Demographic patterns of the purple sea urchin *Strongylocentrotus purpuratus* along a latitudinal gradient, 1985–1987

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ABSTRACT: The abundant center model of geographic distribution has been tested for the purple sea urchin by others who found highest densities and reproduction towards the southern end rather than in the center of the range and so rejected the model. A question is whether size, growth, and survival data would yield other or contrary results. Intertidal densities and size structures were measured for purple sea urchins along the Pacific coast of North America during 1985–1987 from 29.93 to 50.47° N, covering about 65 % of the reported geographic range; these historical data were used to explore latitudinal patterns. Recruitment was based on the fractions of individuals in the smallest mode of the size distributions. Growth was determined by tagging with tetracycline and survival was estimated using size distributions and growth. Density of purple sea urchins was highest between 35 and 37° N and the samples with the highest numbers of recruits occurred between 34 and 38° N. Maximum diameter was largest at 43 to 44° N and smallest at about 34° N. There was no latitudinal pattern to growth or survival. Patterns of population traits did not fit simple models or previously published results. The interplay of coastal topography and currents are suggested as the primary determinants of density and recruitment. No general models for describing geographic distributions predict the observed patterns. The southern range limit is best explained by thermal tolerance and the northern limit by development times of larvae at low temperatures.

KEY WORDS: Geographic patterns · Demography · Size structure · Growth · Recruitment · Survival · Sea urchin

INTRODUCTION

Latitudinal patterns have long been a focus of studies of both theoretical and applied ecology. Across the geographic range of a species there are changes in density that are the result of population processes of growth, survival, reproduction, and recruitment. A common model for density changes is based on Hutchinson's (1957) definition of a niche in which biotic and abiotic factors change in all directions along a gradient from the center of distribution, where conditions are best, out to regions where the species cannot persist. Accordingly, change in density over a species' range is hypothesized to be Gaussian in shape with maximum values in the center of the distribution (e.g. Whittaker 1960, Brown 1984, Guo et al. 2005); this is the abundant center model (e.g. Samis & Eckert 2007).

Climate change coupled with concerns for species conservation have resulted in increasing interest in species distributions and structure within a variety of systems (e.g. Fortin et al. 2005, Guo et al. 2005, Parmesan et al. 2005, Sagarin et al. 2006, Gaston et al. 2008). For marine systems, recent models have emphasized the role of physical transport in shaping structure (e.g. Richards et al. 1995, Ebert 1996, Alexander & Roughgarden 1996, Connolly & Roughgarden 1998, Gaylord & Gaines 2000), but transport alone cannot explain range limits. At a meso-scale, however, physical trans-

port clearly influences pattern (e.g. Ebert & Russell 1988) and is important in understanding changes in distribution or population structure associated with prominent coastal features (e.g. Wares et al. 2001, Zacherl et al. 2003, Herbert et al. 2009, Kelly & Palumbi 2010).

Lewis (1986) developed a model for the geographic distributions of marine species with planktonic larvae that retains physiological elements of a Hutchinsonian niche and focuses on northern range limits set by short breeding seasons that lead to frequent recruitment failures. Reproductive seasons are longer in the south but thermal stress increases mortality. At both extremes temperature sets limits, and has been considered as the driving force for latitudinal changes by others (e.g. Bullock 1955, Frank 1975, Lonsdale & Levinton 1985, Harrington 1987, Defeo & Cardoso 2002).

Several recent papers have tested Brown's model (Brown 1984) of the abundant or domed center for distributions of intertidal species and have failed to support the model. For example, an intertidal limpet failed to show a decline in density and size at the northern edge of its range (Gilman 2005). Sagarin & Gaines (2002) estimated density of 12 intertidal invertebrate species in transects at 42 sites along the Pacific coast of North America from Punta Cabeza Ballena, Baja California Sur (22.92° N) to Shelikof Island, Alaska (57.15° N). They found *Strongylocentrotus purpuratus* from Punta Baja (29.94° N) to Boiler Bay, Oregon (44.83° N). Lester et al. (2007) documented differences in reproduction of *S. purpuratus* from Punta San Carlos, Baja California Norte (29.62° N) to the Bodega Marine Reserve, California (38.32° N). Results from these 2 studies failed to support a model with low density or gonad size towards margins and increases towards the center. In both of these studies, the trend was for density and gonad size to increase toward the south end of the range. An older study of gonad development in *S. purpuratus* from 1958 to 1961 (Boolootian 1966), although complicated by the use of a gonad index, showed greatest gonad development in the north at Sunset Bay, Oregon, through Pacific Grove, California, and lower gonad index values in Mexico. These results are opposite to the results presented by Lester et al. (2007).

To understand population structure over a wide latitudinal range, the best approach is to explore patterns of density, recruitment, size structure, growth, and survival. There are few studies of intertidal populations that span substantial portions of the known range and also include demographic data; therefore, it is reasonable to ask whether, in general, patterns support the abundant center model, a physical transport model (e.g. Ebert 1996, Gaylord & Gaines 2000), the recruitment-survival model of Lewis (1986), or whether pat-

terns are sufficiently species-specific and idiosyncratic that a general model may not be attainable.

The lack of previous publication of the historical data presented here has been associated with problems of analyzing growth of sea urchins. When growth data were gathered in the 1980s, the preferred growth model was the Richards function (Richards 1959, Ebert 1982, Russell 1987). The overall fit of data to this model, however, was not good for small or very large purple sea urchins. The Tanaka growth model (Tanaka 1982, 1988) was much better for growth analysis of sea urchins (e.g. Ebert & Russell 1993); however, the model had an implied time interval, Δt, between marking and recapture of 1 yr. Mostly this was not a major problem (e.g. Ebert et al. 1999), but purple urchin data sets reported here included time intervals as long as 3 yr. Improving the Tanaka model to include different values of Δt (Ebert & Southon 2003, Ebert 2008) left the problem of how to compare growth results because there was no simple summary index. A solution to this final problem with growth analysis is presented here.

MATERIALS AND METHODS

Strongylocentrotus purpuratus has a reported geographic range from Isla Cedros, Baja California Norte (28° N) (Clark 1913) to at least Torch Bay, Alaska (58.33° N) (Duggins 1981). The intertidal distribution is ill-defined but extends at least to Punta San Carlos, Baja California Norte (29.62° N) (Lester et al. 2007). The report of *S. purpuratus* at the southern end of Bahia Tortugas (27.66°) by Olivares-Bañuelos et al. (2008) possibly is a misidentification because a visit to this site in 2009 found just *Echinometra vanbrunti*, a more southern species (J. C. Hernández pers. comm.). Although predominately subtidal at Torch Bay, Alaska, Duggins & Quinn (1975) occasionally found *S. purpuratus* in the low intertidal *Lessoniopsis* zone.

