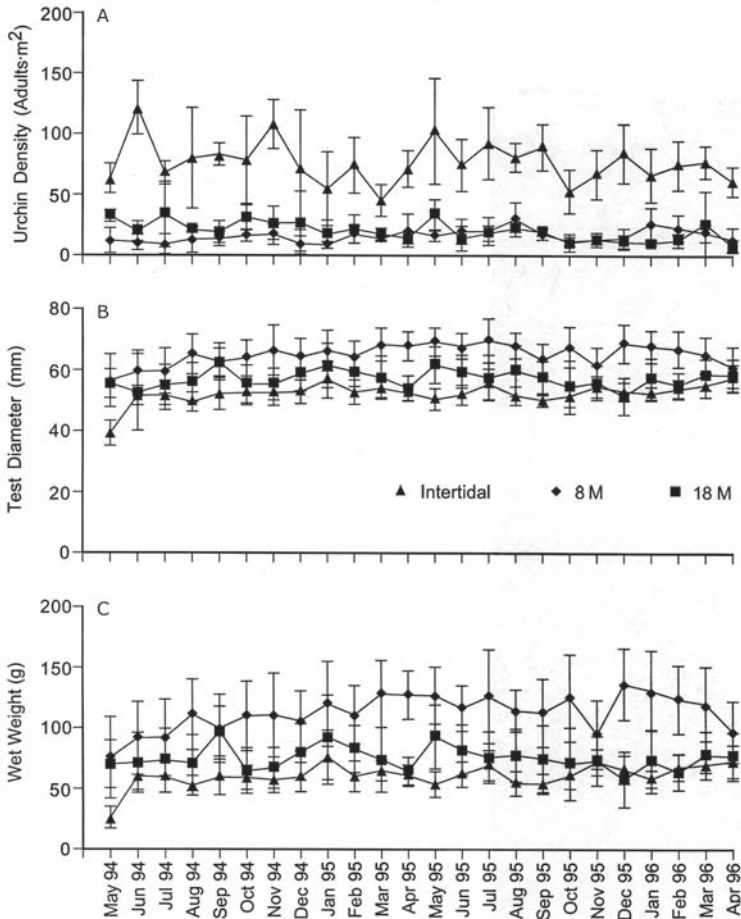


Figure 7. Mean (\pm SD) (A) density, (B) test diameter, and (C) weight of adult *Strongylocentrotus purpuratus*, at the intertidal, 8 m, and 18 m subtidal study sites in the Point Loma Kelp Forest, San Diego, California, USA, May 1994–April 1996.

creased steadily with increasing depth (intertidal [763 g m⁻²] > 8 m [201 g m⁻²] and 18 m [119 g m⁻²]; ANOVA: $P < 0.0001$). Seasonal patterns in GI were non-significant at all sites ($P > 0.05$). Mean GI increased from summer through late autumn with sharp declines indicating spawning in late autumn to early winter. Changes in the gonad index of the three populations were reflected in changes in female reproductive condition during 1994–1995 (Figs. 8–10).

Increasing percentages of females had ovaries in the recovery stage in spring-summer, and in growth stage in summer-autumn (Figs. 9, 10). Ovaries of some females at 18 m were in growth stage in August, one month earlier than those of females at shallower sites, and were in growth stage two months longer at 18 m than elsewhere. Mature ovaries were seen at 18 m in summer-autumn, at 8 m in spring-summer, and intertidally in winter-spring, suggesting that mature ova in subtidal females either develop sooner or are in ovaries longer than in intertidal females. The virtual absence of mature ovaries at other times may be due to maturation of ovaries in ≤ 1 mo or an

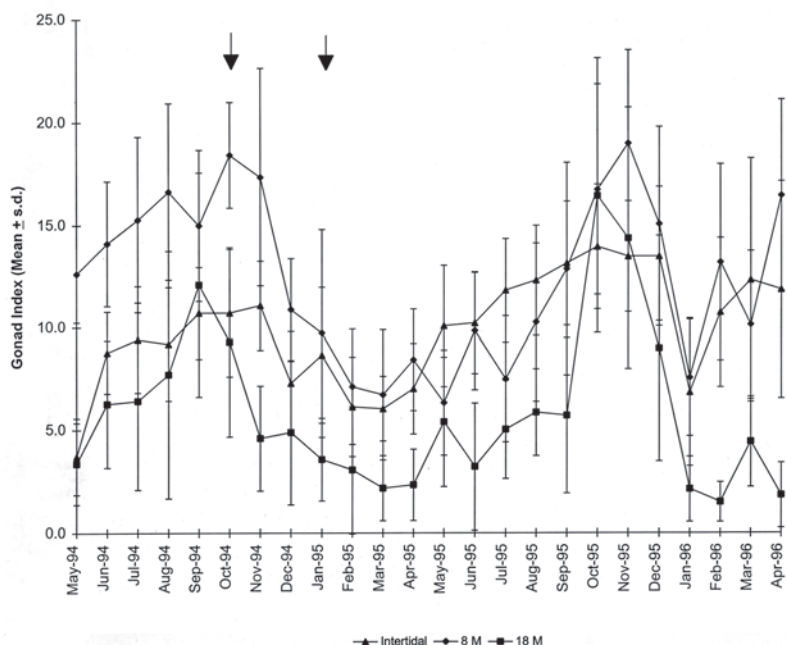


Figure 8. Mean (\pm SD) gonad index (GI) of adult *Strongylocentrotus purpuratus*, at the intertidal, 8 m, and 18 m subtidal study sites in the Point Loma Kelp Forest, San Diego, California, USA, May 1994–April 1996. Sharp declines in GI indicating spawning occurred in period bounded by arrows (October 1994–January 1995), which coincided with significant wave heights ≥ 250 cm (shown in Fig. 3).

