

Spatial variability in red sea urchin (*Strongylocentrotus franciscanus*) recruitment in northern California

LANCE E. MORGAN,^{1,*} STEPHEN R. WING,²
LOUIS W. BOTSFORD,¹ CAROLYN J.
LUNDQUIST¹ AND JENNIFER M. DIEHL¹

¹Department of Wildlife, Fish and Conservation Biology,
University of California, Davis, California, USA

²Department of Marine Science, University of Otago,
304 Castle Street, Dunedin, New Zealand

ABSTRACT

To better understand the spatial distribution of recruitment in the northern California red sea urchin (*Strongylocentrotus franciscanus*) population, we sampled size distributions at each of 12 locations in 1995 and 1996, two of those locations in 1994, and 5 of those locations in 1997. An index of recent recruitment in these size distributions and an estimate of density of recent recruitment reflect a similar spatial pattern of recruitment. This pattern appears to be determined by the effect of coastal circulation on larval delivery during relaxation of upwelling, and not the result of the positive effect of the adult spine canopy on juvenile survival. Recent recruitment of red sea urchins in northern California is higher in areas more frequently subjected to onshore and poleward flow during relaxation of upwelling. These results are consistent with a mechanism by which alongshore spatial variability in southward, offshore flow during upwelling winds allows larvae to maintain latitudinal position, whereas flows during event-scale relaxations in upwelling winds serve to distribute settling larvae alongshore, favouring areas north of promontories. The consequent spatial pattern of red sea urchin settlement varies from year to year, and there are not yet sufficient data to demonstrate the degree to which this spatial pattern in recruitment determines a spatial pattern in fishable adult abundance.

Key words: Larval dispersal, meroplankton, northern California, recruitment varia, red sea urchin, spine canopy, *Strongylocentrotus franciscanus*, upwelling relaxation

INTRODUCTION

The long development times and consequent large distances that planktonic marine larvae may travel result in variable recruitment across broad temporal and spatial scales. The task of understanding the complex association of physical transport and recruitment has been the focus of many studies of meroplanktonic organisms such as crabs (Shanks, 1983; Hobbs *et al.*, 1992; McConnaughey *et al.*, 1992; Botsford *et al.*, 1994a; Wing *et al.*, 1995a, b), sea urchins (Ebert and Russell, 1988; Wing *et al.*, 1995a; Miller and Emlet, 1997), barnacles (Connell, 1985; Gaines and Roughgarden, 1985; Gaines *et al.*, 1985; Shanks, 1986; Farrell *et al.*, 1991; Gaines and Bertness, 1992, 1993; Roughgarden *et al.*, 1992), rockfish (Ainley *et al.*, 1993; Larson *et al.*, 1994), as well as other species (Underwood and Denley, 1984). Despite these efforts, there is still little understanding of the spatial variability in recruitment over the ranges of entire metapopulations connected by larval dispersal (Botsford *et al.*, 1994a). Dispersal patterns can account for a great deal of this variability, and may be as important to metapopulation dynamics as life-history characteristics such as mortality and reproduction (Underwood and Denley, 1984; Pulliam, 1988; Possingham and Roughgarden, 1990; Botsford *et al.*, 1994a; Hastings and Higgins, 1994; Caley *et al.*, 1996) and adult interactions (Connell, 1975; Paine, 1984).

The motivation for this study is the need to know the origins and destinations of recruits when managing fisheries distributed over space. The management of fisheries for sustainability requires maintaining sufficient reproductive capacity, which requires knowing not just the impact of fishing on reproduction at each location, but also the impact of that reproduction on recruitment at other locations. This need is especially acute in the design of marine protected areas and other forms of management based on spatial closures

*Correspondence. L.E. Morgan, Santa Cruz/Tiburon Lab., SWFSC, NMFS, 3150 Paradise Dr., Tiburon, CA 94920, USA. e-mail: lancem@tib.nmfs.gov

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(Botsford *et al.*, 1993; Quinn *et al.*, 1993; Pfister and Bradbury, 1996). The ability to delineate source and sink populations (Pulliam, 1988; Carr and Reed, 1993; Allison *et al.*, 1998) is necessary for the design of spatial management schemes, and is useful in detecting recruitment overfishing. Understanding the spatial pattern of larval dispersal is an important aspect of a complete understanding of the role of recruitment dynamics in determining sustainable catch.

The dispersal patterns of meroplanktonic larvae have been inferred by a variety of means, ranging from direct observations to theoretical models (Allison *et al.*, 1998). Direct observations have been possible for a few species with relatively large larvae that disperse over relatively short distances (Olson, 1985; Davis and Butler, 1989; Carlon and Olson, 1993). Identification of the physical mechanism underlying larval dispersal by sampling larval distributions in the plankton and settlement over space and time concurrently with hydrographic measurements is a second approach (Pedrotti and Fenaux, 1992; Wing *et al.*, 1995b; Miller and Emlet, 1997). Several studies have compared settlement variability over space on a variety of scales from metres to many kilometres (Caffey, 1985; Rumrill, 1988; Judge *et al.*, 1988; Raimondi, 1990; Gaines and Bertness, 1993; Sewell and Watson, 1993; Wing *et al.*, 1995a; Harris and Chester, 1996). Physical oceanographic models of coastal circulation can also contribute to an understanding of the movement of planktonic organisms with specific physical and behavioural characteristics (Hofmann *et al.*, 1991; Botsford *et al.*, 1994a; Keough and Black, 1996).

Here we test whether spatial patterns in recruitment are caused by known aspects of coastal circulation in northern California. The approach taken is to analyse spatial patterns of recruitment from postsettlement observations of size distributions and density. In addition to the effects of circulation prior to settlement, postsettlement processes can also influence recruitment (Connell, 1985; Rowley, 1989; Holm, 1990). We evaluate one of these effects that is known for this species, the protection of newly settled individuals beneath the spine canopy of adults (Tegner and Dayton, 1977), as an alternative explanation of the spatial pattern of recruitment.

Physical oceanographic influences on meroplankton

For the past two decades, increased awareness and understanding of mesoscale variability in coastal circulation off northern California has drawn attention to its implications for meroplanktonic larvae. The presence of strong offshore flows and an equatorward jet during the upwelling season in April to July (Largier

et al., 1993), led to the question of how species with a planktonic stage during these months could persist (Parrish *et al.*, 1981). Research over the past decade indicates the probable answer to this question lies in the combination of: (1) the potential for retention of larvae in alongshore frontal zones (Richardson and Percy, 1977; Shenker, 1988) and areas to the south of coastal promontories termed 'upwelling shadows' (Graham *et al.*, 1992; Graham and Largier, 1997); and (2) the potential for subsequent larval delivery to the coast in flow reversals, both cross-shelf and alongshore, during occasional (event-scale) periods of relaxation or reversal of upwelling winds (Roughgarden *et al.*, 1992; Shanks, 1995; Wing *et al.*, 1995a, b).