During the mid-1980s, intertidal populations of the purple sea urchin were studied from Grant Bay (50.47° N) at the northern tip of Vancouver Island, Canada, to Punta Baja (29.94° N), Baja California Norte, México (Fig. 1). This range encompasses about 65% of the reported distribution. At most sites, pools or channels were located and their dimensions measured. At several sites in southern California where sea urchins occurred under rocks, 1 m belt transects were run parallel with the shore. Surface area of a pool or channel was estimated based on simple measures of the waterline of the surface and general shape such as rectangle, triangle, oval, etc. Pools and channels varied in depth and so there was additional area provided by the sides and complexity (cracks, pits). This increase in area over the estimate of surface area is a source of
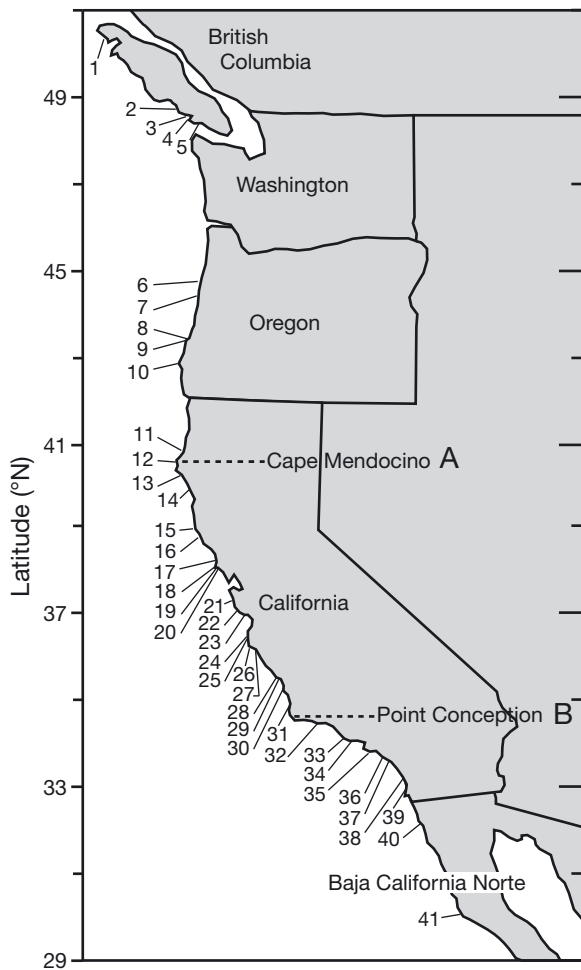
Fig. 1. *Strongylocentrotus purpuratus*. Study sites along the Pacific coast of North America; details of sites given in Table 1. Dashed lines A and B mark positions of Cape Mendocino and Point Conception and are important markers used in other figures

error, but is the same error used in other studies that have attempted to estimate density of organisms in the intertidal (e.g. Sagarin & Gaines 2002). Density in pools potentially was overestimated and with greatest error for deep pools with small surface areas; all densities were scaled to a surface area of 1 m².

At study sites, all sea urchins were collected from a defined area, diameters were measured with vernier calipers to the nearest 0.01 cm, and then urchins were returned. A restriction in sampling was that new individuals had to be large enough to be seen and collected with unaided vision. Although occasionally sea urchins with diameters as small as 0.25 cm were collected, most of this size would have been missed; the lower limit for collection was about 0.5 cm. Size-frequency distributions were separated into 2 or more components using the algorithm of Macdonald & Pitcher

(1979) to determine the fraction of the population that was about 1 yr old.

Size at settlement under laboratory conditions is about 0.03 to 0.04 cm depending on food conditions (Rowley 1989, Miller & Emlet 1999) and settlement time varies year to year from as early as March to as late as August (Rowley 1989, Ebert et al. 1994, Miller & Emlet 1997). At Sunset Bay, Oregon, sea urchins that settled in 1963 in different sites had mean diameters of 1.62 to 1.94 cm in August 1964 (Ebert 1968). In southern California, Rowley (1989) estimated 1 yr old urchins to be ca. 1.90 cm in diameter. These approximate values were used as a gauge to evaluate the appropriateness of using fractions of the first mode in size-frequency distributions as Age ≤ 1, recognizing that the first mode may include some individuals not yet 1 yr old and some older but not equal to 2 yr.

At 5 sites along the coast, sea urchins were tagged with tetracycline (Ebert 1982) to determine growth: Maalth-sit (48.72° N; Site 4 in Fig. 1), Arena Cove (38.92° N; Site 15), Bodega Marine Reserve (38.33° N; Site 17), McClure Beach (38.18° N; Site 18), and Punta Baja (29.93° N; Site 41). The Maalth-sit site was called Flat Top Rock by Russell (1987). Sea urchins generally were collected after about 1 yr, but in one case after 1.5 yr and in another after 3 yr (because the collection was from the wrong pool after 1 yr), and processed as has been previously described (e.g. Ebert 1982).

Growth increments in demi-pyramids (jaws) of Aristotle's lantern were measured under ultraviolet illumination and converted to growth in body (test) diameter after determining the site-specific allometric relationship between test diameter (D) and jaw length (J):

$$D = \alpha J^\beta \tag{1}$$

Data were transformed for analysis using natural logarithms:

$$\ln D = A + \beta \ln J \tag{2}$$

where A is $\ln \alpha$.

The jaw size at the time of tagging, J_t, is the size at subsequent collection, $J_{t+\Delta t}$, minus the jaw increment, ΔJ, which is the sum of the growth increments at the esophageal and labial ends of the jaw. Allometry parameters were used for each sample to estimate the growth increment of the test, ΔD:

$$\Delta D = \alpha \left(J_{t+\Delta t}^\beta - J_t^\beta \right) \tag{3}$$

Two growth models were used for analysis, Tanaka (Tanaka 1982) and Richards (Richards 1959). The Tanaka equation is:

$$\Delta D = -D_t + \frac{1}{\sqrt{f}} \ln\left[2G + 2\sqrt{G^2 + fa} \right] + d \tag{4}$$

where

$$G = E/4 - fa/E + f\Delta t$$
$$E = \exp[\sqrt{f}(D_t - d)]$$

Δt is the time interval between tagging and collection and a, d and f are parameters to be estimated. Further details of the Tanaka equation are given in Tanaka (1988) and Ebert (1999).

The Richards equation is:

$$\Delta D = -D_t + [D_t^{-1/n} + (D_\infty^{-1/n} - D_t^{-1/n})(1 - e^{-K\Delta t})]^{-n} \qquad (5)$$

Comparisons of samples were made by estimating ΔD at an initial diameter of 3 cm and Δt equal to 1 yr. An initial size of 3 cm was selected because it was well within the data clouds of all samples. This is an approach similar to that advocated by Schnute (1981) and implemented in difference-equation form by Francis (1995). Growth parameters were estimated using the nonlinear regression module NONLIN (SYSTAT 2004) and included the function command (FUNPAR) to estimate ΔD at 3 cm together with 95% confidence limits.

Survival was modeled using an exponential equation:

$$N_t = N_0 e^{-Mt} \qquad (6)$$

which assumed that the annual survival rate did not change with age. The parameter M is the instantaneous survival rate and the annual survival rate P^{-1}, is e^{-M}. The estimate of M was obtained using the mean diameter of the size-frequency data, D_T, and the Tanaka growth parameters (Eq. 7) that were obtained from tagging (Ebert 1999):

$$\overline{D_T} = (1 - e^{-M}) \qquad (7)$$

$$\left(\sum_{t=0}^{\varpi} e^{-Mt} \left[\frac{1}{\sqrt{f}} \ln \left(2f((t+T) - c) + 2\sqrt{f^2((t+T) - c)^2 + fa} \right) + d \right] \right)$$

In Eq. (7), the Tanaka growth function (in square brackets) has an additional parameter, T, which is the time of year since annual recruitment. It can be set equal to 0 if the mean of the smallest mode in a size distribution is selected as the size at recruitment, D_0. The mean diameter of Age ≤ 1 individuals, D_0, enters Eq. (7) through c:

$$E = \exp[\sqrt{f}(D_0 - d)] \qquad (8)$$

$$c = \frac{a}{E} - \frac{E}{4f} \qquad (9)$$

The only unknown in Eq. (7) is M, the instantaneous mortality rate, which was estimated using a numerical algorithm called Newton's method. Finding a solution for M starts with a seed value for M such as 1.0 or 0.5 and iterates to improve the estimate until the estimate

of M for the ith + 1 iteration is no more than 1×10^{-6} different from the ith iteration. A BASIC program for solving Eq. (7) by Newton's method is in Ebert (1999). Assumptions in application of Eq. (7) are that Eq. (6) is valid and that the population is seasonally stable and stationary; that is, the population has fixed fractions in each size category if sampling is always done at the same time of year (seasonally stable) and the population is neither growing nor declining (seasonally stationary).