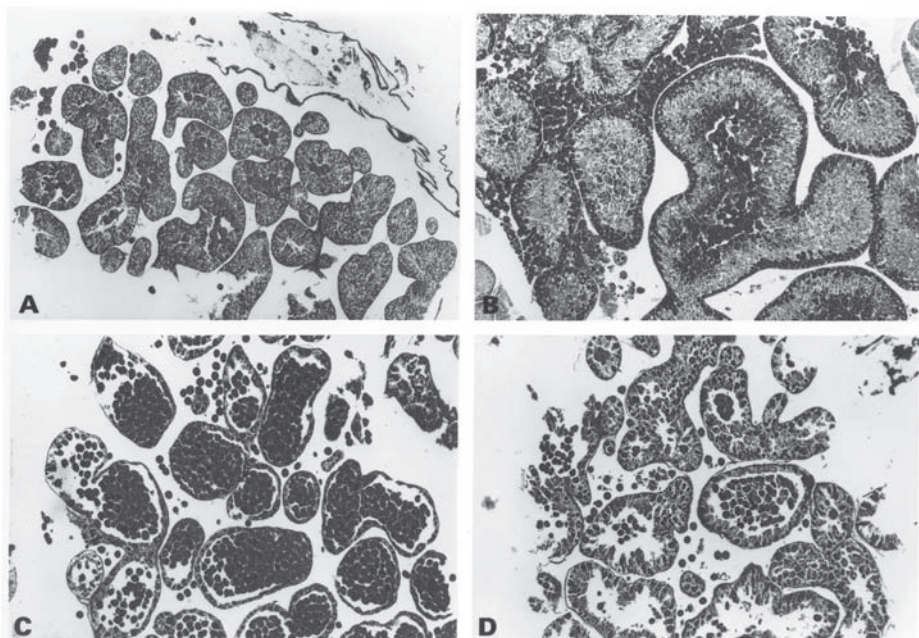


Figure 9. Representative histological sections showing female *Strongylocentrotus purpuratus* reproductive stage (A–D). (A) Stage I: Recovery stage. (B) Stage II: Growth stage. (C) Stage III: Mature stage. (D) Stage IV: Spent stage. Size of mature ova in A–D are approximately 75 μ m. See methods for description of stages.

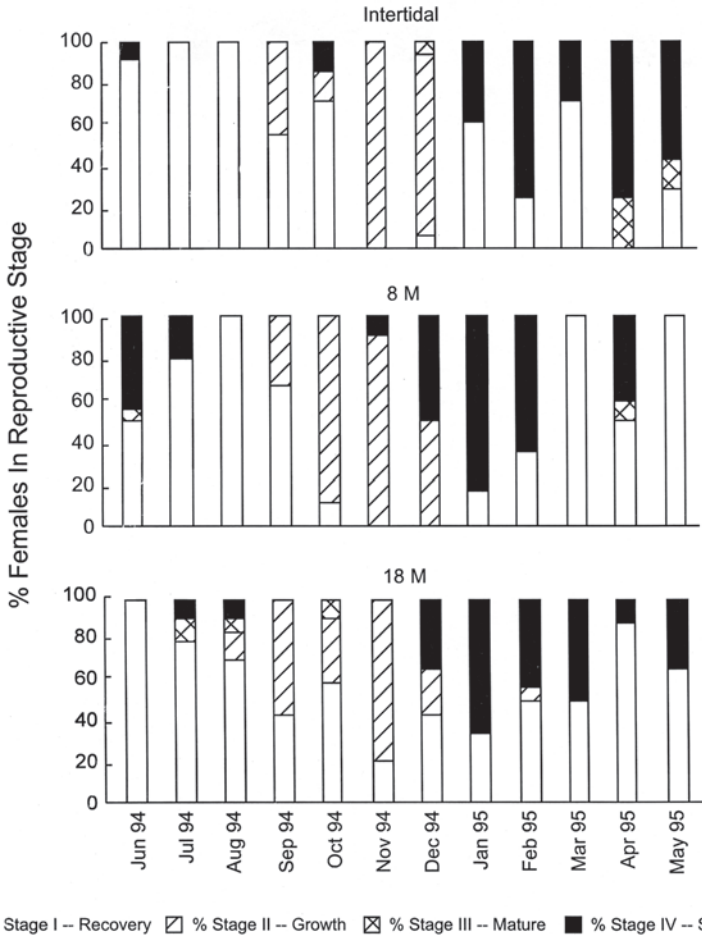


Figure 10. Reproductive stages of female *Strongylocentrotus purpuratus*, from the intertidal, 8 m, and 18 m subtidal study sites in the Point Loma Kelp Forest, San Diego, California, USA, from June 1994–May 1995. Recovery stage–white bars; Growth stage–diagonal bars; Mature stage–cross-hatched bars; Spent stage–black bars. Stages as in Fig. 9.

artifact due to loss of gametes during spawning or processing. Females with spent ovaries dominated in winter-spring at all sites. The mean percentage of time in each stage was very similar among sites. Ovaries were in recovery stage for 49%–54% of the year (~6 mo), followed by spent (24%–27%), growth (17%–23%), and mature stage for only 1%–4% of the year. The size frequency distribution of oocytes and ova reflect patterns in gonad index and female reproductive condition (Figs. 8–11). Ova start to accumulate earlier, and spawn-out faster, at 18 m than in the 8 m or intertidal populations (Fig. 11). Females with measurable germ cells occurred year-round at 18 m, but were absent for up to 4 mo in shallower populations. Nevertheless, ova (mean maximum diameter 75–80 μ m in all populations) were common during more of the year in females from shallower populations. In samples from October through winter, some intertidal females had mature eggs into late spring (Fig. 11).