Cross-shelf flows of water masses driven by event-scale variability in upwelling winds have been shown to influence the timing of barnacle settlement in central California. In studies monitoring barnacle settlement, pulses in recruitment on weekly time scales occurred during relaxation in upwelling winds (Farrell *et al.*, 1991; Roughgarden *et al.*, 1992). Larvae appeared to settle in the intertidal when the upwelling 'front' moved cross-shelf and 'collided' with the shore. Upwelling relaxations also influence transport of pelagic juvenile rockfish in this region, although these are not considered necessary for successful settlement (Larson *et al.*, 1994). Several mechanisms such as internal waves or tidal bores could play a role in the cross-shelf transport during upwelling (review: Shanks, 1995).

In northern California, observations near a major promontory (Point Reyes) have shown that the same event-scale variability in upwelling winds drives alongshore as well as cross-shelf transport of larvae, leading to similar temporal variability in the settlement of crab and sea urchin larvae, and a consistent spatial distribution of settlement along the coast. Observations of planktonic larval distributions and settlement on artificial collectors over space and time concurrent with measurements of hydrographic conditions have led to the conclusion that larvae are retained south of Point Reyes during upwelling winds (Wing *et al.*, 1998), then are transported poleward and shoreward where they settle during upwelling relaxations (Wing *et al.*, 1995a, b). On weekly time scales, crab (primarily *Cancer* spp.) settlement north of Point Reyes increased during periods of upwelling relaxation. Settlement was associated with a sharp increase in hourly temperature, suggesting larvae were transported poleward in the alongshore current identified by Send *et al.* (1987) and Kosro (1987) on the basis of temperature, current meter, acoustic Doppler current profiler and satellite and aircraft surface temperature observations. This coastally trapped flow may

be buoyancy forced, driven in part by freshwater flow from San Francisco Bay. More recent alongshore temperature monitoring indicates that the distance north of Point Reyes reached by this current varies, depending on the duration of the relaxation (Wing *et al.*, 1995b). Poleward alongshore flow was also indicated in geopotential anomalies and in acoustic Doppler current meter records from Bodega Bay to north of Point Arena in 1981 and 1982 (Huyer and Kosro, 1987; Kosro, 1987). Drifters released offshore and south of Point Arena during the upwelling season generally moved south, but with occasional periods of northward movement (Davis, 1985). The temporal pattern of sea urchin (*Strongylocentrotus* spp.) settlement was similar to that described for crabs, but not as predictably tied to relaxation events, suggesting they may either reside in a different water mass than crabs, or may respond in a different manner owing to biomechanical differences (e.g. size, swimming behaviour).

Although less studied from both physical and biological perspectives, the coastal dynamics near Point Arena suggest a pattern similar to that observed at Point Reyes with an onshore and poleward flow during relaxation, with some differences. Observations from AVHRR satellite images of sea surface temperature show that during upwelling relaxation, while a warm band of water flows poleward around the headland at Point Reyes, at Point Arena there is poleward flow of warm water, which affects the coast north of this cape (Fig. 1). Surface waters south of Point Arena appear cold during upwelling and remain cold during relaxation, as compared with the warmer waters in the larval retention zone south of Point Reyes. However, there is a persistent, anticyclonic eddy south and offshore of Point Arena during the upwelling season (Washburn *et al.*, 1993), and this eddy could retain larvae and transport them shoreward during relaxation. The poleward flows in both the computed geopotential anomalies and the acoustic Doppler data cited above (Huyer and Kosro, 1987) continue from south of Point Arena to the north, and data from drifters released near shore north of Point Arena indicated an onshore, downwelling flow north of Point Arena (Davis, 1985).

In addition to this evidence from plankton sampling and settlement collectors in the area near Point Reyes and Point Arena, there is also evidence suggesting that the mesoscale variability in circulation associated with the 100 km scale variability in coastal morphology in northern California and Oregon may influence larval settlement on a larger scale. Ebert and Russell (1988) sampled size distributions of a congener

of the red sea urchin, the purple sea urchin (*Strongylocentrotus purpuratus*), along the west coast from Oregon south to California and concluded that recruitment is strongly influenced by coastal circulation associated with headlands. Based on the coefficients of variation of size distributions at various locations along the coast, they concluded that populations at, and to the south of, headlands had lower recruitment because of stronger offshore transport of larvae at these locations. Areas just to the north of these strong, offshore, upwelling jets had larger coefficients of variation in the sizes of purple sea urchins, which they concluded indicated higher recruitment. Their results, however, leave several unresolved questions regarding the mechanism that would lead to increasing recruitment from south of a headland to the next promontory, the method of estimating recruitment variability, and the long-term population implications of their assumptions.

The explanation for lower recruitment to the south of headlands was that the features associated with headlands affect generally southward transport of larvae in the California Current. While it is true that larvae would generally be transported southward in the California Current, especially under the influence of the strong coastal jet that accompanies upwelling, it does not provide a specific physical mechanism for formation of the gradient in settlement between headlands during active upwelling. Here we interpret our results in terms of a mechanism we have observed near Point Reyes, that explains this gradient in our data and in the observations by Ebert and Russell (1988) in terms of alongshore flow during upwelling relaxation.

While variability in past recruitment affects the coefficient of variation of a size distribution, the coefficient of variation (c.v.) is not a precise indicator of that variability. For example, the denominator of the c.v., the mean size at a location, depends on the pattern of individual growth and mortality rates, which depend on a variety of characteristics other than recruitment, including differences in life-history traits (Russell, 1987), genetics (Edmands *et al.*, 1996), predators (Tegner and Dayton, 1981; Botsford *et al.*, 1994b; Scheibling, 1996), density (Leviton, 1989) and wave action (Edwards and Ebert, 1991). It is difficult to assess how spatial and temporal variability in these affected the computed c.v.s and conclusions. The numerator (the standard deviation) depends on the number of recent recruits, and their ages; recruitment further in the past would have less effect on the standard deviation than would recent recruitment. Variability in recruitment would affect the c.v., only