RESULTS

Density

The pattern of density with latitude (Fig. 2) showed the highest values between 35 and 37° N, which is north from Point Conception to about Bean Hollow
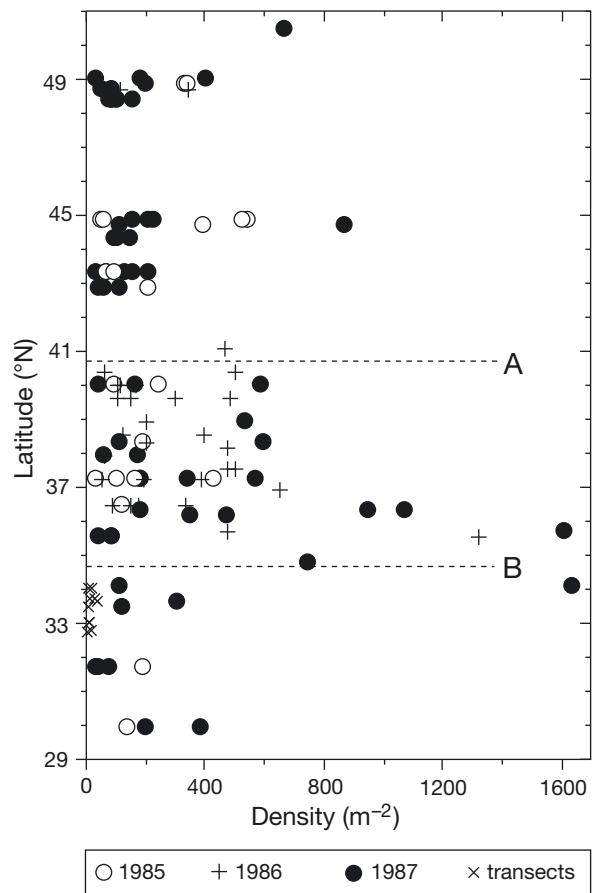

Fig. 2. *Strongylocentrotus purpuratus*. Density as a function of latitude along the Pacific coast of North America. Densities were calculated based on surface area of pools or crevices and then adjusted to a standard m^{-2}; transects were used at cobble beaches. Dashed lines A and B are Cape Mendocino and Point Conception, respectively

(Site 22 in Fig. 1) in central California. Density then declined to low values in Oregon from Cape Blanco (Site 10) to Yaquina Head (Site 7) followed by an increase farther north. At all latitudes there were samples with low densities, which indicates that sites were sampled of varying quality for recruitment, post-settlement survival, or a combination of the two. The low densities in transects in southern California are a reflection of variable micro-site quality on beaches with cobbles and rock slabs interspersed with smaller rocks resting on variable amounts of gravel and sand. The highest density estimates of 1600 m^{-2} were from Piedras Blancas (Site 28) and Leo Carillo State Park (Site 33), both in 1987. At Piedras Blancas on 27 March 1987, 1286 sea urchins were collected in a shallow pool that had an estimated surface area of 0.80 m^2. Most of these sea urchins were very small and mean diameter was just 1.98 cm. In contrast, at Leo Carillo State Park only 193 sea urchins were collected in a small pool that had an estimated surface area of just 0.12 m^2. Sea urchins were larger than at Peidras Blancas and mean diameter was 2.53 cm. The estimate of bottom area based on surface area for the Leo Carillo pool probably contains more error than the estimate of bottom area at Piedras Blancas, but the actual error is unknown.

Fraction of Age ≤ 1 yr

Data of total numbers collected (N), dates, and the fraction in the Age ≤ 1 class are provided in Table 1. Representative size-frequency distributions (Fig. 3) show initial modes of about 1.5 cm, and these would consist of Age ≤ 1 sea urchins. There is clean separation of modes in the samples from Punta Baja (Site 41) and Arena Cove (Site 15) in 1987, but less clear separation at Piedras Blancas (Site 28) and McClure Beach (Site 18). Very few new recruits were observed in the Boulder Field at Sunset Bay (Site 8), Oregon, and there were no recruits at Grant Bay (Site 1) at the north end of Vancouver Island, British Columbia, evident in 1987.

Plotting the Age ≤ 1 data of Table 1 (Fig. 4) shows peak recruitment between 35 and 39° N, a low in Oregon, and a rise on Vancouver Island. The fraction of Age ≤ 1 individuals showed a pattern similar to that of density with a peak in central California, a minimum in Oregon, and intermediate values in both Canada and México. Similarly, there were sites all along the coast with low values for recruitment and a clear indication of annual variation. Samples in central California showed high recruitment in 1987, an indication of high settlement in 1986. The lowest

Table 1. *Strongylocentrotus purpuratus* study sites 1985–1987; site numbers are mapped in Fig. 1. North latitude is expressed with decimal degrees rather than with minutes. Samples include size (N) and Age ≤ 1 fraction of the distributions. SP: state park

No.	Site	Latitude (°N)	Date	Sample 1 N	Sample 1 Age ≤ 1	Sample 2 N	Sample 2 Age ≤ 1	Sample 3 N	Sample 3 Age ≤ 1	Sample 4 N	Sample 4 Age ≤ 1
1	Grant Bay	50.47	29-Apr-87	215	0						
2	Frank Island	49.02	28-Apr-87	63	0	72	0.014	284	0.01		
3	Seppings Island	48.83	2-Aug-85	233	0.285	292	0.273				
4	Maalth-sit	48.72	1-Aug-85	372	0.107	264	0.03				
			13-Nov-85	116	0						
			25-Apr-86	76	0	185	0	194	0.005		
			26-Apr-87	64	0.016	149	0.007	241	0		
5	Botanical Beach	48.38	31-Jul-85	557	0.072						
6	Boiler Bay	44.83	7-Jun-85	175	0.069	233	0.069	86	0.093	55	0.054
			18-May-87	273	0.026	122	0.016	206	0.015		
7	Yaquina Head	44.68	6-Jun-85	646	0.147						
			17-May-87	506	0.109	170	0.196				
8	Sunset Bay	43.33									
	Postelsia zone (PZ)		5-Jun-85	214	0.014						
	Above PZ		5-Jun-85	87	0.011						
	Below PZ and N		5-Jun-85	208	0.091						
	Boulder field		5-Jun-85	57	0	340	0.026				
	Surf grass area		5-Jun-85	203	0.034						
	Below PZ and N		15-May-87	182	0.016						
	Below PZ and S		15-May-87	180	0.038						
	Postelsia zone		15-May-87	206	0.015						
	Above PZ		16-May-87	49	0.02						
	Boulder field		16-May-87	234	0.051						
	Surf grass area		16-May-87	192	0.01						
	South of boulder field		16-May-87	68	0						
9	Cape Arago	43.31	9-Jun-85	109	0.009	131	0				

Table 1 (continued)