Higher percentages of urchins were also induced to spawn during more months of the year in the intertidal relative to animals at 8 m and 18 m (Fig. 12). Urchins spawned during successively fewer months with increasing depth. However, there

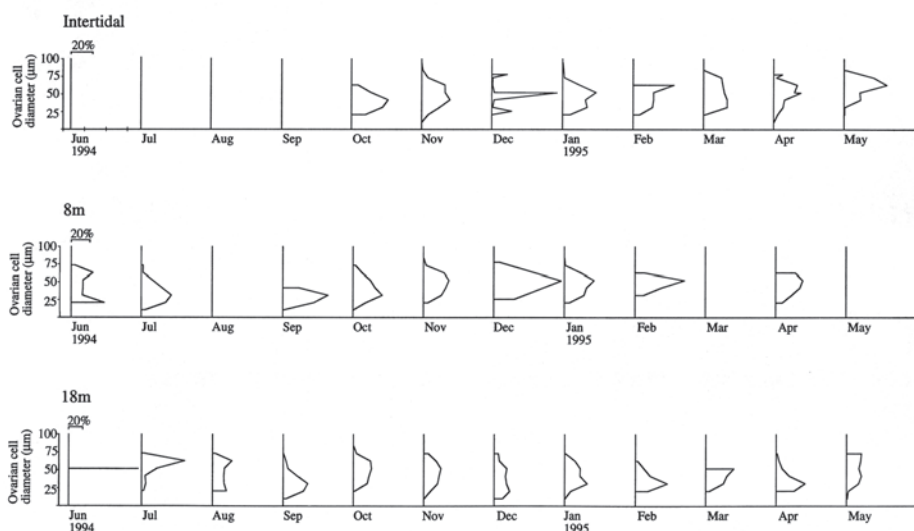


Figure 11. Ovarian cell (oocyte and ova diameters) size frequency distributions of female *Strongylocentrotus purpuratus*, from the intertidal, 8 m, and 18 m subtidal study sites in the Point Loma Kelp Forest, San Diego, California, USA, from June 1994–May 1995. Ova are $\geq 75 \mu\text{m}$.

were no significant differences in spawning among sites or times. In general, urchins spawned more copiously in winter and early spring; animals spawned less, or not at all in late summer to autumn. The frequency of copious spawners typically decreased with increasing depth. Declines in the percentage of induced spawners often coincided with decreases in GI (Figs. 8, 12).

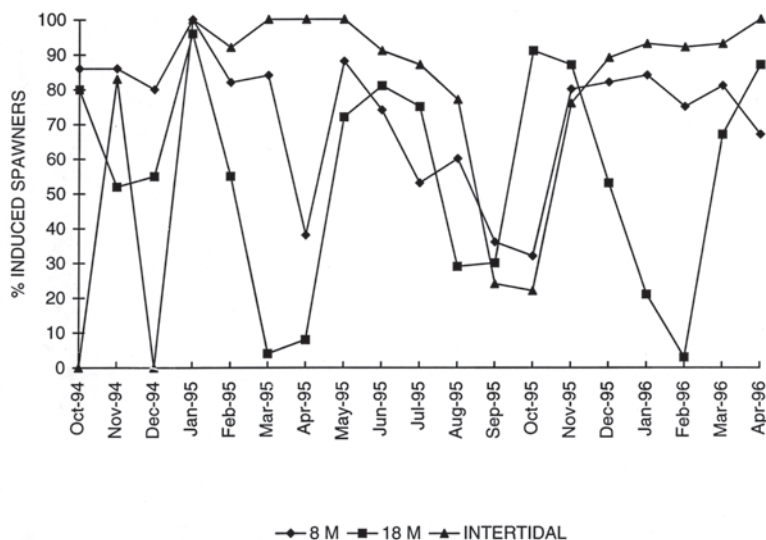


Figure 12. Mean percentage of adult *Strongylocentrotus purpuratus* (females and males pooled), from the intertidal, 8 m, and 18 m subtidal study sites in the Point Loma Kelp Forest, San Diego, California, USA, from October 1994–April 1996, that were induced to spawn in the laboratory.