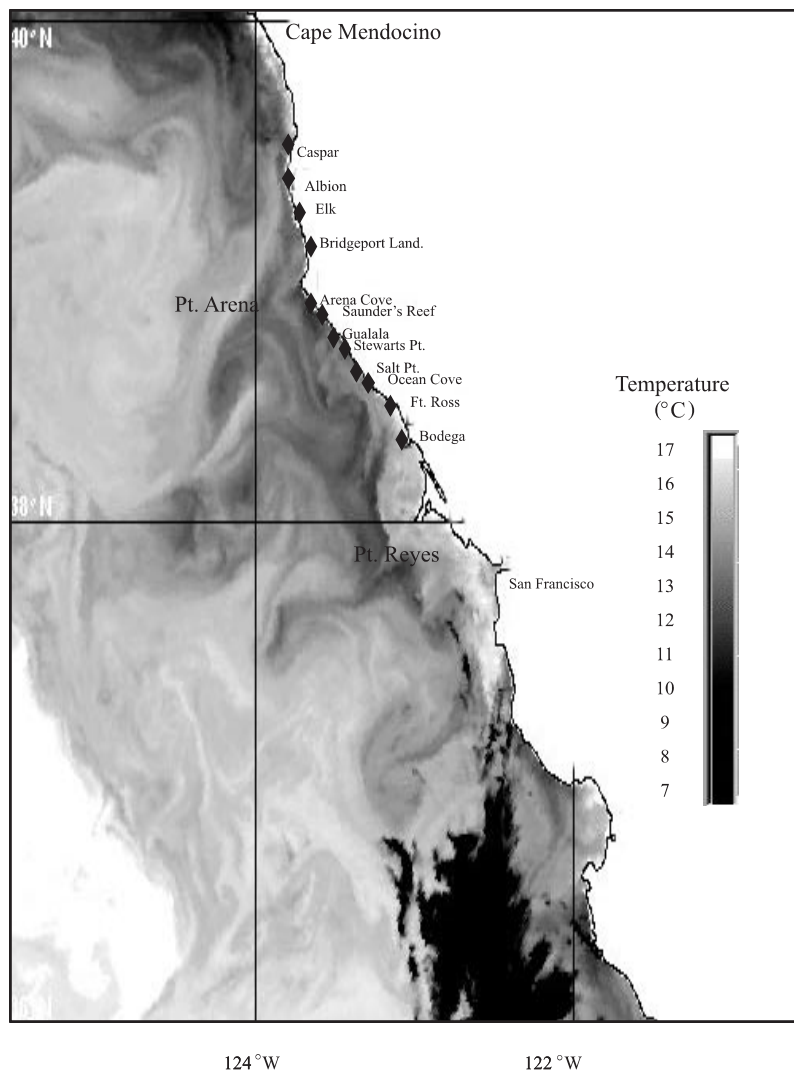


Figure 1. AVHRR satellite image of sea surface temperature from day 207, 1994, showing the poleward and onshore flow above Point Arena (light shades) and the poleward and alongshore flow around Point Reyes out of the Gulf of the Farallones (light shades). Dark areas indicate cooler water (e.g. the filament extending south below Point Arena). Diamonds indicate locations of sites where size distribution data were collected.

in the sense that little or no recruitment over the past 5–7 years would produce a lower c.v. than would recruitment every year. Thus, **at best the c.v. is sensitive only to recruitment variability on long time scales.**

Ebert and Russell (1988) did phrase their conclusions in terms of long-term low or high recruitment at the various locations, but this brings up a second, related difficulty. If we conclude that recruitment is constantly low or high at various locations, how is the upper mode in the size distribution maintained? In a recruitment-driven population with no density dependence in adult mortality, constant lower recruitment at a location would result in size distributions with the same shape as size distributions at locations with constant, but higher recruitment (e.g. Botsford *et al.*, 1994b). A compelling argument for long-term low or high recruitment at various locations on the basis of differences in shapes of size distribu-

tions requires an explanation for how such differences could persist.

The red sea urchin

The settlement pattern of red sea urchins is influenced by the season of spawning, and the development time needed for planktonic larvae. There is a seasonal pattern in the size of gonads and maturity of gametes, with development in late winter and an apparent peak in spawning during the spring (Bernard, 1977; Kato and Schroeter, 1985; Pearse and Cameron, 1991; Wing *et al.*, 1995a). Larvae of the red sea urchin may take 7–19 weeks to metamorphose prior to settlement (Strathmann, 1978; Cameron and Schroeter, 1980; Strathmann, 1987; Rowley, 1989). Several studies have monitored settlement on a weekly basis in northern California. Wing *et al.* (1995a) found peak settlement of red sea urchins during July of 1992 at

Bodega Marine Reserve (BMR) and Salt Point, Sonoma County, though some settlement was observed in all months sampled (May to September). Harrold *et al.* (1991) found settlement of sea urchins in all months except October, with peak settlement in the month of July, during sampling from mid 1988 to mid 1989. They did not distinguish between *S. franciscanus* and *S. purpuratus*. Ebert *et al.* (1994) monitored settlement at three sites in Mendocino County in 1990 and two sites from 1991 to 1993. They found settlement in July and August at Point Cabrillo and Point Arena in 1990, no settlement in 1991, settlement during May to September at Point Cabrillo, and July and August at Westport in 1992, and settlement in March at Point Cabrillo in 1993. Settlement in northern California was described as episodic, suggesting it coincided with occasional, unidentified oceanographic events.

In Oregon, a pattern of variable sea urchin settlement in the spring and summer was observed (Miller and Emlet, 1997) that is similar to the pattern near Point Reyes (Wing *et al.*, 1995a, b). Settlement of red and purple sea urchins was associated with warm-water events characterized by a stratified water column and associated with northward wind stress. Concurrent plankton sampling found higher abundance of larval sea urchins in warm water masses between 11°C and 12°C, near times of settlement. Miller and Emlet (1997) concluded that during the spring and summer upwelling flow regime, settlement of sea urchins occurred with onshore flow during relaxation events forced by winds from the south.

Here we attempt to explain spatial variability in recruitment of red sea urchins, *Strongylocentrotus franciscanus*, in the context of mesoscale features of the circulation associated with two distinct promontories in northern California – Point Reyes and Point Arena. We use an index of recent recruitment based on the shape of the size distribution and an estimate of density along the coast to assess recruitment over several years. Our analysis focuses on the potential for a physical mechanism involving upwelling relaxations that transport larval sea urchins alongshore and to the nearshore for settlement. We test the hypothesis that the spatial pattern of juvenile abundance in the size distribution reflects a pattern in previous settlement owing to this physical mechanism. Specifically, we propose that areas subject to more frequent warming during upwelling relaxations will experience higher recruitment because larvae are retained in this non-upwelled, warmer water and transported to shore. According to this mechanism, recruitment to the north of the two headlands, Point Reyes and Point Arena, would be more frequent than recruitment to the south of Point Arena.

METHODS

Field collection

Size distributions were collected in August, September and October of 1995 and 1996 at 12 locations in northern California (Fig. 1). Some of these sites were also sampled in 1994 and 1997. Two sites, Bodega Marine Life Refuge (BMR) and Salt Point, were sampled four times (1994–1997); four sites, Caspar, Albion, Arena Cove and Gualala, were sampled three times (1995–1997); the other sites were sampled twice (1995–1996). SCUBA divers collected animals from the bottom at a depth of 8–12 m, placed them in canvas bags and brought them to the surface for measurement. Although the substrate was not destructively sampled, the removal of all individuals encountered ensured recovery of protected, smaller individuals, under the adult spine canopy. However, it is unlikely that divers were able to sample individuals under 10 mm in proportion to their true abundance. Test diameter to the nearest 1 mm was recorded, and individuals were grouped into 5 mm size classes for analysis.

In 1996, divers collected red sea urchins for density estimates along 30 × 5 m transects at all sites. Transect lines were positioned along isobaths between 8 m and 12 m. Transect lines were dropped from the surface to minimize bias in selecting areas to sample. The number of urchins encountered in each 1 × 0.5 m quadrat was recorded. Adult sea urchins were examined visually to assess whether juveniles were present underneath the spine canopy, but rocks were not turned over to inspect for smaller individuals. Crevices and holes were searched visually. Site density was calculated as the total number of individuals divided by the total area searched.