No.	Site	Latitude (°N)	Date	Sample 1		Sample 2		Sample 3		Sample 4	
				N	Age ≤ 1	N	Age ≤ 1	N	Age ≤ 1	N	Age ≤ 1
10	Cape Blanco	42.84	4-Jun-85	472	0.025						
			14-May-87	214	0.014	133	0.023	92	0.033		
11	Elk Head	41.07	27-May-86	372	0.121						
12	Devil's Gate	40.4	26-May-86	30	0	200	0.035	100	0.03		
13	Shelter Cove	40.03	3-Jun-85	322	0.05	176	0.045				
			25-May-86	94	0.074	151	0.113	194	0.036		
			13-May-87	129	0.217	58	0.241	73	0.26		
14	Bruhl Point	39.6	28-May-86	103	0.126	163	0.395	151	0.222	269	0.264
15	Arena Cove	38.92	14-Apr-85	280	0.004						
			2-Jun-85	50	0.02						
			29-Apr-86	270	0						
			1-May-87	242	0.24	216	0.268				
16	Windermere Point	38.53	29-May-86	378	0.305	371	0.148				
17	Bodega Marine Reserve	38.33	13-Apr-85	405	0.204						
			28-Apr-86	331	0.203						
			30-Apr-87	74	0.257	390	0.583				
18	McClure Beach	38.18	30-May-86	217	0.859						
19	Palomarin Beach	37.95	24-May-86	241	0.004	177	0				
			3-May-87	126	0.016	207	0.092				
20	Duxbury Reef	37.88	2-Jun-85	107	0.019	316	0.071				
21	Fitzgerald Marine Reserve	37.53	23-May-86	142	0.021	240	0				
22	Bean Hollow	37.22	1-Jun-85	65	0.062	33	0.091	88	0.136	120	0.447
			22-May-86	95	0.039	58	0.086	192	0.223		
			12-May-87	130	0.507	118	0.327	46	0.413		
23	Natural Bridges	36.95	17-Oct-86	488	0.336						
24	Garrapata SP	36.47	1-Jun-85	333	0.069						
			22-May-86	160	0.156	229	0.109				
25	Soberanes Point	36.45	22-Jun-86	62	0.113	81	0.025	456	0.363		
26	Andrew Molera SP	36.28	26-Mar-87	183	0.651	101	0.521	333	0.686		
27	Partington Cove	36.17	25-Mar-87	81	0.463	234	0.59				
28	Piedras Blancas site #1	35.68	23-Jun-86	167	0.042						
	Piedras Blancas site #2	35.66	27-Mar-87	1286	0.684						
29	Cambria	35.54	23-Jun-86	291	0.217						
			28-Mar-87	232	0.392	119	0.302	128	0.193		
30	Montana de Oro SP	35.27	4-Jul-85	40	0	176	0.095				
31	Purisima Point	34.76	26-Jan-87	80	0.605						
32	Coal Oil Point	34.47	5-Jul-85	102	0.336						
33	Leo Carillo SP	34.04	27-Jan-87	193	0.359	413	0.189				
34	Paradise Cove	34.01	25-Jan-87	169	0.388	51	0.381				
35	White Point	33.71	3-Jul-85	195	0.005						
			12-Jan-87	176	0.626	179	0.557				
36	Pelican Point	33.58	10-Jan-87	248	0.27	147	0.088				
37	Dana Point	33.45	11-Jan-87	63	0.105	140	0.231				
38	Encinitas	33.03	28-Jan-87	112	0.696						
39	False Point	32.8	14-Jan-87	74	0.176						
40	S of Papalote Bay	31.71	2-Jul-85	332	0.015						
			11-Mar-87	447	0.129	224	0.04	44	0.091		
41	Punta Baja	29.94	1-May-85	212	0.009						
			12-Mar-87	680	0.418	195	0.249				

recruitment in central California occurred in 1985, meaning poor settlement in 1984. Recruitment in Canada showed a pattern opposite to California, i.e. settlement in 1984 was good as shown by the recruitment of Age ≤ 1 sea urchins in 1985. Settlement in 1986 was poor as shown by poor recruitment in 1987.

Changes in maximum test diameter with latitude

Maximum diameter, the largest measured sea urchin in a sample, provides additional insight into pattern with latitude. Maximum measured diameter is a better measure than mean or mode because it is not influenced by differences in recruitment events. Maximum
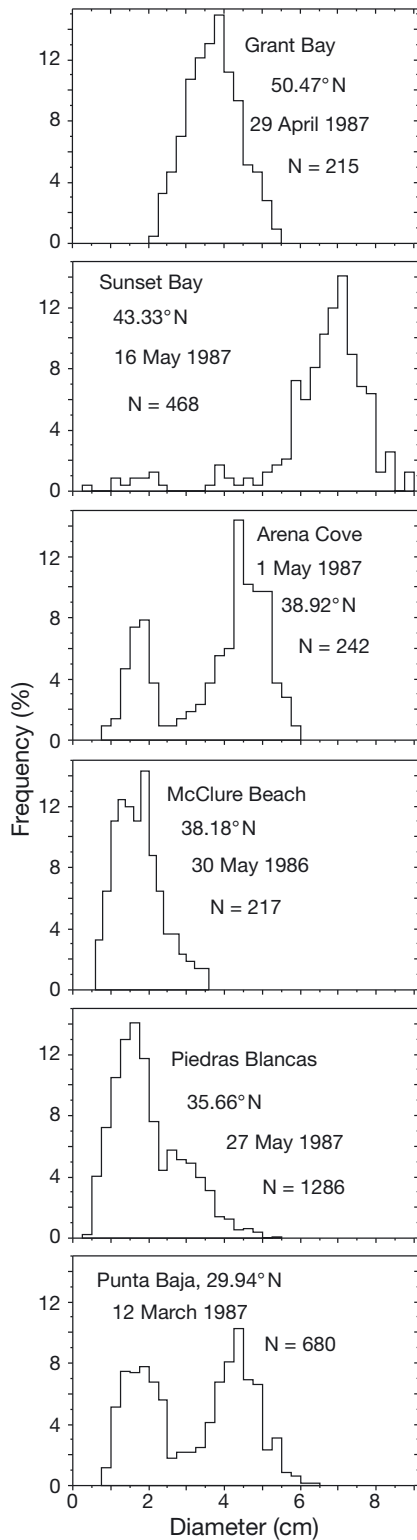
Fig. 3. *Strongylocentrotus purpuratus*. Representative size structures arranged from north to south to illustrate fractions present in the smallest size class, which is approximately Age ≤ 1: Grant Bay (Site 1, Fig. 1), Sunset Bay (Site 8), Arena Cove (Site 15), McClure Beach (Site 18), Piedras Blancas (Site 28), and Punta Baja (Site 41)
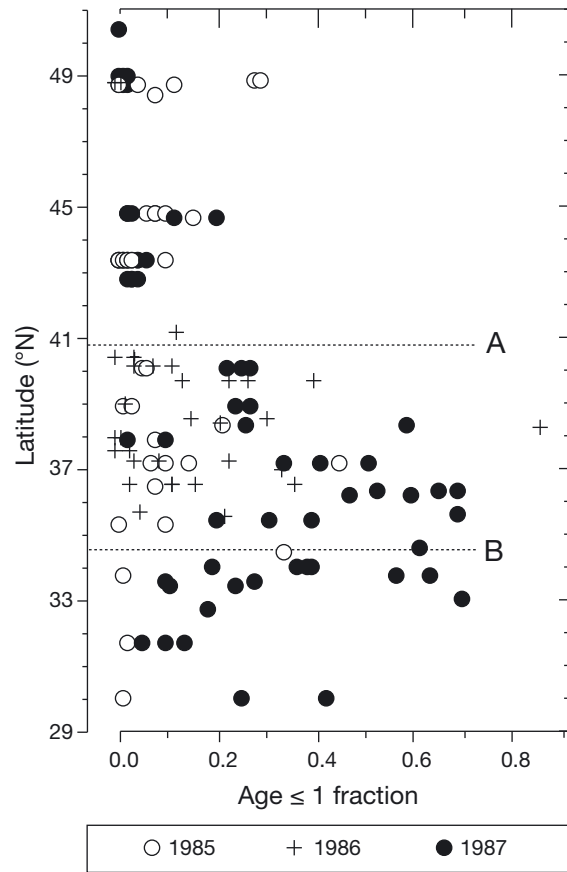

Fig. 4. *Strongylocentrotus purpuratus*. Fraction of Age ≤ 1 individuals in size distributions along the Pacific coast of North America. Dashed lines A and B are Cape Mendocino and Point Conception, respectively

observed diameter (Fig. 5) changed with latitude first with a drop at Point Conception followed by a steady rise past Cape Mendocino and attaining largest individuals in Oregon from Cape Blanco (Site 10) to Yaquina Head (Site 7). This was followed by a drop in maximum diameter on Vancouver Island. The greatest inter-sample variation occurred at about 38° N, with large individuals over 8.0 cm at Palomarin Beach (37.95° N, Site 19) and, close by, very small sea urchins a McClure Beach (38.18° N, Site 18). It is important to note that there were areas, such as along the Oregon coast, where no sites were sampled where maximum sizes were less than 6.0 cm.