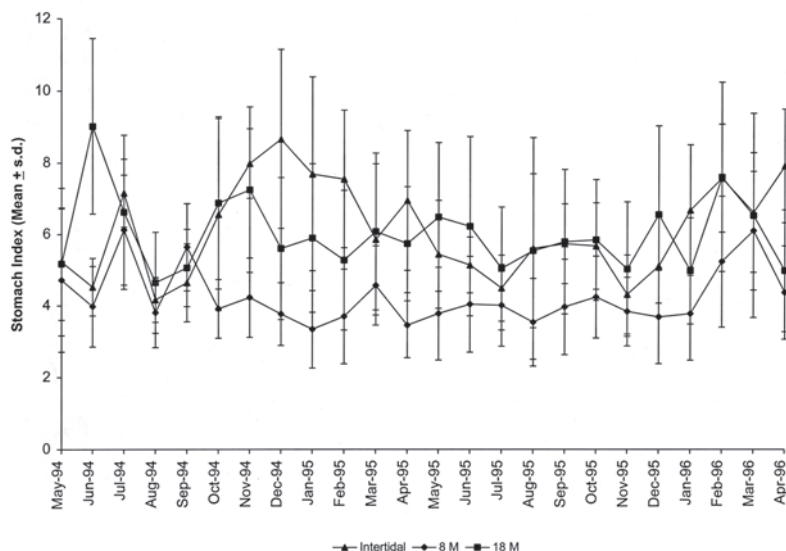


Figure 13. Mean (\pm SD) stomach index (SI) of adult *Strongylocentrotus purpuratus*, from the intertidal, 8 m, and 18 m subtidal study sites in the Point Loma Kelp Forest, San Diego, California, USA, from May 1994–April 1996.

Sex ratios in each population were near even but slightly skewed toward females at all sites, in most months; there were no significant seasonal trends (ANCOVA: $P = 0.15$). Among sites, sex ratio differed significantly only between the intertidal and 18 m populations (ANCOVA: $P = 0.01$).

Although egg quality (i.e., volume, energy content) was not measured directly, there were no differences among populations in success at fertilization, embryogenesis, or early larval development (ANOVA: $P > 0.05$).

NUTRITIONAL CONDITION

Stomach index (SI) at 8 m was less than at 18 m or intertidal sites but, like drift abundance (Fig. 4), did not vary significantly among sites (ANCOVA: $P = 0.869$) due to high sample variances (Fig. 13). SI was significantly different among dates (ANCOVA: $P = 0.001$); generally SI peaked and declined in spring-summer, then increased again in autumn-winter. Increases in SI coincided with, or followed after a brief lag, consistent peaks in drift plant abundance in both years of this study (Figs. 4, 13). Increases in SI tended to precede increases in GI (Figs. 8, 13).

Gut contents in all populations were usually dominated by laminarian brown algae, mostly *Macrocystis*, followed in decreasing order of abundance by crustose and articulated coralline algae, and surf grass, *Phyllospadix* spp. (Fig. 14). Other, uncommon food items included a few other species of brown algae, and at the intertidal site, eel grass, *Z. marina*. Rank order abundance of gut contents generally reflected available drift composition (Figs. 5, 14) except for intertidal urchins which often appeared to feed more on abundant attached articulated coralline red algae in the autumn due to inconsistent, limited supplies of drift kelp (Figs. 4, 5, 14). When drift kelp occurred in the intertidal even rare bladeless stipes were always actively grazed by many urchins.

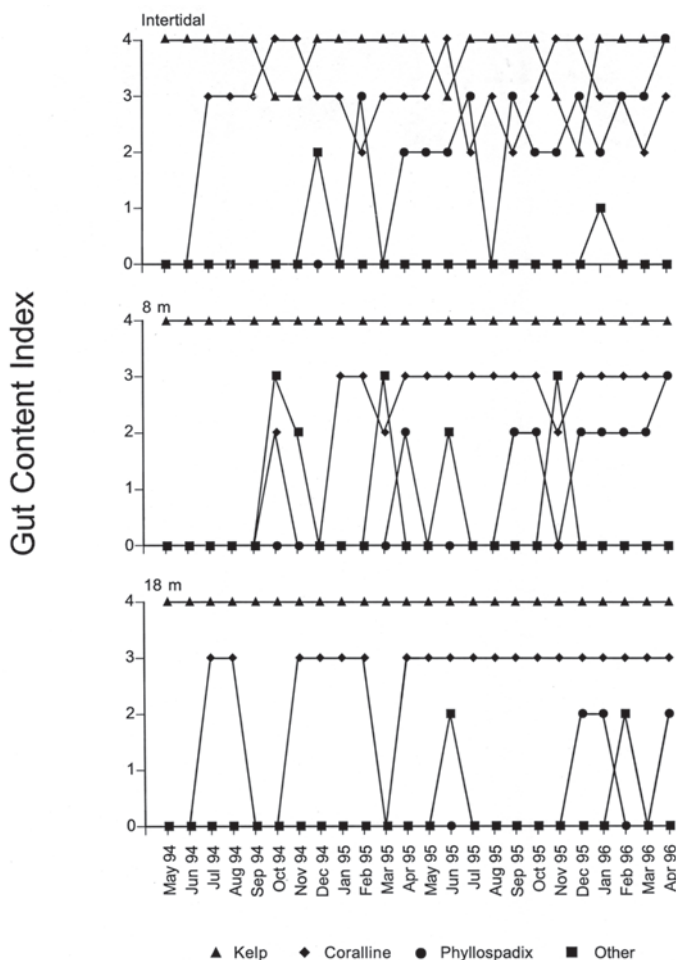


Figure 14. Gut content index of adult *Strongylocentrotus purpuratus*, at the intertidal, 8 m, and 18 m subtidal study sites in the Point Loma Kelp Forest, San Diego, California, USA, from May 1994–April 1996 (major food categories, estimated volume; 4 = most abundant food, 0 = absent).

