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Latitudinal variation in size structure of the west coast purple sea urchin: A correlation with headlands[1]

Abstract—Size structure of the purple sea urchin *Strongylocentrotus purpuratus* was sampled from central California to central Oregon (36°–45°N). Size frequency and inferred recruitment events are correlated with major topographic features. Capes and headlands—predictable sites of upwelling and locations of cold water plumes—show size frequencies indicative of low recruitment rates. Sites without predictable upwelling or regions that are between headlands have size frequencies that indicate substantial annual recruitment.

Planktonic larvae of marine organisms may spend many weeks at sea during which time they may travel hundreds of kilometers from their origin before they are competent to metamorphose and settle. They may be moved offshore, brought back onshore, or kept at or away from suitable settlement sites by processes acting at several scales.

Differences in settlement and recruitment at a specific site represent an integration of processes acting over many degrees of latitude (Efford 1970; Frank 1975; Parrish et al. 1981; Ebert 1983) as well as very locally (Kendall et al. 1982; Shanks 1983; Gaines and Roughgarden 1985; Connell 1985; Kingsford and Choat 1986). The purpose of this note is to show a correlation between population size structure and coastal features, with associated oceanographic processes, that exists at a scale of one hundred to several hundreds of kilometers. These medium-scale features are important in understanding the dynamics of species with planktonic stages (Cowen 1985) as well as interactions within nearshore communities (cf. Dayton and Tegner 1984).

Features at a scale of one to several hundreds of kilometers can be seen in infrared images from satellites (Bernstein et al. 1977; Mooers and Robinson 1984). Along the Pacific coast in the region from Cape Blanco, Oregon, to Point Conception, California, large cold plumes or jets, extending tens of meters vertically from the surface and two hundred or more kilometers offshore, may form during spring and summer. They recur in about the same places, both between years and within a given year (Kelly 1985). The jets may form in response to local topography and winds (Kelly 1983, 1985; Davis 1985), but there are alternative

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hypotheses for their formation (e.g. Huyer and Kosro 1987) as well as additional effects of headlands on oceanographic features (Beardsley et al. 1987).

Places along the California coast that are the sites of intense upwelling and plume formation are Point Reyes with a wide shelf that extends down to San Francisco Bay, Point Arena, and Cape Mendocino, which has very rough bottom topography. In Oregon, Cape Blanco and Heceta Banks have offshore extensions in bottom topography and are recognized regions of upwelling (Ikeda and Emery 1984). Eddy formation is more energetic south of Cape Mendocino where winds that are favorable for upwelling are stronger than in Oregon (Davis 1985). Late spring and early summer mark the onset of wind stress that is favorable to upwelling and jet formation, and it continues episodically through late fall, although upwelling is possible at any time during the year (Chelton 1981; Parrish et al. 1981). The west coast purple sea urchin *Strongylocentrotus purpuratus* spawns during winter to early spring (Pearse et al. 1986) and has a planktonic larval period of probably 9–12 weeks before larvae become competent to settle (Strathmann 1978). Therefore, initial upwelling and jet formation coincides with the time when urchins start to settle. We were interested in discovering whether upwelling and jet formation, which could modify larval density in coastal waters, would be reflected in the population structure along the coast. Specifically, we wished to test the null hypothesis that population size structure was independent of sites where cold water jets form.

Analysis of satellite images for this study was done at the Scripps Institution of Oceanography Satellite Facility with training and help by R. Whritner and J. Svejkovsky. The manuscript benefited from the comments of C. Barilotti, C. E. Dorman, and R. L. Bernstein.