Data analysis

Analysis of size-distribution data to determine the factors causing recruitment requires an estimate of the correspondence between the data, which are in terms of abundance-at-size, and past recruitment, as indicated in abundance-at-age. As a rough indicator of the recruitment cohort responsible for abundance at each size, we used a size-structured model of growth to establish the upper and lower sizes for each cohort in the first three years following settlement. Growth estimates (Morgan *et al.*, 2000) and seasonal settlement patterns (Wing *et al.*, 1995a) were used in a size-structured model based on von Bertalanffy growth with individual variability in L_{∞} (Botsford *et al.*, 1994b; Smith *et al.*, 1998). We assumed that growth and mortality were similar between sites and that settle-

ment follows a similar monthly pattern at each site and in each year, but that the magnitude of annual settlement could vary with location and year. These results were then used to classify the year of recruitment responsible for abundance at each size in the collected size distributions.

We tested whether recent recruitment indicated in the size distributions collected at each site reflected the spatial pattern expected on the basis of circulation patterns during upwelling relaxation. There are several approaches to quantifying recent recruitment, and each has limitations. Direct estimates of density per unit area are desirable, but precise estimates require sampling a significant proportion of the area of interest, hence are expensive. As described above, we collected data in transects of quadrats at each site for cursory density estimates. The number of quadrats at each location ranged from 300 to 1650. We calculated density by estimating abundance in an assumed large area, $2S \text{ m}^2$ (S is the total number of quadrats of 0.5 m^2 in this area). The estimate of abundance is $A = nS$, where n is the mean abundance in a quadrat (Seber, 1982). The variance of this estimate is:

$$\sigma^2 = vS^2 \left(\frac{1}{s} - \frac{1}{S} \right) \quad (1)$$

where v is the variance of the quadrat counts and s is the number of quadrats sampled at each location. From this expression and the expression for abundance, we can see that the coefficient of variation (i.e. σ/A) goes to a constant as S becomes large. We therefore assumed that S was an arbitrarily large area so that its specific value did not influence the coefficient of variation in our density estimates. We calculated recruit density by multiplying the estimated site density by the percentage of individuals less than 60 mm in the size distribution at each location. Based on estimates of growth rate, individuals less than 60 mm include the first 3 cohorts in the size distribution.

The alternative to estimating density is to describe recent recruitment in terms of an index, by dividing the abundance of recent recruits by the abundance of larger individuals in the size distribution. The overlapping of several year classes at larger sizes is presumed to be a reasonably constant indicator of long-term average recruitment. This index is more precise, but it is an indicator of recruitment relative to long-term recruitment at that site, rather than density. To obtain such an index, we divided abundance at small sizes (0–60 mm) by abundance at large sizes (70–89 mm). We could not use urchins larger than the

legal size (>90 mm) because of potential bias due to differential harvesting between sites. This index is somewhat problematic in that abundance in the range of 60–89 mm involves summing over only 4 or 5 year classes, which limits its usefulness as an indicator of long-term variability.

We examined the potential influence of adult spine canopy on recruitment by computing an index of the amount of spine canopy available. The middle value of each 5 mm size increment was converted to an area, assuming each urchin to represent a horizontal circle. The spine canopy index was the sum over all size classes greater than 90 mm of that area multiplied by the percentage in the size increment. We multiplied density times spine canopy index to provide an estimate of total spine canopy density (SCD) at each site.

We examined the influence of spine canopy index, density and minutes of latitude north of a headland (Point Arena or Point Reyes) on recruitment index and recruit density with pairwise correlations.

RESULTS

Size distributions from the 12 sites show a variety of shapes (Fig. 2a,b,c), but the fraction of individuals in the smaller size classes appears to follow the spatial pattern hypothesized on the basis of known circulation near Point Reyes (Send *et al.*, 1987; Wing *et al.*, 1995a, 1995b, 1998) and proposed circulation near Point Arena (Davis, 1985; Huyer and Kosro, 1987). Sites to the north of Point Arena show larger proportions of small individuals than sites immediately to the south of Point Arena. BMR, the site closest to Point Reyes, also shows a larger number of small sea urchins in the size distribution. Areas closed to fishing, BMR and Caspar, also stand out from the others because of the presence of large individuals (>110 mm).

The index of recent recruitment computed from these size distributions indicates that recruitment is higher for areas north of Point Arena and at BMR (Fig. 3a). These areas are the most likely to encounter warm-water flows during relaxations from upwelling (e.g. Fig. 1). This pattern is consistent between 1995 and 1996, the two years that all sites were sampled. The size distribution at Fort Ross is the single exception, suggesting lower recruitment than one would expect on the basis of this mechanism. This general pattern is a better match to our prediction based on circulation patterns than would be expected by chance alone, as evidenced by a significant correlation between minutes of latitude north of a headland and the recruitment index (Table 1). Values of recruit density

Figure 2a.