Growth

Examination of growth across latitude provides a clear test of the abundant center model. Expectation is that growth should be highest in the middle of the range and lowest at the northern and southern ends of
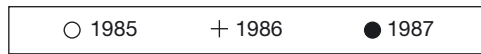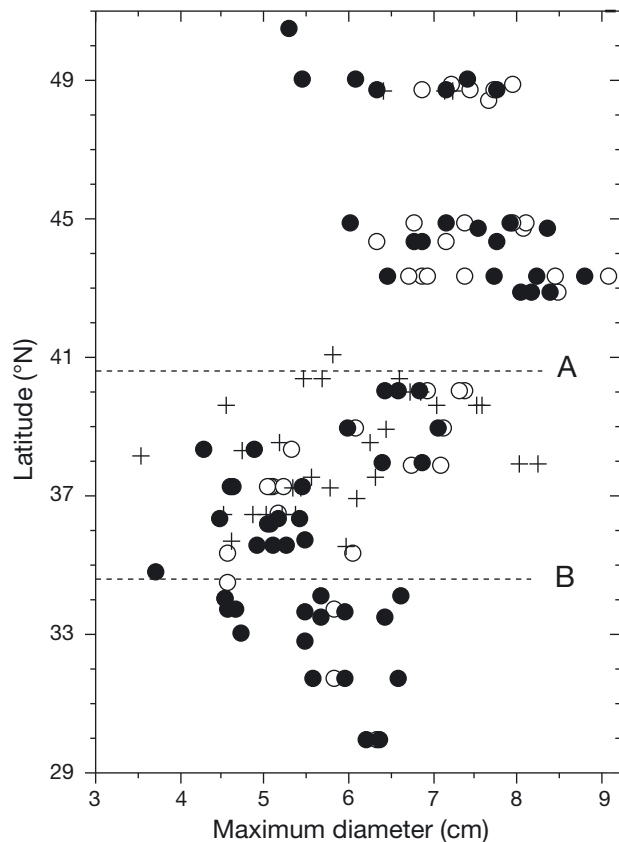
Fig. 5. *Strongylocentrotus purpuratus*. Maximum diameter in samples measured along the Pacific coast of North America. Dashed lines A and B are Cape Mendocino and Point Conception, respectively

Growth parameters of the Tanaka function were determined (Eq. 4) for each sample. The correlation between parameters *f* and *d* ranged from 0.390 to 0.997 with a weighted mean of 0.91. Also, the 95% confidence intervals of *f* overlapped for all samples, which suggested that *f* could be fixed and estimation reduced to just 2 parameters. The weighted mean value for *f* was 1.3 and analyses were redone for each sample (NONLIN; SYSTAT 2004), testing the null hypothesis that there was no difference in fit between estimating 3 parameters, *f*, *a*, and *d*, and fixing *f* at 1.3 and estimating just 2 parameters. No p-value was < 0.05 and all but one was > 0.10 (Table 3), so fixing *f* to reduce the number of fitted parameters is reasonable.

Parameters *n*, *k*, and D_∞ of the Richards function (Eq. 5) were estimated for all samples. Correlation of parameters and 95% confidence intervals were examined to see whether parameter number could be re-

the range. To convert jaw growth to test growth, the first test was whether common allometry parameters could be used for all sites. Jaw lengths, *J*, and test diameters, *D*, were transformed using natural logarithms (Eq. 2) and then used in an ANCOVA (GLM; SYSTAT 2004) with ln*D* as the dependent variable, Sample as a grouping variable, ln*J* as a covariate, and an interaction term of Sample × ln*J* (Table 2A). The interaction term indicated that slopes were not homogeneous ($F_{12,2243} = 6.129$, p < 0.0001). Accordingly, individual regressions were determined for each sample (Table 2B) and the parameters α and β were used to convert jaw growth to diameter growth, Δ*D* (Eq. 3). Numbers associated with Maalth-sit are pools where urchins were collected so 2_85 is Pool 2 collected in 1985 and where urchins had been tagged in 1984. Maalth-sit W_85 was collected in 1985 as Pool 1 but was the wrong pool. Pool 1 where urchins had been tagged in 1984 was collected in 1987 and called Pool 4_87 because there were 3 pools that had been tagged in 1986 (Tables 2 to 4 and Figs. 6 & 7).

Table 2. *Strongylocentrotus purpuratus*. Allometric parameters for ln diameter (ln*D*) as a function of ln jaw length (ln*J*). (A) ANOVA with ln*D* as the dependent variable and an interaction term of Sample × ln*J* to determine homogeneity of slopes. (B) Individual regression parameters for sites estimated because the interaction term in (A) was significant at p < 0.0001

A. ANOVA

Source	SS	df	MS	*F*	p
ln*J*	41.817	1	41.817	12363.4	0.000
Sample	1.407	12	0.117	34.662	0.000
Sample × ln *J*	0.249	12	0.021	6.129	0.000
Error	7.587	2243	0.003		

B. Allometric parameters with 95% CI for individual samples
(arranged from north to south)

Sample	Date	N	ln(α)	95% CI	β	95% CI
Maalth-sit 2_85	13-Nov-85	54	1.492	1.473–1.510	1.167	1.118–1.217
Maalth-sit 3_85	13-Nov-85	17	1.478	1.458–1.498	0.949	0.838–1.059
Maalth-sit W_85	13-Nov-85	202	1.476	1.467–1.484	1.075	1.039–1.111
Maalth-sit 1_87	26-Apr-87	62	1.485	1.469–1.500	1.103	1.031–1.175
Maalth-sit 2_87	26-Apr-87	145	1.455	1.445–1.466	1.102	1.042–1.161
Maalth-sit 3_87	27-Apr-87	239	1.507	1.500–1.514	1.193	1.159–1.227
Maalth-sit 4_87	5-Nov-87	189	1.469	1.461–1.476	1.105	1.069–1.141
Arena 86	29-Apr-86	217	1.502	1.493–1.511	1.113	1.053–1.173
Arena 87	1-May-87	176	1.469	1.458–1.480	1.107	1.075–1.139
Bodega 85	13-Apr-85	123	1.476	1.458–1.494	1.124	1.085–1.163
Bodega 86	26-Apr-86	340	1.473	1.464–1.482	1.134	1.114–1.154
McClure	2-May-87	105	1.596	1.572–1.619	1.210	1.185–1.234
Punta Baja 85	10-Oct-85	400	1.540	1.534–1.547	1.042	0.996–1.088

Table 3. *Strongylocentrotus purpuratus.* Tanaka parameters *d* and *a* with parameter *f* fixed at 1.30. The p-value is the probability that the fit with *f* fixed at 1.30 does not differ from the fit when *f*, *d*, and *a* all were estimated. Degrees of freedom for all tests is N – 3. The conclusion is that fixing *f* at 1.30 is justified for all samples at α = 0.05

Sample	N	*d*	95 % CI	*a*	95 % CI	*F*	p
Maalth-sit 2 85	43	1.859	1.544–2.175	2.737	2.014–3.461	0.148	0.70
Maalth-sit 3 85	15	1.817	1.470–2.164	1.214	−0.045–2.474	0.866	0.37
Maalth-sit 1 87	55	1.960	1.775–2.145	1.320	0.810–1.830	1.251	0.27
Maalth-sit 2 87	140	1.522	1.396–1.648	1.735	0.891–2.579	2.336	0.13
Maalth-sit 3 87	35	2.355	2.175–2.535	3.741	2.874–4.609	0.713	0.41
Maalth-sit 4 87	129	1.441	1.322–1.561	2.470	1.347–3.594	0.163	0.69
Arena 86	182	1.701	1.585–1.818	1.190	0.586–1.793	2.666	0.10
Arena 87	137	1.595	1.451–1.738	0.294	−0.893–1.482	3.139	0.08
Bodega 85	13	0.951	0.256–1.647	−0.739	−8.915–7.436	1.143	0.31
Bodega 86	141	1.432	1.339–1.524	0.558	0.470–0.647	1.661	0.20
McClure	22	0.667	0.315–1.018	1.873	0.828–2.917	1.712	0.21
Punta Baja 85	286	1.522	1.440–1.604	1.103	0.200–2.007	1.278	0.26

Table 4. *Strongylocentrotus purpuratus.* Richards function growth parameters (*n*, S_∞, *K*) at sites along the Pacific coast from 1985 to 1987