DISCUSSION

Ecological processes affecting the reproduction of sea urchins and other marine invertebrates have been identified, but how reproduction in echinoid populations—including the well-studied *S. purpuratus*—is influenced by the combined set of naturally integrated environmental factors experienced is still unresolved (Giese and Pearse, 1974; Giese and Kanatani, 1987; Pearse and Cameron, 1991). Changes in environmental factor(s) can maintain, synchronize, or cause differences in reproductive patterns within or among populations; factors vary with environmental conditions and may act together or cancel effects of others. Studies have attempted to correlate variation in reproductive responses with one or two natural environmental factors; results have often been unsupported by experiments. Those on photoperiod have been most definitive, and there is still need for systematic, concurrent field data on reproduction and environmental conditions and their interplay (Giese and Pearse,

1974; Pearse and Cameron, 1991). Differences among local populations in their reproductive responses to contrasting or changing environmental conditions may determine their abilities to: (1) withstand potentially stressful physical or biotic environmental changes, (2) persist in space and time, (3) contribute to the metapopulation larval pool, or (4) sustain a fishery.

AGE-SIZE EFFECTS, PHYSIOLOGICAL ECOLOGY

Urchin age and size are both important with respect to reproduction since urchin physiology and nutritional requirements vary accordingly. For example, *Strongylocentrotus intermedius* A. Agassiz, 1863 fed *Laminaria japonica* J. E. Areschoug, 1851 showed higher somatic growth in young animals than in old ones, and much more gonadal growth in old animals (Fuji, 1967). Adult size differences among the three populations in this study were small, but significant. We have no information on urchin age-size relationships in these populations. Since larger organisms have lower surface area-to-volume ratios than smaller ones, larger, subtidal urchins may be better able to withstand changing environmental conditions and control internal ones. Large size can increase an individuals' persistence or reproductive output. Large urchins have more volume for development of gonadal tissue (hence higher fecundity), and may be better able to catch and eat more food. Large animals also have a more efficient metabolism—i.e., a lower metabolic rate per unit body mass—than smaller ones (Schmidt-Nielsen, 1984).

Sea urchin size and reproductive output depend on resource availability relative to metabolic needs (Ebert, 1968). The dense intertidal population of small urchins, with comparatively small gonads, is limited by generally poor food quality, inconsistent drift supply, and habitat-typical physiological stresses (e.g., air exposure, high temperature). Intertidal urchins did not feed when exposed at low tide, and were observed to move into deeper water during storm-induced swell or surge, as did *Strongylocentrotus droebachiensis* O. F. Müller, 1776 (Himmelman and Steele, 1971). Input of drift to the intertidal was extremely patchy; even rare bladeless stipes of low food quality (Leighton, 1968; Lawrence, 1975) were always actively grazed by many urchins. The intertidal population often fed on nutritionally poor coralline algae, and had higher frequencies of individuals with empty guts, extremely small, dark, non-reproductive gonads, and other indicators of poor condition such as thin test walls, injuries, or infections, relative to subtidal urchins. Subtidal animals were larger, lived at lower density in more protected habitats favorable for drift accumulation, and experienced less stressful environments than intertidal populations. These factors suggest lower competition for food.

ENVIRONMENTAL CONTRASTS

Photoperiod.—Photoperiod, conclusively shown to regulate the timing of gametogenesis in *S. purpuratus* (Pearse et al., 1986; Bay-Schmith and Pearse, 1987), is similar from latitudinal to local scales. Hence change in daylength would not be expected to cause marked interpopulation differences in reproduction. Light intensity decreases with depth. Changes in light level affect spawning in various invertebrates, but this has not been demonstrated for echinoderms (Giese and Kanatani, 1987; Strathmann, 1987; Pearse et al., 1988; Byrne, 1990).

Water Movement.—Water movement in the vicinity of our study sites has been characterized for typical and storm periods. Jackson and Winant (1983) found that

current speeds within the PLKF are one third of those outside. In normal conditions flow is highest at the seaward edge of the forest, typified by 18 m, and much lower inside the bed at areas like 8 m, since currents entering the kelp forest slow to typical inside-forest velocities within 100 m of the edge. Seymour et al. (1989) studied water movements near our sites during unusual periods with large storm waves. U^2 , mean maximum surface flow speed squared (highest wave in a thousand), over three winter storm periods was highest at 18 m ($6.29 \text{ m}^2 \text{ s}^{-2}$) and decreased with distance into the bed ($5.76 \text{ m}^2 \text{ s}^{-2}$ and $4.55 \text{ m}^2 \text{ s}^{-2}$ at 15 m and 12 m, respectively). Maximum significant wave heights at the Mission Bay Channel entrance were 5.1 m (Seymour et al., 1989). The intertidal site, about 1 km inside the channel, is relatively protected from storm waves, but storm surge does occur. Concurrent data on maximum significant wave height suggest strongest effects of water motion on the bottom mainly during winter and spring, and occasional autumn storms. All data combined indicate a reduction in flows from deep to shallow sites.