During late spring 1985 and 1986 we sampled rocky intertidal sites along the Pacific coast from about 36° (central California) to 45°N (central Oregon). Intertidal pools with sea urchins were bailed to remove as much water as possible and then thoroughly searched. In channels or boulder
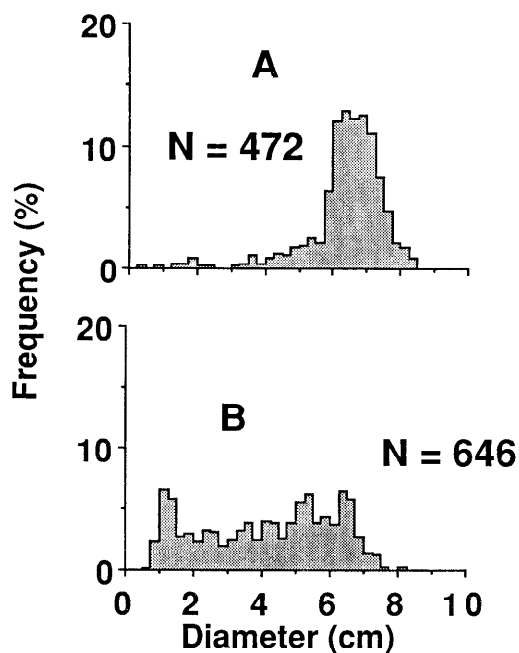

Fig. 1. Size frequency distributions of *Strongylocentrotus purpuratus*. A. Cape Blanco, Oregon, 4 June 1985. B. Yaquina Head, Oregon, 6 June 1985.

fields an arbitrary area was delimited and then searched. When time permitted during a low tide, several pools or areas were sampled. The diameters of animals were measured with knife-edged vernier calipers to the nearest 0.01 cm, and then animals were returned to their intertidal habitats.

The original intention of the sampling was to obtain further documentation of a latitudinal cline in recruitment where previous data supported the hypothesis that annual recruitment was good in the south and became progressively worse with increasing latitude (Ebert 1983). In 1985, samples were spaced irregularly from central California to central Oregon in the expectation that the size structure of populations would show ever greater concentration of individuals at a single mode of large individuals, thus reflecting sporadic recruitment. Samples in Oregon showed that this simple cline did not exist.

Recruitment has been poor for many years at Cape Blanco (Fig. 1A): there are very few small animals or individuals of intermediate sizes. The mode of large animals represents an accumulation of many year

Table 1. Summary statistics of population size structure of *Strongylocentrotus purpuratus* from central California to central Oregon. °S column is degrees south of a major headland (Point Reyes, Point Arena, Cape Mendocino, and Cape Blanco); for Soberanes Point and Garrapata State Park, °S values in parentheses are degrees south of Pigeon Point (37°10.9′N).