Sample	n	95 % CI	S_∞ cm	95 % CI	*K*	95 % CI
Maalth-sit 2 85	0.533	−0.130 – 1.197	5.082	4.572–5.592	0.542	0.199–0.885
Maalth-sit 3 85	−0.375	−1.215 – 0.466	6.015	−1.346–13.38	0.130	−0.704–0.964
Maalth-sit 1 87	−0.393	−0.621 – −0.164	6.024	5.233–6.815	0.135	0.010–0.260
Maalth-sit 2 87	−0.332	−0.451 – −0.213	6.435	5.235–7.635	0.063	−0.003–0.130
Maalth-sit 3 87	4.288	−26.61 – 35.19	6.721	6.240–7.201	0.211	0.097–0.324
Maalth-sit 4 87	−0.380	−0.573 – −0.186	5.845	5.061–6.630	0.095	0.014–0.177
Arena 86	−0.294	−0.376 – −0.212	5.814	5.367–6.262	0.103	0.045–0.160
Arena 87	−0.246	−0.351 – −0.140	6.544	3.805–9.283	0.047	−0.073–0.167
Bodega 85	−0.346	−1.708 – 1.015	4.043	2.371–5.716	0.350	−1.092–1.792
Bodega 86	−2.223	−4.408 – −0.037	4.443	4.275–4.612	0.564	0.430–0.698
McClure	−1.000		4.772	2.829–6.715	0.227	0.049–0.405
Baja 85	−0.274	−0.351 – −0.196	5.695	5.124–6.267	0.092	0.026–0.159

duced; this was not possible, so 3 parameters were estimated for all individual samples. Parameter estimates would not converge for data from McClure Beach and so the shape parameter *n* was arbitrarily set at −1.0, which is the Brody-Bertalanffy growth model (Table 4).

The scatter of data and fitted lines for both growth models and all samples (Fig. 6) indicate general agreement of the 2 models in the midrange of initial diameter sizes. Differences, however, are apparent at both the upper and lower initial sizes. A lack of very small sea urchins at the time of tagging at most sites precludes comparison of growth for individuals with diameters < ~2.0 cm. The fitted Tanaka lines below an initial diameter of 2 cm show great variation including no initial diameter with a maximum growth rate, ΔD, and decline in the rate at smaller sizes. The fitted line for the Bodega 1985 sample (Fig. 6) continues to rise whereas in the 1986 sample a maximum growth rate was estimated to be at an initial diameter of about 1.25 cm. The lack of a peak in the growth rate in the 1985 sample is also indicated by the estimated negative value for the parameter *a* (Table 3).

A comparison of annual growth of a 3 cm sea urchin (Fig. 7) showed no pattern with latitude using either the Tanaka or Richards functions. The 1985 sample from the Bodega Marine Reserve as well as the sample from McClure Beach showed the least annual growth as well as being in the central portion of the range of sites studied. Sample sizes for both of the samples, however, were small, 13 and 22 respectively, and the 95 % confidence intervals for the Bodega 1985 sample (Fig. 7) extended into the range of the Bodega 1986 sample. Furthermore, the 1985 sample had a Δ*t* of 1.59 yr where the half year included winter months and so would be expected to lower the overall estimate of growth. Using the Richards function (Fig. 7), confidence intervals for both Bodega 1985 and McClure Beach extended into the ranges of the other samples. The significant conclusion from this analysis is that there was no latitudinal trend and growth at the extremes was similar to that in the middle. The highest growth rates occurred in the north at Maalth-sit (Site 4), but overlapping confidence intervals should be taken to mean that there was no difference in growth with latitude.
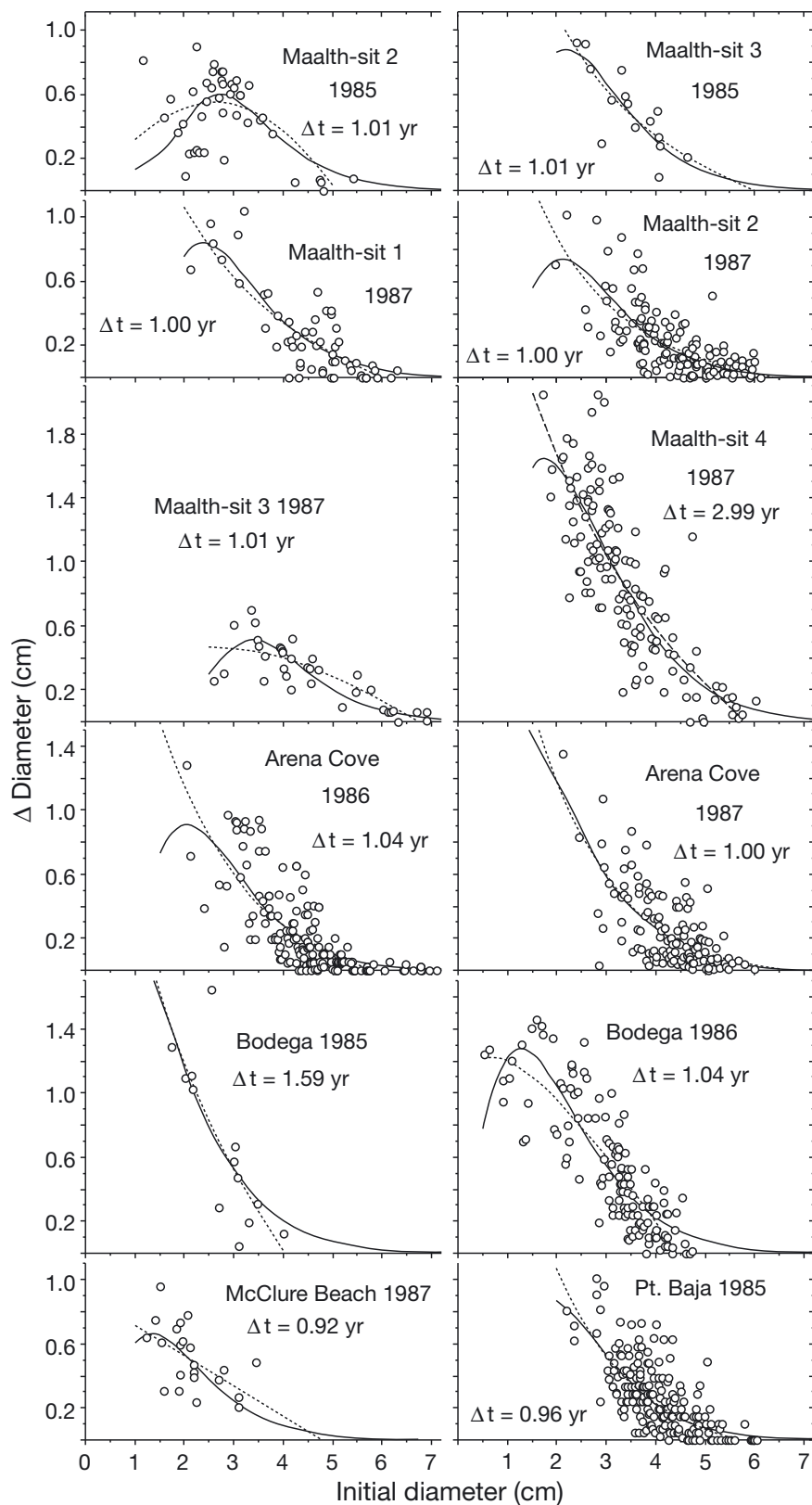
Fig. 6. *Strongylocentrotus purpuratus*. Scatter plots of Δdiameter as a function of initial diameter arranged from north to south; Tanaka function with 2 parameters (solid lines) and Richards function with 3 parameters (dashed lines); Maalth-sit (Site 4, Fig. 1), Arena Cove (Site 15), Bodega Marine Reserve (Site 17), McClure Beach (Site 18), and Punta Baja (Site 41). N for each sample is given in Table 3
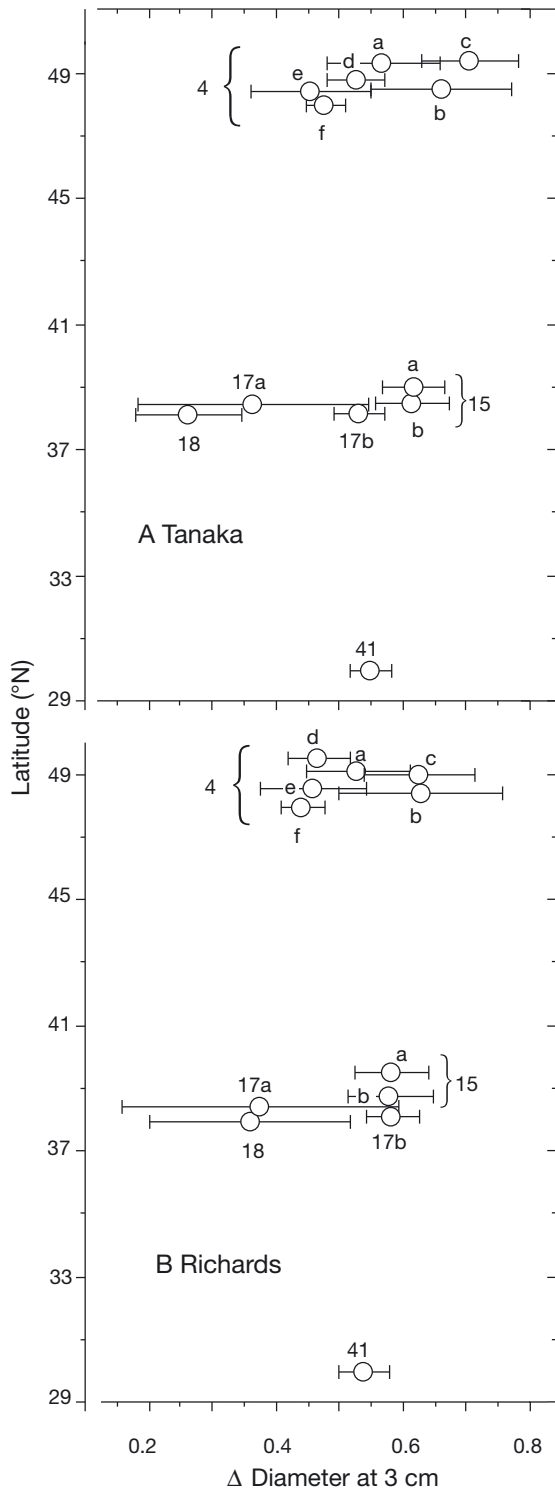
Fig. 7. *Strongylocentrotus purpuratus.* Δdiameter estimated at an initial diameter of 3 cm using (A) the Tanaka function and (B) the Richards function. Error bars are 95% confidence intervals. Site 4, Maalth-sit: (a) pool_2 1985, (b) pool_3 1985, (c) pool_1 1987, (d) pool_2 1987, (e) pool_3 1987, and (f) pool_4 1987; Site 15, Arena Cove: (a) 1986, (b) 1987; Site 17, Bodega Marine Reserve: (a) 1985, (b) 1986; Site 18, McClure Beach 1987; Site 41, Punta Baja 1985
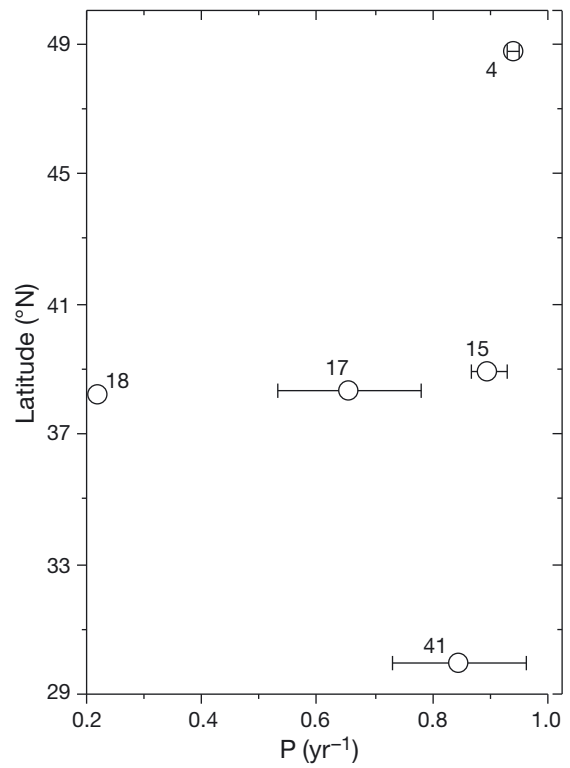