Water motion has direct and indirect effects on reproductive processes. Higher flows and lower *Macrocystis* stipe carrying capacity at 18 m (Dayton et al., 1992) may limit drift availability relative to shallower, internal locations within the kelp forest. Direct effects of, for example, increasing tidal flows, wave action, turbulence, and other flow-related physical shock have not been clearly shown to trigger spawning in marine benthic invertebrates. However, Young (1945) suggested that California mussels are stimulated to spawn by high wave action. Higher flows can produce indirect effects—changes in concentrations of phytoplankton, gametes, pheromones or other chemicals, temperature, or turbidity affecting light conditions, any of which induce spawning in urchins or other invertebrates (Himmelman, 1975; Giese and Kanatani, 1987; Starr et al., 1990; Babcock et al., 1992). We observed corresponding changes in our study populations in the level and timing of reproductive processes, indicating spawning of reproductively mature adults after high storm wave periods. High wave heights preceded several steady or sharp declines in GI, percent of induced spawners, and numbers of mature eggs in ovaries. These events also occurred earlier and sometimes more precipitously at deeper, higher flow sites. Urchins at 18 m spawned earlier in 1994 than in 1995. This interannual variability in spawning may be due to anomalously high waves in October 1994. Winter storms causing high waves in this region typically do not occur until late November or December, as was the case in 1995 (based on closest available wave data from the SIO Pier; SIO Coastal Data Information Program), when spawning also occurred later than in 1994. Since reductions in GI are mainly due to spawning, if spawning is mechanically triggered by direct physical disturbance from water movement (via changes in pressure, velocity, acceleration, etc.), then it is likely that not just wave height, but the frequency and cumulative number of waves in a given period are also important variables affecting reproduction.

Temperature.—There are direct and indirect effects of temperature on reproduction of *S. purpuratus*. Seasonal changes in temperature have been invoked as the cause for temporal and interpopulation patterns in sea urchin reproduction (Cochran and Englemann, 1975). Laboratory experiments on *S. purpuratus* in southern and central California showed that gametogenesis and gamete storage were inhibited above 17°C (Cochran and Englemann, 1975; Pearse, 1981). This corresponds with the typical summer regression in reproductive state of most individuals. Temperatures were $\geq 17^\circ \text{C}$ from May to November during both years at the intertidal site, and from

July to November 1994 at 8 m. This corresponds with the period when non-mature gametes predominated in ovaries. These observations support Cochran and Englemann's (1975) and Pearse's (1981) experimental results: temperatures $\geq 17^\circ\text{C}$ appear to negatively influence gametogenesis. This effect is likely to be greater at shallower sites and negligible at deeper ones. In contrast with gametogenic patterns, during warm water periods we saw large increases in GI in all populations. Also, GI was generally higher in warm, shallow, food-rich populations, and gonad production per unit area was highest intertidally and decreased with depth. These findings corroborate Pearse (1981) who found higher GI's in a Baja California Norte, Mexico, population in warm, shallow water, relative to another shallow population only 4 km away in much colder, upwelled water. Unlike GI, both populations typically had strikingly similar gametogenic patterns and reproductive timing, despite very different environmental temperatures, except during a high temperature period when gametogenesis was slowed at the warm water site. The annual reproductive cycle (as generally measured by GI) is similar for populations throughout the species range, from the north, where the temperature range is small with a 15°C maximum, to southern and Baja California. In the present study, the temperature range and maxima are greater: $11\text{--}23^\circ\text{C}$. Temperature does not tightly synchronize the timing of the annual reproductive cycle, however, higher temperatures do appear to limit gametogenesis.

High temperatures increased feeding rate, which sustained higher respiration, not growth of *S. purpuratus* (Pearse, 1981). These somatic processes put potential limits on reproduction, such as the observed reductions in gametogenesis (Cochran and Englemann, 1975; Pearse, 1981; this study). Other indirect effects of temperature on reproduction include temperature-mediated nutrient content of plant foods, rates of food decomposition, and resource abundance for urchins (see below). In summary (1) temperatures near 17°C appear critical for progression of gametogenesis or gamete storage, but (2) do not directly limit gonad growth by proliferation of nutritive cells. (3) Populations of *Strongylocentrotus* spp. in warmer, or shallower, potentially more food-rich waters tend to have higher gonad production (e.g., *S. purpuratus*: Pearse, 1981, and this study, *S. droebachiensis*: Keats et al., 1984, *Strongylocentrotus franciscanus* A. Agassiz, 1863: Carney, 1991, and Rogers-Bennett et al., 1995), but the opposite occurs for some noncongeners (e.g., *Evechinus chloroticus* Valenciennes, 1846: Dix, 1970, *Paracentrotus lividus* Lamarck, 1816: Byrne, 1990), suggesting other factor(s) are important.

Food Availability.—Average drift abundances were significantly higher at shallower subtidal sites from 1983–1987, and of the same order of magnitude as seen in this study, but up to five times lower than peak intertidal drift levels (Tegner and Dayton, 1991: figs. 1, 2, based on numerous 400 m^{-2} samples). Drift peaks occurred in summer to autumn, as seen in previous years at the intertidal, and at the Point Loma Kelp Forest (see Baker, 1973; Tegner and Dayton, 1991, respectively).

Links between nutrition and reproduction are known for many echinoids (Lawrence, 1975, 1987; Lawrence and Lane, 1982; Thompson, 1982; Pearse and Cameron, 1991), but underlying mechanisms integrating feeding and reproduction are not fully resolved. For example, the dependence of gonad development on food supply suggests that gonad condition is a good index of urchin nutrition. However, relationships among these processes are influenced by the role of the gonad as a principal energy storage organ that can buffer effects of extremes in food availability on reproduction (reviewed by Lawrence, 1987; Pearse and Cameron, 1991). The relative size of

the gut (e.g., height of gut wall epithelium), or volume of its contents, often shows annual variations reflecting urchin nutritional state (Lawrence et al., 1965), perhaps sooner, or over a shorter term than gonadal changes. The fairly low seasonal variation in gut and gonad size in populations of *S. purpuratus* and *S. franciscanus* in the 1960s (including 14 m depth in the PLKF; Pearse et al., 1970; Pearse, 1981) suggested a relatively constant, low food supply at that time (visually estimated in the 1960s). In contrast, we saw seasonal patterns in gut and gonad size; their cycles were roughly inversely related, with successive peaks in drift abundance, gut, and gonad size.