Location	°S	1985					1986				
		N	Range	Mean	SD	C.V. (%)	N	Range	Mean	SD	C.V. (%)
Soberanes Point									22 June		
36°27′N	1.55						62	0.32–4.53	2.98	1.08	36.4
	(0.73)						81	0.78–4.88	3.00	0.84	28.0
							456	0.17–5.38	2.33	1.32	56.9*
Garrapata State Park				1 June					22 May		
36°28′N	1.53	333	0.68–5.18	3.15	0.87	27.8	160	0.21–5.01	2.77	1.03	37.3
	(0.71)						229	0.22–5.20	3.16	1.18	37.6*
Bean Hollow				1 June					22 May		
37°31′N	0.78	65	0.25–5.24	3.14	1.10	35.1	95	0.73–5.33	3.03	1.00	32.9
		33	0.38–5.06	3.01	1.13	37.7	58	0.30–5.42	3.15	1.21	38.3
		88	0.17–5.10	3.00	1.23	40.7	192	0.20–5.77	2.64	1.39	52.5
		120	0.33–5.12	2.24	1.55	69.3*					
Fitzgerald Marine Reserve									23 May		
37°32′N	0.47						142	0.27–5.55	4.02	0.86	21.3
							240	0.19–6.33	4.04	1.05	26.1*
Duxbury Reef				2 June							
37°53′N	0.12	107	1.71–6.77	4.38	0.97	22.1					
		316	1.17–7.12	4.48	1.26	28.1					
Palomarin									24 May		
37°57′N	0.05						241	1.39–8.26	5.67	1.28	22.6*
							177	2.86–8.03	5.91	1.21	20.5
1. Point Reyes 38°00′N											
McClure Beach									30 May		
38°11′N	0.77						217	0.65–3.55	1.75	0.62	35.5
Bodega Marine Reserve				13 April					28 April		
38°20′N	0.62	405	0.44–5.34	2.98	1.08	36.1*	331	0.85–4.74	2.74	0.80	29.0
Windemere Point									29 May		
38°32′N	0.42						378	0.19–6.25	3.34	1.49	44.6*
							371	0.19–5.17	2.70	0.83	30.6
Arena Cove				14 April					29 April		
38°55′N	0.03	280	1.08–7.13	4.50	0.96	21.3*	267	1.77–6.46	4.32	0.86	19.8
				2 June							
		50	0.70–6.11	4.49	0.98	21.8					
2. Point Arena 38°57′N											
Bruhel Point									28 May		
39°36′N	0.83						103	1.09–4.56	2.87	0.74	25.7
							163	0.26–7.53	4.08	1.79	43.8*
							151	0.30–7.59	4.15	1.57	37.8
							269	0.20–7.04	3.55	1.51	42.5
Shelter Cove				3 June					25 May		
40°2′N	0.40	322	0.68–7.34	4.91	1.41	28.7*	94	0.58–6.95	4.55	1.30	28.7
		176	0.65–7.38	4.78	1.23	25.7	151	0.59–6.72	4.52	1.26	28.0
							194	0.80–6.86	4.53	1.13	24.9
Devils Gate									26 May		
40°24′N	0.03						30	2.52–5.69	4.09	0.72	17.7
							200	1.11–6.60	3.62	1.12	30.9*
							100	1.02–5.47	3.24	0.86	26.5
3. Cape Mendocino 40°26′N											

Table 1. Continued.

| Location	°S	1985					1986				
		N	Range	Mean	SD	C.V. (%)	N	Range	Mean	SD	C.V. (%)
Elk Head									27 May		
41°4′N	1.76						372	0.85–5.60	3.59	0.95	26.6*
Cape Blanco				4 June							
42°50′N	0.0	472	0.44–8.50	6.37	1.18	18.5*					
4. Cape Blanco 42°50′N											
Cape Arago				9 June							
43°18.5′N		109	0.99–6.94	4.77	1.14	23.9					
		131	2.56–6.90	4.97	0.82	16.6					
Sunsct Bay				5 June							
43°20′N		87	1.39–6.74	4.23	0.96	22.8					
		203	1.07–6.35	4.83	0.96	19.8					
		208	0.80–7.40	4.63	1.27	27.4*					
		214	1.50–7.18	4.70	1.07	22.8					
		57	3.25–8.48	6.82	1.14	16.7					
				8 June							
		340	0.78–9.09	6.37	1.42	22.2					
Yaquina Head				6 June							
44°40′N		646	0.75–8.08	4.17	1.95	46.7*					
Boiler Bay				7 June							
44°50′N		175	0.74–7.96	5.01	1.89	37.7					
		233	0.64–7.40	4.68	1.67	35.8					
		86	0.91–6.78	4.14	1.33	32.1					
		55	1.11–8.12	4.79	1.89	39.4					

* Distributions with largest C.V. for each site that are plotted in Fig. 2.

classes. In contrast, the sample from Yaquina Head (Fig. 1B) shows very good recruitment: there arc many small animals as well as all intermediate sizes up to the mode of large animals. Progressive changes in size-frequency distributions have been followed in Sunset Bay, Oregon, since 1964 (Ebert 1968, 1983) and show that a substantial recruitment event can be recognized as a distinct mode for at least 7 yr, so the single mode at Cape Blanco in 1985 indicates poor recruitment at least since 1978 and the lack of an obvious gap in the Yaquina sample indicates good recruitment during this same time.