Fig. 8. *Strongylocentrotus purpuratus.* Survival estimates (annual survival rate, P yr^{-1}) based on Tanaka growth parameters and mean diameter of size distributions. Error bars are ±1 SE. Site 4, Maalth-sit; Site 17, Bodega Marine Reserve; Site 15, Arena Cove; Site 18, McClure Beach; Site 41, Punta Baja

Annual survival

The parameter M (Eq. 7) was calculated for each site where growth parameters had been estimated and the mean size of individuals in the first mode was used as D_0 in Eq. (7). Annual survival rate, P yr^{-1}, (e^{-M}) and mean annual survival were calculated for each site. Survival rates were similar at both northern and southern sites (Fig. 8). The estimates for sites between 38 and 39° N showed great variation over short distances, with the highest survival estimate for Arena Cove and the lowest for McClure Beach. Survival estimates for Bodega Marine Reserve were intermediate and these 3 sites emphasize that variation in both growth and survival can be expected over short distances.

DISCUSSION

There are very few studies with sea urchins that span a wide latitudinal range; however, previous studies of *Strongylocentrotus purpuratus* at some of the sites (e.g. Ebert 1968, 1983, Russell 1987, Ebert & Russell 1988) showed patterns similar to those presented here. The

red sea urchin *Strongylocentrotus franciscanus*, studied from Alaska to southern California (Ebert et al. 1999), showed patterns similar to those found for *S. purpuratus*. Growth varied from north to south, but there was no latitudinal trend; survival was better in the north. The largest red sea urchins were found in the San Juan Islands, Washington, not at the most northern sites in Alaska. The largest red sea urchins have been reported towards the northern end of Vancouver Island (Bureau 1996) and the largest recorded *S. purpuratus* (10.4 cm) was at a subtidal site off the southern coast of Vancouver Island (48.38° N, Kramer & Nordin 1975). Farther north, in Torch Bay, Alaska (58.33° N), Duggins (1981) did not find purple sea urchins larger than 8 cm. The pattern for both of these *Strongylocentrotus* species is an increase in the maximum observed size towards the northern end of the range and then a decline out to where the studies have ended.

The number of sites where growth and survival was determined was small; therefore, complex patterns cannot be determined. It is expected, however, that patterns such as the latitudinal changes in maximum diameter (Fig. 5) can be interpreted in terms of growth or survival (or both), which will then focus on the environmental factors that determine these demographic attributes. It also is unknown whether patterns presented here have changed during the past 20 yr.

Latitudinal patterns of size, growth, and survival have been described for a number of intertidal and nearshore species. Survival has been reported to increase towards higher latitudes (e.g. Weymouth et al. 1931, Gilbert 1973, Frank 1975, Lewis 1986, Harrington 1987). In general, the pattern for growth rate is the opposite, with a higher growth rate at lower latitudes (e.g. Weymouth et al. 1931, Hall et al. 1974, Frank 1975, Wright 1975, Appeldoorn 1983) but with some complications. *Macoma balthica* showed an increase in growth rate to the south along the Atlantic coast of the US, but on the European coast growth was highest at intermediate latitudes (Beukema & Meehan 1985). Maximum size often has been reported as greater at high latitudes (e.g. Weymouth et al. 1931, Frank 1975, Lewis 1986), but the pattern was reversed for *M. balthica* (Beukema & Meehan 1985) and Gilman (2005, 2006) found no latitudinal trend in maximum size or short-term growth and survival of the limpet *Collisella scabra* (now *Lottia scabra*, see Lindberg 2007)

It is unclear whether all of the latitudinal trends that have been reported are correct. For example, *Tegula funebralis* (now *Chlorosoma funebralis*, see McLean 2007) showed a trend of increasing maximum size to the north (Frank 1975), but Wright (1975) examined populations both farther north and south. He found the largest individuals at North Cove of Cape Arago,

Oregon (43.30° N), a decrease in maximum size at Mukkaw Bay, Washington (48.37° N), and a further decline at Chesterman Beach, Vancouver Island (49.10° N). This pattern is similar to the pattern shown by *Strongylocentrotus* spp. It also must be emphasized that all of these studies represent snapshots of the populations and long-term sampling of purple sea urchins has been restricted to just a few sites. For example, at Sunset Bay, Oregon (Site 8, Fig. 1), size structure has been documented since 1964 (Ebert 1968, 1983, unpubl. data) and is strongly influenced by rare recruitment events that change the fraction of Age ≤ 1 individuals but not maximum size. At another site, False Point, California (Site 39, Fig. 1), where sea urchins have been studied since 1970, density, size structure, and maximum observed size have fluctuated due to both frequent recruitment events and catastrophic mortality (Ebert 1983, unpubl. data).