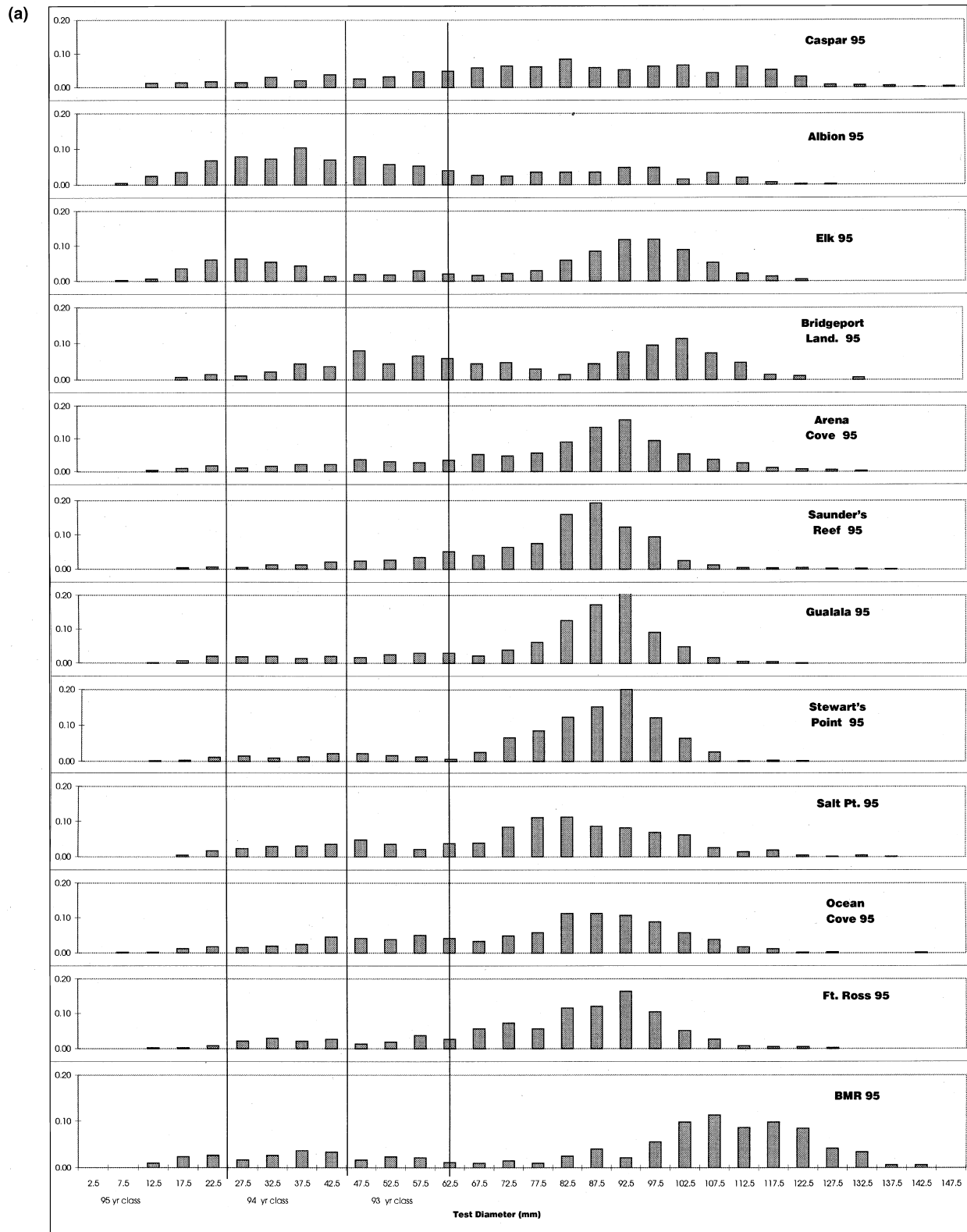


Figure 2b.

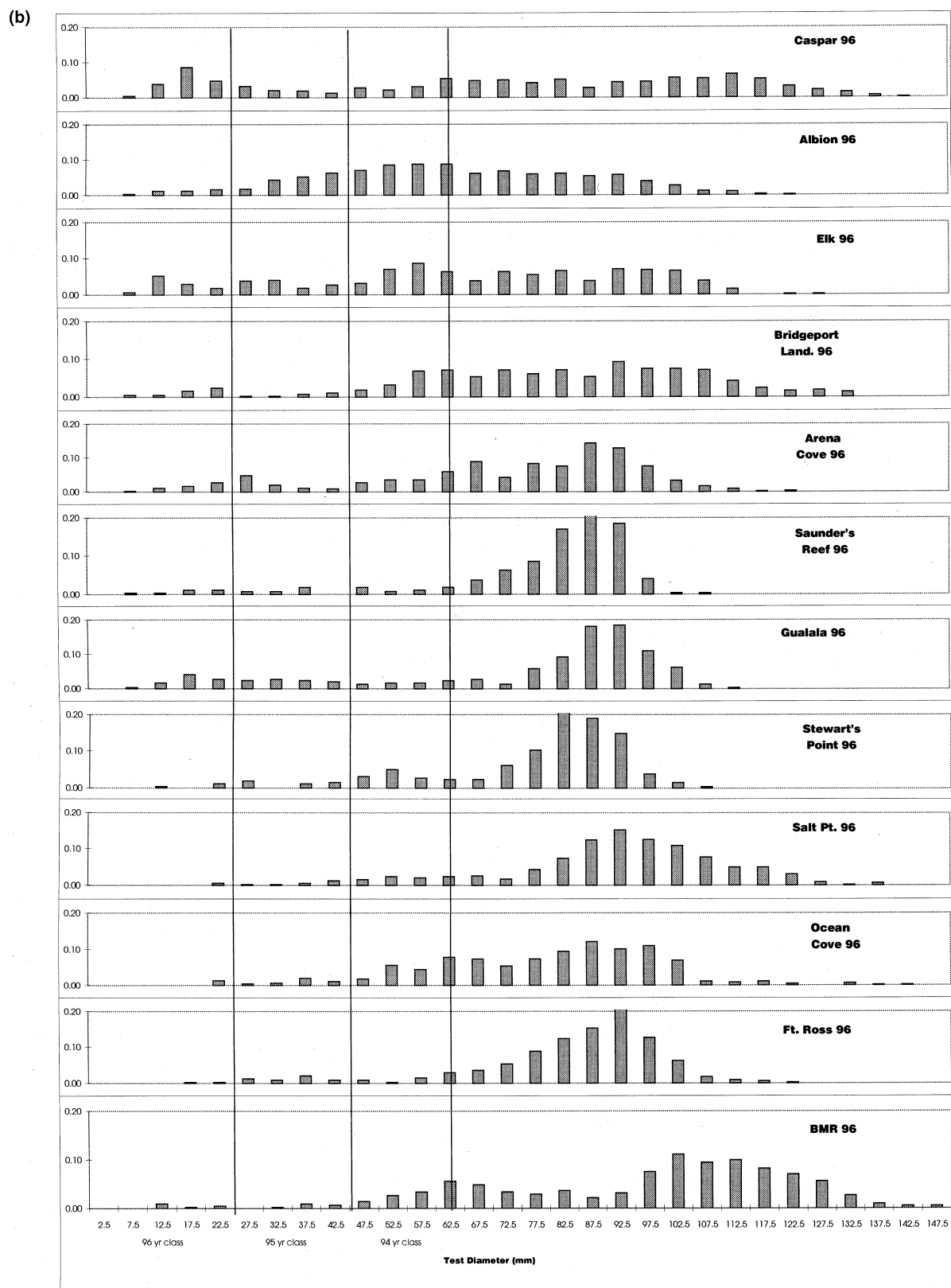


Figure 2. Fraction of each size in the field-collected size distributions of red sea urchins during: (a) 1995; (b) 1996; and (c) 1994 and 1997. Vertical lines indicate approximate ages based on estimates from size-structured growth model. The first category is recruitment in the current year, then one year earlier, then two years earlier. Beyond that point, age classes overlap to a large degree.