A general test of thc cline hypothesis for central California to central Oregon was done using the coefficient of variation (C.V. = SD/mean × 100%) for all size distributions gathered in this region during 1985 (Table 1). A large C.V. indicates a distribution with a wide range of sizes relative to the mean and so is an indication of frequent recruitment. For example, the C.V. for Yaquina Head is 46.7% and that for Cape Blanco is 18.5%. There was a nonsignificant correlation between latitude and C.V. ($r = -0.22$, df = 24, $r_{crit} = 0.39$: fail to reject H_0).

The consistently good recruitment at Yaquina Head and consistently poor recruitment at Cape Blanco suggested that a major component of recruitment was physical rather than biotic, which provided the motivation for exploring patterns of water movement. Sampling in 1986 was designed to evaluate the relationship between size structure and major headlands that have been reported to have frequent and recurrent jets (Kelly 1983, 1985). The proposed mechanism for the relationship is that intense upwelling or cold water jets would advect larvae away from the coast and hence would modify settlement and recruitment.
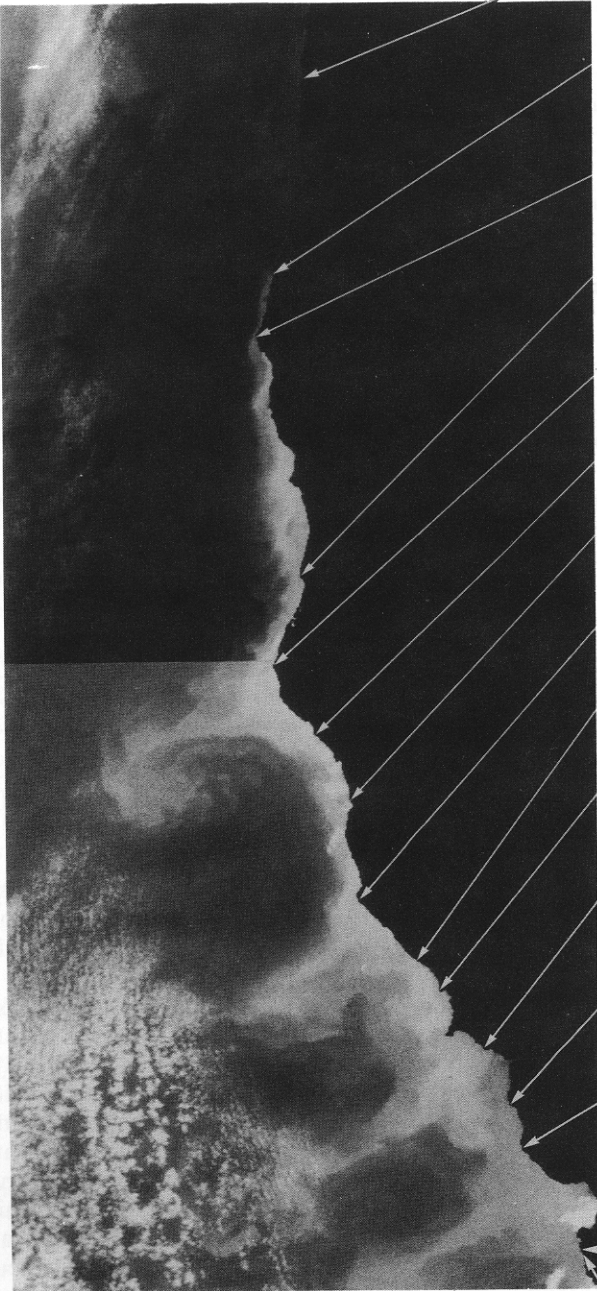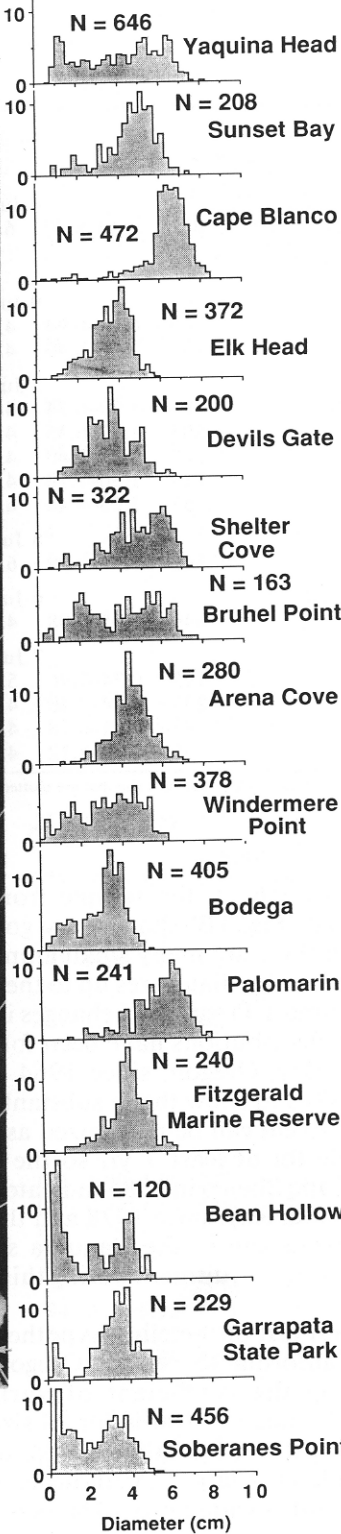
An assumption we make is that recruitment differences reflected in the size frequency distributions result from settlement differences rather than from processes that act after settlement (cf. Connell 1985).