The models describing population structure across a geographic range by Brown (1984) and Caughley et al. (1988) were developed based on life cycles where offspring develop in the same location as parents (e.g. birds, mammals, plants). These models are not appropriate for marine species with planktonic larvae that spend weeks in the plankton, are obligate dispersers, and hence violate the assumption that offspring develop close to the adults that produced them. Although the shape of the density versus latitude distribution (Fig. 2) tapers at both ends, it should not be considered to support these models. Growth and survival of purple sea urchins as well as other marine invertebrates with planktonic larvae show patterns that are not consistent with the assumptions of the Brown and Caughley models, and so they should not be used to test hypotheses related to latitudinal structure of marine species with planktonic larvae.

Transport of larvae by ocean currents is important and recruitment has been correlated with distance from headlands (Ebert & Russell 1988). Given the long larval period of ≥5 wk in *Strongylocentrotus purpuratus* (Strathmann 1978), the patterns of density (Fig. 2) and fraction of Age ≤ 1 individuals (Fig. 4) are probably best considered in the context of patterns of water movement along the coast (e.g. Ebert 1996, Gaylord & Gaines 2000). These physical models are useful in focusing attention on currents and coastal topography, but were not developed as general models that include mechanisms responsible for geographic limits or patterns of growth and survival. The obligate planktonic stage uncouples settlement from post-settlement processes and so a site that is good for settlement may or may not be a good site for future growth, survival, and reproduction (Ebert 1982, Gilman 2005).

The model developed by Lewis (1986) comes closest to fitting the purple sea urchin distribution. In this

model, physical conditions were suitable for adults much farther to the north beyond the normal range and good survival coupled with uncertain recruitment resulted in low densities of large, long-lived individuals. Reproductive seasons lengthened in the south so recruitment failures would be fewer and densities would be higher, but thermal stress would result in smaller and shorter-lived individuals. Some portions of these patterns, such as a general increase in size and improved survival with latitude together with a trend towards increased settlement in the south, have been shown for both red and purple sea urchins (Ebert et al. 1994). Growth rates of red and purple sea urchins, however, do not conform to all aspects of Lewis's model.

Reproduction, based on a gonad index, is difficult to compare across sites because different authors have used different measures, but in general there appears to be no trend in gamete production so northern sites are as productive as southern sites but with substantial variation. For example, sea urchins at Bodega Marine Reserve had gonads smaller than those farther to the south (Lester et al. 2007), but Bodega Marine Reserve was also a site with slower growth than that reported here. Boolootian (1966) determined gonad indices at a site called Shell Beach, close to the Bodega Marine Reserve, as being as high as at sites farther north into Oregon; he concluded that gonad indices were considerably higher for northern populations. The important point is that gamete production is not low in the north and high in the south, which is required in Lewis' (1986) model.

Thermal stress for intertidal species is not a simple function of latitude (e.g. Dahlhoff 2004, Helmuth et al. 2006, Sagarin & Somero 2006). The tidal wave along the Pacific coast of North America sweeps from south to north and so low tides occur earlier in the south where the lowest summer tides occur before sunrise. Farther north, extreme low tides can occur midmorning and so thermal stress may be greater in the north (Helmuth et al. 2002). The lethal upper limit for *Strongylocentrotus purpuratus* is about 24°C (Farmanfarmaian & Giese 1963) and there is evidence that purple sea urchins do not tolerate temperatures ≥22°C for prolonged periods (Ford et al. 1978). For shorter periods, however, individuals can tolerate higher temperatures as shown by Gonor (1968), who measured internal body temperatures for intertidal urchins, but 3 to 5 hr of exposure can be fatal. A sample of 27 individuals at Boiler Bay, Oregon, with internal temperatures above 26°C were taken back to Hatfield Marine Laboratory in Newport and held in running seawater where all died within 24 hr (Gonor 1968). There was also substantial mortality in the field at this time: farther south, a mass mortality was observed in the inter-

tidal at False Point, La Jolla, California, in 1971 (Ebert 1983), associated with a combination of warm water, high air temperatures, and fall low tides.

Lewis (1986) interpreted southern limits as set by thermal stress and, in combination with changes in nearshore oceanographic processes, this may explain the southern distribution of purple sea urchins. Upwelling can reduce the frequency of high temperature events nearshore and both Punta Baja and Punta San Carlos, Baja California Norte, are within upwelling regions; however, south of Punta San Carlos there is a long stretch of the Baja California coast without predictable upwelling (Zaytsev et al. 2003). Given available information, temperature limitation by physiological stress at the southern end of the distribution is the most reasonable explanation for why *Strongylocentrotus purpuratus* stops occuring in the intertidal at about Punta San Carlos (Lester et al. 2007) and possibly also the reason for the southern subtidal limit at Isla Cedros.

The cause of the northern limit is unknown, but temperature effects on adults do not seem likely, and in this regard Lewis (1986) is probably correct that adults could be transported many kilometers to the north and they would survive and reproduce. The disconnect between recruitment and adult survival also has been observed across sharp boundaries (e.g. Zacherl et al. 2003, Herbert et al. 2009). Poor recruitment success in *Strongylocentrotus purpuratus* certainly occurs given the size structure shown at Grant Bay (50.47° N) or that found by Duggins (1981) in Torch Bay, Alaska (58.33° N). Recruitment frequency at these northern sites is not known, but it is likely that a combination of temperature effects on development coupled with physical transport of larvae account for highly variable success and at some point total numbers recruited cannot balance adult survival and the geographic limit is reached. This limit may move back and forth along the coast, but farther extension becomes unlikely. Interaction of currents and coastal topography alone, however, cannot be the answer because there are other sea urchin species present in Alaska that have similar larvae. *S. franciscanus* extends to the west at least to Kodiak Island, Alaska (57° N, 153° W; Mortensen 1943), *S. droebachiensis* and *S. palidus* both are present in Torch Bay as well as farther west along the Alaskan coast, and *S. polyacanthus* is present farther west in the Aleutian chain (Estes & Duggins 1995). These species have planktonic larvae physically similar to those of *S. purpuratus* and current patterns are such that they arrive at suitable rocky locations. The limitation of both *S. purpuratus* and *S. franciscanus* may be due to temperature effects on larval development and so fit with the model of Lewis (1986). At 10°C, early development rates to the pluteus stage were similar for *S. purpuratus*, *S. droebachiensis*, and *S. franciscanus* (Strath-

mann 1987), but Farmanfarmaian & Giese (1963) reported that no fertilization membrane or development occurred at 5°C in *S. purpuratus*.

Appropriate questions for future research are whether demographic patterns shown by *Strongylocentrotus purpuratus* in the late 1980s have persisted and whether other nearshore species display similar patterns of size, recruitment, growth, and survival. The lack of a cline of growth may be unique to sea urchins or possibly echinoderms generally, but there are no comparable studies that help in answering this. Molluscs certainly have different growth responses and the few available studies show faster growth at lower latitudes. The difference with echinoderms may be related to internal (echinoderms) versus external (molluscs) skeletons. There is a lack of demographic studies over many degrees of latitude for a diversity of marine invertebrates (cf. Sagarin et al. 2006) that could aid in answering these questions, and a single model may not be appropriate.

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