



Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses

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Abstract

Aim It is often assumed that species generally reach their highest densities in the centre of their range and decline in abundance towards the range edges. A number of mechanisms have been proposed that could theoretically support this pattern, and several ecological theories have been developed based on the assumption that this pattern occurs in nature. However, few studies have quantified geographical patterns of species abundance throughout species ranges. This is largely because of the logistical challenges of sampling throughout the large spatial areas of most species ranges. We use intertidal invertebrates, which have relatively well defined linear ranges, to test the hypothesis that species are most abundant in the centres of their ranges.

Location Our sampling programme covered all or most of the ranges of twelve intertidal invertebrate species along the Pacific coast of North America, from Cabo San Lucas (Baja California, Mexico) to Shelikof Island (AK, USA).

Method We sampled invertebrate density at forty-two field sites using quadrat and transect methods. We used a shape fitting procedure to find idealized range shapes that best fit the sampled distributions of abundance. The idealized range shapes represented both a distribution where abundance was highest at the range centre and distributions where abundance was highest at one or both of the range edges.

Results Overall, this suite of species did not show the expected pattern of high abundance near the range centre. Six of the species showed patterns indicative of high densities near one of their range edges, whereas only two showed patterns with high densities near their range centres. Furthermore, nine of the twelve species had sites near the range edges in which density ranked in the top 20% of all sites.

Main conclusions The hypothesis that species are most abundant in the centre of their ranges cannot be generalized to this diverse suite of intertidal organisms. The diversity of distribution shapes that we found suggest that evolutionary and ecological theories that assume high abundance at range centres should be re-examined with consideration of alternative abundance distributions. We suggest that sampled geographical distributions of abundance can be combined with demographic and physical factor data taken at the same scale to test hypotheses related to the causes of range boundaries and the responses of species ranges to climatic change.

Keywords

Intertidal invertebrates, range limits, abundance distributions, Pacific coast of North America.

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INTRODUCTION

Patterns of species geographical abundance may provide insights into several central questions in ecology including: What determines or sets range boundaries? How will ranges respond to climate change? How do species evolve within their ranges? What areas of ranges should be the foci of conservation efforts? It is widely assumed that species reach their highest densities at the centre of their range and decline in density toward the range edges (Wulff, 1950; Andrewartha & Birch, 1954; Udvardy, 1969; Naumov, 1972; Kendeigh, 1974; Whittaker, 1975; Rapoport, 1982; Brown & Gibson, 1983; Cox & Moore, 1985; Hengeveld, 1990; Maurer *et al.*, 1994).

Several explanations of why such an 'abundant centre' pattern should develop in natural populations have been posited in the biogeographic literature. Grinnell (1922) and later Cain (1944) suggested that individuals disperse outward from a central point where favourable environmental conditions lead to maximal densities. Other authors linked species abundance distributions to environmental gradients, and proposed that species are physiologically limited and reach lower maximal densities at extreme values of these gradients (Shelford, 1911; Andrewartha & Birch, 1954; Kendeigh, 1974; Cox & Moore, 1985). Brown (1984) formulated a more encompassing mechanistic explanation for the abundant centre distribution by arguing that local abundance is a reflection of how well a particular site meets the needs of a species along many niche axes. These axes include the physiological characteristics of the species (e.g. temperature tolerance) as well as ecological characteristics (e.g. response to competitors or predators). Brown argued that these parameters are spatially autocorrelated, so that sites farther from the optimal site in any direction are less optimal and lead to declining densities until the range edge where suitability and density drop to zero.

That abundant centre patterns exist in natural populations has often been assumed in discussions of several ecological and evolutionary hypotheses including theoretical studies of species responses to climate change (Hengeveld, 1990; Mehlman, 1997; Sagarin *et al.*, 1999), spatially explicit approaches to population dynamics (Andrewartha & Birch, 1954; Ratcliffe, 1968; Richards & Southwood, 1968; Maurer & Brown, 1989; Hengeveld, 1990; Maurer, 1994; Enquist *et al.*, 1995; Curnutt *et al.*, 1996; Mehlman, 1997), the analysis of habitat reserve strategies (Lawton, 1993; Brown *et al.*, 1995), species conservation models (Lomolino & Channell, 1995), predictions of pest outbreaks (Birch, 1957; Hengeveld & Haeck, 1981), examinations of genetic population structure (Antonovics, 1976; Hoffman & Blows, 1994), models for speciation (Wulff, 1950; Brown, 1984), studies of the evolution of species range limits (Kirkpatrick & Barton, 1997), and explanations of ecological patterns such as the positive relationship between local abundance and the extent of geographical distributions (Gotelli & Simberloff, 1987).

Despite its prevalence in the literature, little empirical work has rigorously examined the abundant centre pattern

in nature (Sagarin & Gaines, 2002). Because most species inhabit large geographical ranges, it is often logistically difficult to consistently sample density throughout the range. Perhaps the most challenging problem is adequately sampling the range edges, where there typically is far more area than near the range centre (Sagarin *et al.*, in preparation).