Earlier field observations suggested that reproduction was correlated with algal food abundance (reviewed by Giese and Pearse, 1974; Pearse and Cameron, 1991). However, food abundance is too variable in time and space to produce the similar reproductive timing observed either in geographically widespread populations, or at the same site over time (Pearse and Cameron, 1991). Variation in food abundance, preference, assimilation, and nutritive value directly affects metabolism, and seasonal patterns in feeding and somatic growth of *S. purpuratus* and other echinoids (Ebert, 1968; Leighton, 1968; Lawrence, 1975, 1987; Vadas, 1977; Pearse, 1981). Less clear are separate or combined effects of food amount, type, or nutritional quality on reproduction. Holland (1964) and Russell (1987) quickly enhanced and advanced the time of gonad growth or gametogenesis in laboratory experiments by feeding *S. purpuratus* unlimited amounts of *Macrocystis*. Only two field studies (Lees, 1970; Baker, 1973), which were near our study sites, have had a few overlapping, quantitative samples of GI and food availability for two urchin populations. These studies suggested urchin populations having more high-quality food produced larger gonads, and that gonads were larger in the PLKF than at shallow Mission Bay sites, similar to our findings. Neither previous study had sufficiently long, overlapping time series needed to assess food or other environmental effects on reproduction, and seasonal or interannual variation. Thompson's (1982) experiments on effects of food on reproductive effort of *S. droebachiensis* suggested that when preferred algae are limited (as often occurs for the intertidal population), animals allocate resources to reproduction over somatic growth, since urchins would gain little from further growth in a food-stressed environment. This, along with the long-term nutrient storage capability of the gonad, may partly explain why intertidal urchins continue to reproduce. Moreover, although corallines were the most abundant attached intertidal algae, and often made up a large volume of gut contents, our data suggest that occasional large pulses of preferred drift *Macrocystis* constitute the most important energy source for reproduction. Dix (1970) also associated larger gonads of *E. chloroticus* with greater food supply (but the latter was not quantified). Although difficult to extrapolate to natural populations, field caging experiments in which *E. chloroticus* density and unialgal diets were varied suggested that algal availability and individual preference directly influenced gonad size and condition (Andrew, 1986). Offshore populations of *Lytechinus variegatus* Lamarck, 1816 and *Arbacia punctulata* Lamarck, 1816, relative to individuals in shallow water, had low gut and gonad indices suggesting food limitation and low production, but an extended reproductive potential by existing at greater depths (Hill and Lawrence, 2003).

Food Quality.—Gonad development, the proportion of gonad tissue types, and somatic growth vary with diet in *S. purpuratus* and other urchins (reviewed by Pearse and Cameron, 1991). *Strongylocentrotus purpuratus* showed highest preference, di-

gestibility, and gonad growth on *Macrocystis* relative to five other algae (Leighton, 1968; Lawrence, 1975, table 8).

Drift species composition in the present study was very similar among sites and times; *Macrocystis* dominated drift and gut contents. Thus drift composition is unlikely to account for observed reproductive differences. Intertidal urchins ate relatively high percentages of coralline algae; presumably most corallines were grazed from rocks. The nutritional value and absorption efficiencies of corallines are low for urchins (Lawrence, 1975), and likely contribute little to reproduction.

The nutritive value of drift algae can vary with species composition, production location, seasonal growth conditions for source plants, part of plant, or drift plant tissue senescence and degradation time (since drift was produced) (e.g., Niell, 1976; Gerard, 1982, 1984; Hanisak, 1983; Zimmerman and Kremer, 1984; Reed et al., 1996). C:N ratio is an indicator of both nitrogen content and senescence in various algal tissues; C:N differs significantly for live brown, green, and red algae; brown algae have higher C:N (lower nitrogen content). Low algal C:N ratios are characteristic of rapid growth in biomass, while higher values occur when algal productivity is low. Species that grow primarily in colder periods or places have lower C:N (i.e., relatively enhanced N content) (Niell 1976). Mann (1972) found similar trends for two laminarian kelps during favorable and unfavorable growth seasons.

Variation in algal nutrient and energy content has many potential consequences for urchin reproduction (reviewed by Lawrence, 1975; Lawrence and Lane, 1982). Algal composition varies with age, structure, season, and locality. Few studies address these factors (however, see Percival, 1968). As kelp ages, tissue sloughing often occurs, leading to a loss of structural integrity and materials like structural polysaccharides and photosynthates, e.g., mannitol. Food value varies with algal structure due to differences in preference, nutrient content, or absorption efficiency (Leighton, 1968; Lawrence, 1975). Growth, and presumably other processes, were reduced in *S. purpuratus* and *S. franciscanus* when fed *Macrocystis* haptera vs blades (Leighton, 1968). Urchins grew faster when fed kelp covered with the bryozoan *Membranipora* Linnaeus, 1767 than with epiphyte-free kelp (Jensen, 1969; Nestler and Harris, 1994). There is seasonal and spatial variation in algal epiphyte cover at Point Loma and elsewhere (Pearse et al., 1970; Bernstein and Jung, 1979; Yoshioka, 1982). More epiphytes occur at 18 m than at our other sites, suggesting that epiphytized plants yield more nutrition for urchin reproduction.