Plumes or jets for 27 April 1984 together with selected size distributions from 1985 to 1986 are shown in Fig. 2. Size distributions that were selected for the figure are those with $N > 100$ and with the largest C.V. for each site. Because of the general southward flow of the California Current, there is a southward displacement of the jets. Plumes are evident extending offshore from Cape Mendocino (north of Devils Gate), Point Arena (north of Arena Cove), Point Reyes (north of Palomarin), and Pigeon Point (south of Bean Hollow [=Arroyo de los Frijoles Beach]). It must be emphasized that although Fig. 2 is a snapshot for just 1 d, it shows some areas that have predictable and frequent jet formation in California (Kelly 1983, 1985; Davis 1985), namely Point Reyes, Point Arena, and Cape Mendocino. Upwelling at Cape Blanco is frequent (Ikeda and Emery 1984) but was not particularly strong on 27 April 1984. Pigeon Point does not appear in the literature as a predictable location for jet formation.

There are differences in the size frequency distributions of populations from central California to central Oregon. At some areas, such as Yaquina Head, Bruhel Point, Windermere Point, and Soberanes Point, the distributions show a wide range of sizes, including small individuals <1.0 cm. In these areas we infer successful recruitment each spring extending over at least 5 yr and possibly longer. Other areas, such as Sunset Bay, Cape Blanco, Devils Gate, Arena Cove, and the Fitzgerald Marine Reserve lack small individuals and show negative skew. We infer that they have had substantially lower recruitment rates during at least the past 7 yr. At Sunset Bay, the last major recruitment event was in 1963.
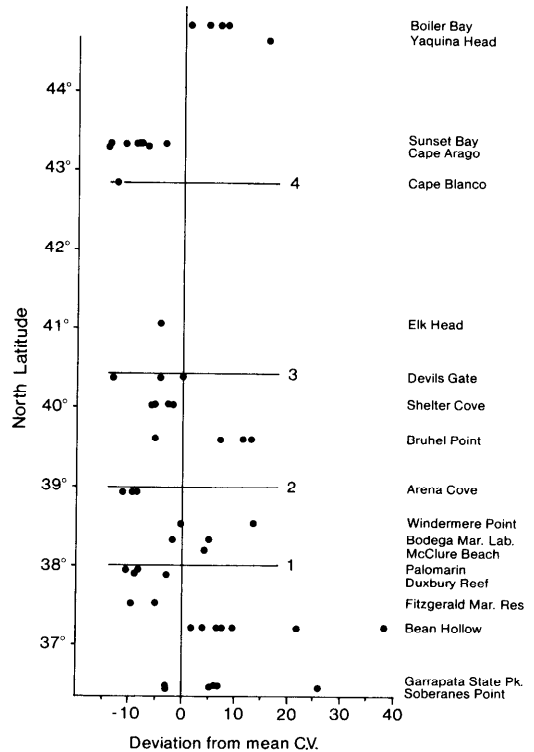