Here, we present results of surveys of intertidal invertebrate density along the Pacific Coast of North America that were designed to test the hypothesis that species abundances are highest in the centre of the range and decline towards the edges (i.e. the abundant centre hypothesis). Intertidal invertebrates represent an ideal system for this study because they occupy ranges that are essentially one-dimensional. They occupy a narrow strip of shoreline habitat, and their range can be characterized by two points – their northern and southern geographical limits. In the special case of one-dimensional ranges, edge areas are no larger than areas at the centre of the range and abundance distributions can be drawn directly from surveys taken at multiple points across the range. Moreover, intertidal invertebrates are generally conspicuous and slow moving or sedentary, making them relatively easy to sample. Because their ranges are constrained to the coastline, a single team of observers can sample densities over the entire species range.

These surveys provide a 'snap shot' of abundance distributions vs. position within the range that we use to assess the generality of abundant centre distributions. We discuss how geographical abundance distributions might be combined with demographic and physiological data to form testable hypotheses about the causes of species range limits and to further improve predictions of species responses to climate change.

METHODS

Survey methods

We sampled densities of intertidal invertebrates at forty-two sites across all or most of their known geographical ranges during low tides between December 1998 and August 2000 (Table 1, Fig. 1). We sampled twelve species that were easily identifiable, conspicuous, and diverse in both their habitat use and life-history strategies (Table 2). Identifications were made in the field by the first author (RDS). At each site, voucher specimens were collected for later verification using taxonomic guides (Smith & Carlton, 1975; Morris *et al.*, 1980; Lindberg, 1981; Kozloff, 1993). It is likely that our records for the whelk *Nucella ostrina* include both *N. ostrina* and its cryptic sister species *N. emarginata*. These two recently divided species overlap in distribution between Pt. Conception, California and San Francisco Bay (Marko, 1998). Whelks we encountered more closely resembled the 'northern form' described by Palmer *et al.* (1990) and later named *N. ostrina* by Marko (1998), and the area we studied largely covers the range of *N. ostrina*. However, within the region of species overlap, we cannot be certain of our whelk identifications.

Table 1 Sites sampled from south to north with dates and coordinates

ID	Site	Date	Latitude (N)	Longitude (W)
1	Pta. Cabeza Ballena, Mexico	3 April '00	22°55'	109°50'
2	Pta. Chileno, Mexico	4 April '00	22°58'	109°48'
3	Milgriño, Mexico	2 April '00	23°01'	110°05'
4	Los Cerritos, Mexico	1 April '00	23°19'	110°10'
5	Pta Marquez, Mexico	4 April '00	23°57'	110°52'
6	Pta Tosca, Mexico	6 April '00	24°18'	111°43'
7	El Palito, Mexico	7 April '00	26°14'	112°29'
8	Pta. Abreojos, Mexico	26 October '99	26°42'	113°35'
9	Bahía Tortugas, Mexico	27 October '99	27°42'	114°53'
10	Pta. Lobos, Mexico	28 October '99	28°53'	114°26'
11	Pta. San Carlos, Mexico	2 January '99	29°37'	115°30'
12	Pta. Baja, Mexico	1 January '99	29°57'	115°49'
		25 October '99		
13	Pta. Clara, Mexico	30 December '98	31°32'	116°40'
		29 October '99		
14	El Zepelin, Mexico	3 January '99		
		24 October '99	31°42'	116°41'
15	Playa Encantada, Mexico	21 May '00	32°18'	117°03'
16	Bird Rock Road, CA, USA	4 January '99	32°49'	117°16'
17	Crescent Bay, CA, USA	18 May '00	33°33'	117°48'
18	Flat Rock Point, CA, USA	17 March '99	33°47'	118°50'
19	Sycamore Cove, CA, USA	16 March '99	34°09'	119°20'
20	Arroyo Hondo, CA, USA	16 May '00	34°28'	120°09'
21	Lompoc Landing, CA, USA	15 March '99	34°44'	120°39'
22	Piedras Blancas, CA, USA	28 February '99	35°40'	121°32'
		6 June '00		
23	Oystercatcher Point, CA, USA	4 June '00	36°05'	121°33'
24	Soberanes Point, CA, USA	1 March '99		
		17 February '00	36°26'	121°56'
25	Hopkins Marine Station, Pacific Grove, CA, USA	17 February '99	36°38'	121°55'
		21 December '99		
26	Natural Bridges, Santa Cruz, CA, USA	26 February '99	36°57'	122°01'
		23 December '99		
27	Pigeon Point Lighthouse, CA, USA	15 February '99	37°11'	122°23'
		23 December '99		
28	Fitzgerald Marine Reserve, CA, USA	14 February '99	37°31'	122°31'
		23 December '99		
29	Bodega Marine Laboratory, CA, USA	28 June '99	38°18'	123°03'
		20 December '99		
30	Jug Handle, CA, USA	7 May '00	39°22'	121°23'
31	Palmer's Point, CA, USA	29 June '00	41°08'	124°09'
		8 May '00		
32	South Cove, OR, USA	30 June '99	43°18'	124°24'
		9 May '00		
33	Boiler Bay, OR, USA	1 June '99	44°50'	124°03'
		10 May '00		
34	Falcon Point, OR, USA	2 July '99		
		11 May '00	45°46'	123°58'
35	Point Grenville, WA, USA	29 June '00	47°18'	124°16'
36	Beach 4, WA, USA	3 July '99	47°39'	124°23'
37	Hole in the Wall, WA, USA	4 July '99	47°57'	124°39'
		30 June '00		
38	Sepping's Island, BC, Canada	1 July '00	48°50'	125°12'
39	Florencia Beach, BC, Canada	2 July '00	49°00'	125°39'
40	Nawisnuk, BC, Canada	3 July '00	51°08'	127°44'
41	Makhnati Island, AK, USA	14 August '00	57°02'	135°23'
42	Shelikof Island, AK, USA	13 August '00	57°09'	135°45'