The biomass and nutritional quality of kelp, and possibly drift, depend on earlier oceanographic conditions that affect the production and tissue composition of algal stands; cooler water containing high nutrient levels results in favorable growth and accumulation of nitrogen in macroalgal tissues (Gerard, 1982, 1984; Zimmerman and Kremer, 1984; Reed et al., 1996). Drift from kelp produced in colder seasons, or from plants in deeper, colder water presumably contains higher levels of carbon and nitrogen, and decomposes at slower rates than drift produced at higher temperatures.

C:N ratio is used to assess animal dietary requirements since it effectively measures the percentage of nitrogen in food (Russell-Hunter, 1970). Grazers do not use all of the nutrient and energy content of algae since they contain indigestible structural polysaccharides. Thus, it is inappropriate to use total carbon or energy content of food to assess its nutritional value (Lawrence, 1975).

We know of no comparisons of nutrient content, absorption efficiency, or food value for reproduction of live, attached algae and drift at various stages of decomposition. Live and drift *Macrocystis* C:N and percent N values (range 0.7%–3.7%) in the present study were similar to ones for live *Macrocystis* at Point Loma (Tegner and Dayton, 1987) and elsewhere in southern California, and were generally consistent with expectations based on differences in temperature, dissolved nitrogen, and live kelp C:N in this region (Gerard, 1982; Reed et al., 1996). We saw generally higher C:N and lower N values at shallower sites, or in periods with higher temperatures. Reduced nitrogen levels in drift compared to live kelp at 18 m may be due to drift decomposition. Tissue nitrogen levels limiting growth of *Macrocystis* (1.1%, Gerard, 1982) were generally more common at shallower, warmer sites, suggesting that, on average, the nutritional value of kelp for urchin reproduction may decline with decreasing depth. Temporal or spatial variation in drift kelp condition could be due to uncertainty about the location and prevailing environmental conditions where drift was produced, and in the length of time and distance moved since drift was detached from source plants. We need more information on the production, change in composition, and fate of drift to determine its importance for urchin nutrition and reproduction. Regardless of drift nutrient content, temporal changes in gonad size and condition are directly related to changes in drift *Macrocystis* abundance and urchin gut contents.

SUMMARY

The range in urchin GI values in the PLKF was similar in the 1960s (Pearse et al., 1970; Pearse, 1981) and the 1990s (present study), suggesting that environmental effects on GI were similar during both periods. The range in urchin GI in the PLKF is high and similar to that of populations from central California northward. In contrast, range in GI at the intertidal site is lower and similar to other southern and Baja California populations (see also figs. 25–28 in Boolootian, 1966; Pearse, 1981). There is high intrapopulation variation in GI in this and other echinoids (reviewed by Pearse and Cameron, 1991 and Lozano et al., 1995). Reproductive patterns in the three populations studied reflect those seen throughout the species range (reviewed by Pearse and Cameron, 1991), but interpopulation differences we observed closely tracked variation in local environmental conditions, e.g., in temperature, rates of accumulation of drift, and spawning cues. Sequential peaks in drift kelp abundance, urchin nutritional, and reproductive measures demonstrate the strong influence of food availability on gonad production in all populations. Our study, like earlier ones of this and other species of urchins, indicates that *S. purpuratus* allocate available resources to reproduction before the start of gametogenesis. Food amount regulates reproductive output, but not timing. Food availability is too variable to provide consistent cues for reproductive timing, which is most tightly regulated by photoperiod in *S. purpuratus* (Pearse and Cameron, 1991). The large temperature differences among sites undoubtedly regulate physiological and reproductive rate processes; higher temperatures can severely limit reproduction in shallow water. High temperatures, $\geq 17^{\circ}\text{C}$, occur annually for several months in the intertidal zone, and correlate with lower gametogenic activity. In contrast, reproduction in subtidal populations is not affected by high temperature episodes, which may partly explain why gametogenesis and spawning occur earlier in deeper water.

Differences in, and interactions among, environmental conditions affecting the reproduction of ecologically and economically important animals like sea urchins require careful consideration at different space and time scales as we attempt to predict the outcome of changing environmental conditions, fishing, or management practices. Even small differences in the relative reproductive contributions of local populations in contrasting environments hint at potential multi-scale consequences which may influence their relative contributions to successive generations; shallow populations have greater total reproductive output (e.g., Rogers-Bennett et al., 1995 for *S. franciscanus*, this study), are capable of spawning for longer periods during the year, may have higher fertilization rates, and be a larger, or more consistent source of larvae. If so, shallow populations may have more influence on overall metapopulation and genetic structure. A fishery for *S. purpuratus* occurred on the heels of declining catches of red sea urchins *S. franciscanus* (Kalvass and Hendrix, 1997). Given the apparent importance of populations of *S. purpuratus* and other urchins, and their susceptibility to heavy fishing pressure, environmentally-influenced differences in life history and population characteristics need to be factored into management efforts to ensure population persistence. Local differences in reproduction among populations may confer ecological or evolutionary advantages to various *S. purpuratus* populations, or may reflect differential susceptibility among populations to changes in environmental conditions.

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