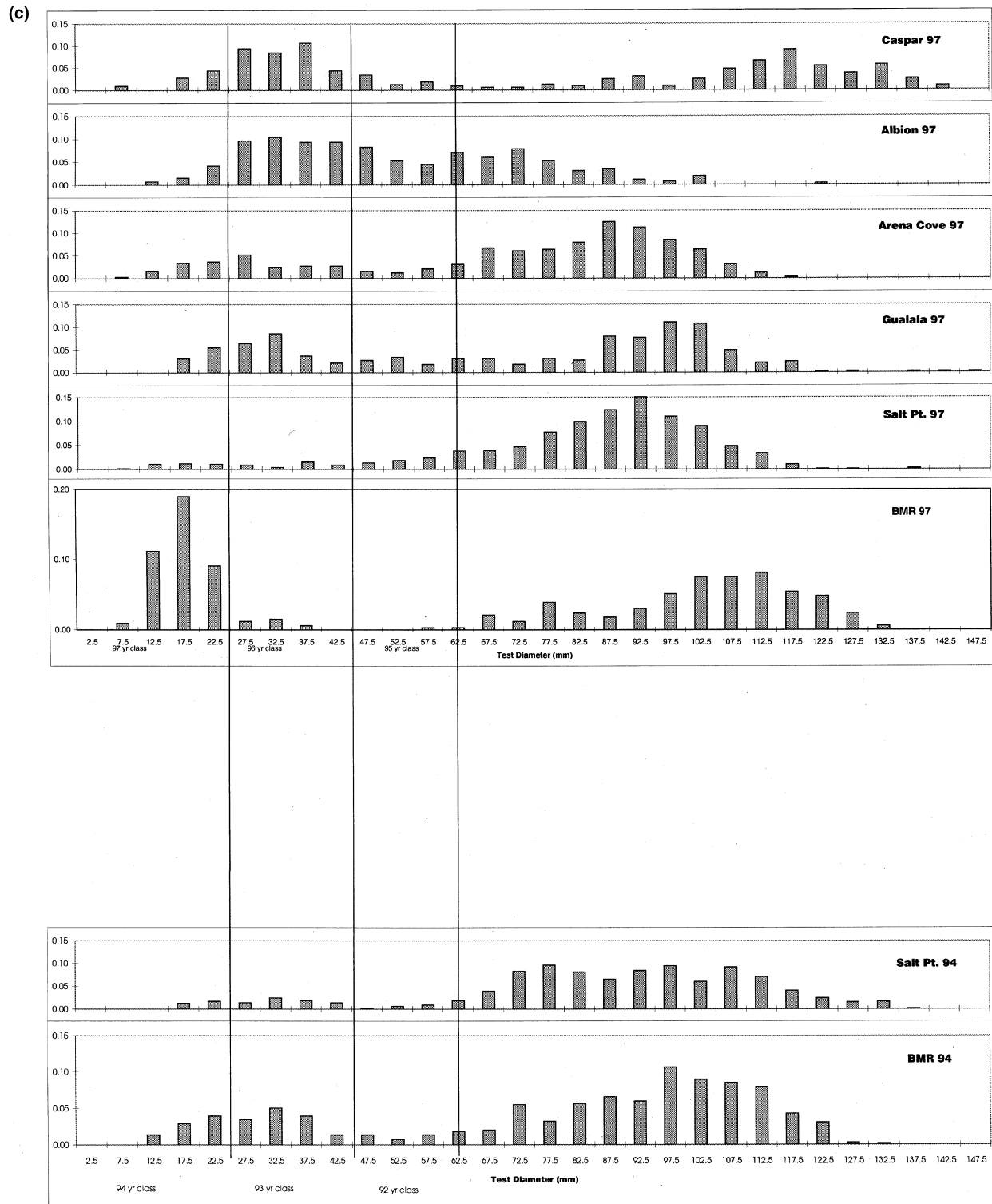
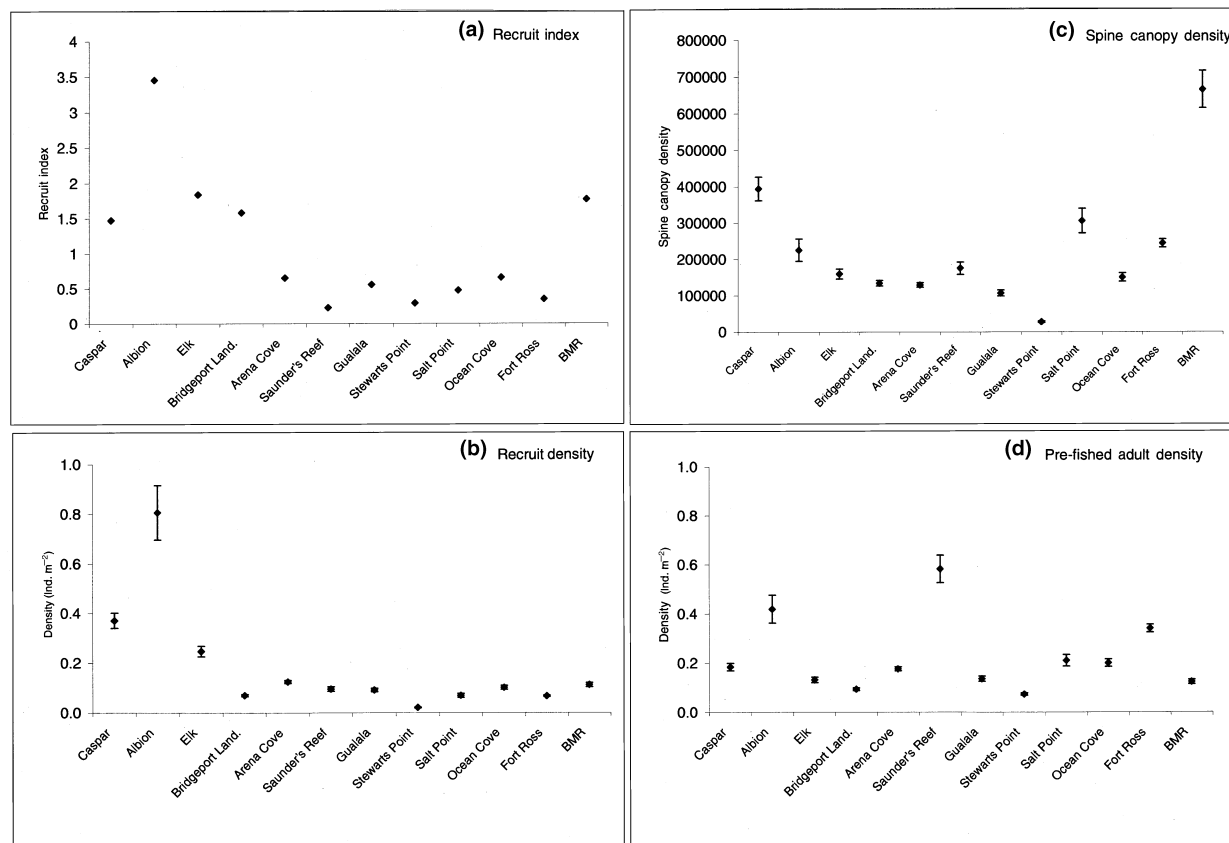


Figure 3. (a) Recruitment Index (number of sea urchins from 0 to 60 mm divided by the number of sea urchins from 70 to 89 mm) averaged for 1995 and 1996, the two years when all sites were sampled. (b) Recruit Density (density multiplied by the fraction of individuals in the 1996 size distribution smaller than 60 mm). (c) Spine Canopy Density (sum of: density \times area covered by sea urchins \times fraction in size distribution for each 5 mm increment over 90 mm). (d) Density of prefished adults (the fraction of sea urchins smaller than the minimum fishable size \times density). Error bars are calculated based on the variance in density estimates (see text).



show a spatial pattern of red sea urchin recruitment similar to the indices of recruitment, except that sites just north of Point Reyes have densities that are lower than expected (Fig. 3b). However, sites to the north of Point Arena have higher recruitment density (Fig. 3a) than sites to the south of Point Arena.