Fig. 3. Deviation of the C.V. of each sample from the mean C.V. for 54 size distributions (mean C.V. = 31.1%). Numbered horizontal lines are major headlands: 1—Point Reyes; 2—Point Arena; 3—Cape Mendocino; 4—Cape Blanco.

A mean of 54 C.V. values (Table 1) was calculated ($\overline{C.V.} = 31.1\%$) and the deviation of each from the mean ($31.1\% - $ C.V.) was plotted (Fig. 3). Sites with inferred low recruitment have C.V. values that are below the mean, whereas sites with better recruitment have values above the mean (Fig. 3). The numbered lines in Fig. 3 show the positions of sites where jets are likely to form.

It is unclear how to classify Cape Arago and Sunset Bay with respect to upwelling. As shown in Fig. 2, Cape Arago is at the northern end of a coastal bulge that has Cape Blanco at its southern end. Satellite images tend to show that when cold water is present near the coast at Cape Blanco, it also is pres-

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Fig. 2. Size frequency distributions of *Strongylocentrotus purpuratus* from central California to central Oregon; *x*-axis is body diameter (cm) and *y*-axis is frequency in the sample (%); NOAA-7 satellite image is from 27 April 1984 with channel 4 (11 μm) of the AVHRR; light areas are regions of cooler water; sea surface in lower left is obscured by clouds.

Table 2. Stepwise multiple regression coefficients (BMDP2R: Dixon and Jennrich 1985) with the C.V. of size for *Strongylocentrotus purpuratus* as a function of distance south of prominent headlands and location along the coast, both in degrees of latitude. $N = 41$ size distributions from Cape Blanco, Oregon, to Soberanes Point, California; R is the multiple correlation coefficient. Part A excludes and part B includes Pigeon Point, California, as a prominent headland. Step is number of steps in the multiple regression before no additional variables were significant at $P \leq 0.05$.

			Distance from			Partial correlation coefficients	
	Step	R	headland	Latitude	Intercept	Distance	Latitude
Part A	1	0.48	9.90*	−1.69 (ns)	25.79*	0.48*	−0.23 (ns)
Part B	2	0.59	12.87*	−2.15*	108.01*	0.46*	−0.34*

* Significant at $P \leq 0.05$.

ent at Cape Arago; however, no work on upwelling specific to Cape Arago has been conducted (A. Huyer pers. comm.).

The regions between jets in California show similar patterns of size structure changes; namely, small values of C.V. at or immediately south of a major cape or headland and increasing values moving south from the headland. This southward skew would be expected if features associated with headlands affect generally southward transport of larvae in the California Current. The relationships between C.V., latitude, and degrees south of a major headland were examined by stepwise multiple regression (Table 2). Only data in the area between Soberanes Point and Cape Blanco were included in the analysis because Cape Blanco is the northernmost headland that is listed in the literature as a major site of upwelling and jet formation. The literature may be biased, however, by the ability to sample from satellites (Pan et al. 1988). Two regressions were explored, one excluding Pigeon Point as a significant site for jet formation (part A, Table 2), in which the locations of Soberanes Point and Garrapata State Park were made relative to Point Reyes, and a second regression that included Pigeon Point (part B, Table 2).

With or without Pigeon Point, there is a significant relationship between distance south of a major headland and the C.V. of size (both parts A and B, Table 2). If Pigeon Point is excluded as a major headland, latitude does not provide any significant reduction of residual sums-of-squares; if Pigeon Point is included, then both distance south of a major headland and latitude are significant. Distance south of a headland en-

ters the regression first in both cases and explains more of the relationship, as shown by the partial correlation coefficients (Table 2).

Our interpretation of the results is that they are best explained by physical events. Intense upwelling advects competent larvae away from the coast and hence reduces the numbers that are available for settlement. Eddies that form due to the plumes may bring larvae back to the coast or hold them near it while they develop. Advection of larvae due to upwelling has been proposed as a way of explaining latitudinal recruitment patterns in fish (Parrish et al. 1981), and return of larvae in large eddies has been proposed as a way of accounting for population maintenance of spiny lobsters (Johnson 1960, Phillips 1981). Recruitment of crabs has been related to oceanographic events (briefly reviewed by Jamieson 1986) including upwelling (Botsford 1986; Botsford and Wickham 1975) and shelf water retention (Sulkin and Epifanio 1986; Johnson et al. 1984), but the focus of these studies was annual variation rather than spatial differences.

Contrasting results for *S. purpuratus* to those presented here occur in a region without intense upwelling—southern California—where years of relatively frequent upwelling events are associated with improved recruitment (Ebert 1983). These contrary results suggest that low levels of upwelling may enhance recruitment, but intense upwelling may inhibit settlement. Also, the California Bight has a gyre, the southern California eddy (Owen 1980), that helps retain water within the bight.

Because we have samples at most sites for

just 2 yr, we cannot address the significance of temporal variation, which can only be done with longer time series (e.g. Ebert 1983; Pearse and Hines 1987). At Sunset Bay, size-frequency distributions have been gathered since 1964. In 1963 a massive recruitment event was observed (Ebert 1968), which was evident as a major mode in size distributions from 1964 onward until the year-class fused with the mode of large individuals by about 1970 (depending on the area in Sunset Bay). There were minor recruitment events in 1970 and in 1980 or 1981 (Ebert 1983 and unpubl.). Paine (1986) observed a major recruitment event for purple sea urchins in Washington in 1963 but has also observed significant recruitment in 1969 and a massive event in 1982–1983. The similarity between Sunset Bay, Oregon, and Mukkaw Bay, Washington, in 1963 and differences between Sunset Bay and sites close to Mukkaw Bay in other years emphasize not only temporal variation but also spatial differences through time.

The nearshore effects of upwelling are complex and controversial and there is some evidence that upwelling may result in both onshore and offshore movements of water and that offshore transport may be confined to a very narrow layer (Peterson et al. 1979). Although the effects of jets have not been analyzed closely enough to describe their importance in the intertidal, upwelling circulation at headlands seems to extend close to shore (Kelly 1985). Although our explanation is a parsimonious one, our correlational study cannot exclude other effects associated with headlands or nearshore water movement. The dynamics of mass exchange between the surf zone and regions offshore may be modulated, for example by wave exposure.

The implications of our work clearly are important in evaluating studies of marine populations that focus on demography or deduce life history strategies from recruitment data. An intertidal study conducted at a cape or headland may have different results from one conducted at a site between headlands. Community structure caused by interspecific relationships can be modified by the intensity of recruitment of species, and hence it is to be expected that the timing of spawning and onset of upwelling would modify significantly the suite of species and the intensity of interactions. Comparative studies that emphasize recruitment patterns and measure circulation effects directly are needed to test this prediction and to elucidate the mechanisms that affect settlement success.

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