An alternative explanation of the spatial pattern in the recruitment index, that it is a result of spatial variability in the amount of protective habitat under adult spine canopies, is not supported by a comparison with the spatial distribution of computed spine canopy density (Fig. 3c, Table 1). The distribution of the spine canopy density is dominated by the two reserve sites (BMR and Caspar) where harvest is not allowed, as expected. However, these are not the sites with the highest values of recruitment density or recruitment index.

An approximate assessment of the relative contributions of recruitment in different years to the size

distributions indicates that the recruitment seen in Fig. 2 occurred at different locations in each year. Based on the growth model described above, we can roughly separate the age classes of recent recruitment into 0–25 mm for 0 to one-year-olds, 25–45 mm for two-year-olds, and 45–60 mm for three-year-olds. In the 1994 size distributions, there is evidence of little settlement in 1992, slightly more settlement in 1993 and even less in 1994. Although this 1992–1994 pattern of settlement does not show up clearly in Fig. 2(a,b) because of the scale of these plots, it was clear enough to be followed through 1997 at BMR and Salt Point in Morgan *et al.* (2000) as a test of the growth estimates. This 1993 cohort appears in the 1995 size distributions at Albion, Bridgeport Landing, Salt Point and Ocean Cove, along with contributions from the 1994 year classes at Albion and Elk. This same pattern of settlement generally carries over into the 1996 size distributions; Albion and Elk indicate

Table 1 Correlations between recruitment index, recruit density, and adult density and factors that could influence the observed spatial pattern of recruitment: (i) the availability of adult spine canopy (SC density); and (ii) relative position with regard to upwelling relaxation flow moving poleward above headlands (Mins lat. North). * indicates significant correlations at $P < 0.05$.

	Recruitment index	Density			Mins lat. North
		Recruit	Adult	SC	
Site					
Caspar	1.47	0.371	0.185	394 459	24
Albion	3.46	0.806	0.420	225 634	16
Elk	1.84	0.248	0.131	160 170	10
Bridgeport Land.	1.58	0.070	0.093	134 659	6
Arena Cove	0.65	0.124	0.176	129 802	55
Saunder's Reef	0.23	0.095	0.583	175 764	51
Gualala	0.56	0.091	0.136	107 689	47
Stewarts Point	0.29	0.021	0.073	28 525	39
Salt Point	0.48	0.069	0.210	306 197	34
Ocean Cove	0.66	0.102	0.199	150 828	33
Fort Ross	0.35	0.067	0.340	244 590	31
BMR	1.77	0.112	0.122	665 838	19
Correlations					
Recruitment index	1				
Recruit density	0.859*	1			
Adult density	0.038	0.343	1		
SC density	0.307	0.134	-0.013	1	
Mins lat. North	-0.716*	-0.387	0.267	-0.321	

strong 1994 year classes. The 1996 size distributions also indicate little recruitment in 1995, but recruitment at Caspar and Elk from 1996. In the 1997 size distributions there is evidence of that recruitment in 1996 at Caspar, Albion, Arena Cove and Gualala, and a strong pulse of 1997 recruitment at the Bodega Marine Reserve.

DISCUSSION

Observed spatial patterns in the size distributions, indices of recent recruitment, and recruit density, as well as negative correlations of these with distance north of headlands, all indicate that locations subject to more frequent upwelling relaxation flows show a greater abundance of recent recruits. At the southern sites, the pattern of crab settlement described in Wing *et al.* (1995b), i.e. that during relaxation, settlement was greater at sites closer to Point Reyes (such as BMR) than sites further to the north (Salt Point), is reflected in the postsettlement size distributions of red sea urchins. This mechanism is supported by physical data from AVHRR, flow meters, geopotential anomalies and drifters. At the northern sites, a similar pattern at Point Arena consistent with a similar relaxation flow is also observed. Sites to the north of this promontory, points at which AVHRR satellite observations of

surface temperature indicate that a relaxation flow would first contact the shore (e.g. Fig. 1), show the highest rates of recruitment in recent years. The areas south of Point Arena, which are only infrequently visited by the relaxation flows from south of Point Reyes seen in AVHRR images, show very low rates of recent recruitment.

This spatial pattern is also consistent with transport implied by larger-scale flows observed in the region between Cape Mendocino and Point Reyes. Dynamic heights from a hydrographic survey in early May of 1987 (Hayward and Mantyla, 1990) indicate flow offshore at Cape Mendocino, turning southward about 100 km from shore, then shoreward, affecting the coast north of Caspar (Fig. 5 of Hayward and Mantyla, 1990). Flow is then alongshore to Point Arena, where it turns offshore, then south, then again shoreward, affecting the coast near Salt Point (Fig. 5 of Hayward and Mantyla, 1990), and turning to flow south. Such a current could disperse larvae from north of Cape Mendocino to both of the areas of high settlement identified here. These observations are not completely synoptic, hence may not reflect actual flows. This 12 day survey moved from near shore to offshore, and winds were from the south for the first few days, then were from the north for the remainder.

This mechanism could also be responsible for similar spatial patterns further north along the coast. In Oregon, Miller and Emlet (1997) focused on the temporal variability in red sea urchin settlement, associating settlement pulses with upwelling relaxation events concurrent with northward winds. However, there was also significant spatial variability in their observations. Their site 10 km south of Cape Blanco had much lower densities of red sea urchins in the plankton and lower settlement than their site 50 km north of that promontory. This pattern of settlement is consistent with greater onshore flow to the north of promontories, as proposed for Point Arena.

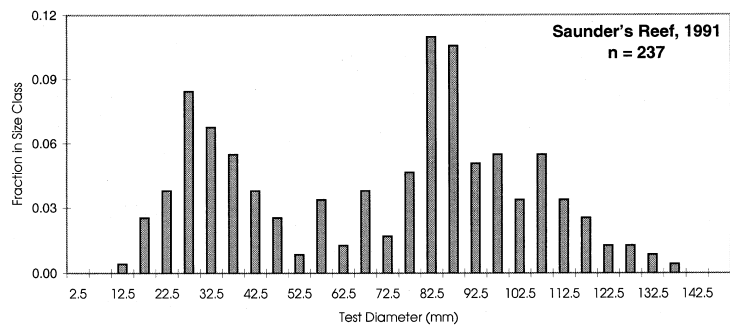
This mechanism would have important implications for populations distributed along the coast. For example, it explains how populations with planktonic larvae in the California Current during the upwelling season can maintain themselves despite strong offshore, equatorward mean advection during the upwelling season (cf. Parrish *et al.*, 1981). Also, to the extent that larvae are retained at the 'downstream' (southern) end of embayments and returned to their embayment of origin, this mechanism sets a scale for dispersal (Botsford *et al.*, 1998 discuss the consequences of this mechanism in the context of Dungeness crab). The degree of 'leakage' between embayments cannot be determined from the type of data collected here, but may be testable through population genetic methods (Palumbi, 1994; Burton, 1995).

Our results are similar to those of Ebert and Russell (1988) in that they describe differences in settlement north and south of promontories, but they extend them in several respects, providing an explanation that is applicable to the purple sea urchin as well as the red sea urchin. Here we quantify the relative amount of recruitment at each location, rather than just proposing that recruitment is greater or less at each location on the basis of the coefficient of variation of the size distribution. We also explain the observed spatial pattern of recruitment in terms of a specific mechanism for larval delivery, alongshore poleward flows during upwelling relaxation. Location of larval settlement is based on specific mesoscale circulation patterns, not just position with respect to headlands and presumed patterns of offshore flow. Our analysis based on minutes of latitude north of a headland is appropriate because of the significance of poleward flow leading to settlement north of promontories, but is not fundamentally different from the significant positive correlation with minutes of latitude south of a headland noted by Ebert and Russell (1988).

The data presented here provide evidence for a mechanism underlying a spatial pattern in recent recruitment; however, the implications for the spatial distribution in long-term abundance are not as clear. The long-term consequences of the spatial pattern of recent recruitment are relevant both to the consistency of our explanation and the implications for the relative densities that can be expected for fishery management of these populations. The primary question is whether we can expect the same spatial pattern in population density that we have seen in recent recruitment. That would require that the pattern actually have an effect on adult density, and that the spatial pattern persist from year to year. With regard to the latter, the size distributions presented here indicate that the spatial pattern expected from the relaxation mechanism does not appear as an exact replicate each year, but it may predominate. More frequent settlement at some locations would lead to higher average density at those locations.

To test whether higher recent recruitment at a location influences adult density, we examined the pattern in density with the effects of recent recruits and fishing removed, by computing a correlation between location and the abundance between 70 mm and 89 mm. The spatial pattern of density of individuals between 70 mm and 89 mm (Fig. 3d) does not show as clear a spatial pattern as the recent recruitment index (Fig. 3a) or recruit density (Fig. 3b). The correlation with latitude north of a point is 0.267, which is not significant at the 0.05 level, and the opposite sign of our expectation. Thus the effect of frequency of settlement on a narrow range of adult sizes is likely confounded either by longer time scale patterns such as very large, but infrequent recruitment classes, or by local site factors related to postsettlement survival. This low correlation is not unexpected, because a strong correlation between the abundance less than 60 mm and abundance between 70 and 89 mm would be high if the size distribution had a constant shape over those sizes, rather than the pattern of recent recruitment seen here. This is because the data presented here do not contain an independent estimate of long-term density of different size classes; we have estimated density in only one year. To determine whether this spatial pattern in recruitment ultimately drives a spatial pattern in adults entering the fishery, we would need to estimate density in several years or make use of fishery data under constant conditions. Because this fishery has developed so recently, data from the fishery are not yet appropriate for this purpose.

Figure 4. Fraction at each size in the field distribution from Saunder's Reef in 1991. Note the large number of small sea urchins, a lower mode nearly as large as the upper mode. (Data from California Department of Fish and Game, Fort Bragg.)



The density at Saunder's Reef is an exception to a general association between recruitment and adult density, having low relative recruitment and recruitment density, but high adult density. This combination could be explained by very high recruitment at this location in the recent past. We were able to locate a size distribution from surveys made by the California Department of Fish and Game in 1991. In 1991, there appeared to be a recruitment event equal in size to the upper mode (Fig. 4). In relative terms, the recruitment pulse in Fig. 4 is larger than any in Fig. 2, except the 1997 recruitment at BMR.

The fact that the age of sea urchins cannot be confidently determined limits our ability to identify abundance at a certain size with its year of recruitment. Here we have used an age-length association derived from a model fitted to size increment data and size distribution data (Smith *et al.*, 1998; Morgan *et al.*, 2000). While this relationship is useful in interpreting size distributions, it should be kept in mind that an error of a year in either direction would not be improbable. Early or late settlement within a year can lead to mistakes in assigning the year of settlement; also, associating age with size for very small urchins (<30 mm) is uncertain because growth estimates are based on larger animals. While the growth patterns from Morgan *et al.* (2000) appear to be consistent with laboratory growth (Morris and Campbell, 1996) and observations from cultured individuals planted in the field (Rogers-Bennett, 1994), these uncertainties are highlighted by the 1996 cohort. This cohort is strong in the 1997 size distributions, but relatively small in the 1996 size distributions. In part this is expected owing to the difficulty in finding and sampling the smallest urchins, but may reflect small discrepancies between our estimates of the cohort boundaries because of the reasons mentioned above.

Because our interpretation of the size distributions presented here depended on relative abundance at different sizes, it is useful to assess the variability that might be expected from general biological and

physical conditions in this region over the past 10 years. Local manifestations of ENSO events could affect sea urchin recruitment through effects on larval transport and food availability. Growth rates of sea urchin larvae depend on food levels (Hart and Scheibling, 1988) and presumably mortality rates would also. The ENSO event that began in 1997 was preceded by several years of cooler, non-ENSO conditions, 1994–1996. The period between 1991 and 1993 is considered an ENSO period on this part of the coast (Lynn *et al.*, 1995), with anomalous poleward flows in 1992 (Sakuma and Ralston, 1995) and lower primary productivity (Lenarz *et al.*, 1995). The period from 1988 to 1990 was an exceptionally cool period (Lenarz *et al.*, 1995).

If ENSO events had a negative effect on sea urchin larval productivity, most of the recruitment seen here would have occurred during relatively good years, 1994 to 1996. The relatively good recruitment seen here in 1993 is not consistent with that scenario, nor is the pulse of recruitment at BMR in 1997, but the 1991–1993 ENSO was waning in 1993, and the 1997–1998 ENSO was evident on this part of the coast only as lower local winds in the spring and summer. We would expect higher abundance at adult, fishable sizes (greater than 90 mm) in, for example, the 1996 size distribution, with a possible dip in abundance between 60 and 90 mm owing to the 1991–1993 ENSO conditions. One of the consequences of such a scenario would be lower-than-usual recruitment to the fishery in the next few years.

The observed pattern of recruitment is consistent with an independent analysis of the decline in catch per unit effort (CPUE) in the red sea urchin fishery in northern California. Botsford *et al.* (1998) showed that at three of the four ports in northern California, CPUE had declined faster than would be expected in 'fishing up' an unharvested stock. This would imply that in these three locations, recruitment to the fishery had declined. The only port at which recruitment was not adversely affected was Albion, an area that receives

relatively high recruitment according to the interpretation we present in this study.

Mesoscale patterns of circulation in northern California, and the delivery of larvae to the coast during upwelling relaxation, is the explanation most consistent with the observed pattern of recent recruitment. We are using this information to assess potential impacts on fishery yields, but it will be more useful in fishery management once we understand how recruitment contributes to a spatial pattern in harvestable abundance. Now that the fishery has reached a state such that annual catch is dependent on recruitment from only one or two years, we will be able to observe spatial variability in production, and possibly explain that variability on the basis of physically mediated differences in recruitment. Continued monitoring of settlement, plankton and hydrographic features will improve our understanding of the complete larval dispersal path. This information is topical in light of current increasing interest in marine protected areas (Carr and Reed, 1993; Rowley, 1994; Allison *et al.*, 1998) and spatial management of fisheries in general (Dugan and Davis, 1993; Botsford *et al.*, 1993; Quinn *et al.*, 1993).

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