ID column numbers refer to map in Fig. 1.



Figure 1 Map depicting approximate locations of study sites. Numbers refer to study sites identified in Table 1.

Sites were mainly chosen based on accessibility and the availability of rocky substrata. All were exposed outer coast sites. We avoided sites in calm bays or inland waterways, such as Puget Sound, Washington. Geographical coordinates for each site were taken with a handheld Global Positioning System receiver (ETrex, Garmin Ltd, Olathe, USA). Although sites covered the entire range of most of the focal species, sample coverage is much more sparse in the northern part of the range because of the relative rarity of rocky sites in Washington and the difficulty of accessing many sites in British Columbia and Alaska.

At each site, we established two to eight transects ranging from 4 to 50 m in length. Transect length and number of quadrats sampled varied with site depending on the area of habitat available. Sampling was conducted by trained volunteer researchers under the guidance of RDS. At each site we attempted to sample six zones: (1) the high barnacle zone, (2) the rockweed zone, (3) the 'mid'-intertidal zone (characterized by macroalgae, especially brown turf algae), (4) the low-intertidal zone (characterized by short-term exposure to air at low tide and the

appearance of fleshy red algae), (5) surge channels or boulder fields, and (6) the exposed zone (characterized by direct exposure to wave action and the frequent occurrence of mussel beds). We counted target species in 0.25 m² quadrats spaced at every metre along transects. At sites where the target species were rare, and thus not found along transects, we conducted intensive searches in appropriate habitat for the species. Search areas were marked and measured, so that species abundances for rare taxa could be reported per m². In addition, the anemones *Anthopleura sola* and *A. xanthogrammica*, the urchin *Strongylocentrotus purpuratus*, and the sea star *Pisaster ochraceus* were sampled along band transects where an observer walked an 8–25 m path through the low or exposed zones and counted individuals of the species within 1 m on either side of the transect line.

Densities of the mussel *Mytilus californianus* are difficult to measure without distinctive sampling, because they form multilayer beds at high densities. To convert visual estimates of percent mussel cover from quadrats to a density estimate, we cleared 10 × 10 cm quadrats with 100% mussel cover at each site near the transect. We sorted all the mussels collected by size using a graduated sieve. These site specific density estimates were then used to scale quadrat percent cover to densities. In some sites, collection restrictions prevented the use of this technique. In these cases counts of mussels from 10 cm² samples taken at the nearest site were multiplied by the average percent cover at the local site to estimate mussel density.

Although we did not design this study to determine the mechanisms responsible for the observed distribution patterns, we did want to examine if patterns within the range arose solely because of the lack of habitat. Abundances might decline near the edge of the range if the prevalence of available habitat declined. Dimensions of rocky benches at each site were measured to estimate total area available to intertidal invertebrates. At each site, the areas of high, middle, low and exposed tidal zones were measured with their boundaries delineated by their positions on shore and the taxa that were present. In addition, percent cover of the following habitat attributes for the entire site was estimated visually by RDS: cobble, flat bench area, large boulders (greater than 0.5 m³), massives (rock formations whose vertical surfaces were greater than their horizontal top surface areas), calm pools, surge channels (narrow inlets of c. 2 m or less in width with moving water), surge pools (rock surfaces which experience high wave action, even at low tide), and overall algal and bare rock cover.

For each target species except the mussel *M. californianus*, available appropriate habitat was defined as the area of the species preferred tidal zone(s) multiplied by the proportion of preferred habitat type within that zone (see Table 2). The relationship between average and maximum species densities (see below) to total areas of the sites and total areas of appropriate habitat within the sites was evaluated using least squares linear regressions. Obviously, the measurements give only gross estimates of available habitat for the species, but these measures were consistent across sites and were used to

Table 2 Species used in surveys and criteria used for assessing appropriate habitat

Species	Common name	Geographic range	Tidal zone/association	Habitat
<i>Anthopleura sola</i> (Pearse & Francis, 2000)	Anemone	Northern California to central Baja	Entire mid-zone	Rock surfaces, crevices, calm pools
<i>A. xanthogrammica</i> (Brandt, 1835)	Anemone	Northern Baja to Alaska	Mid to low and exposed zone	In tide pools, surge channels and crevices
<i>Fissurella volcano</i> (Reeve, 1849)	Keyhole limpet	Crescent City, California to Bahia Magdalena, Baja	Mid and lower mid zone	Amid turf and crustose corraline algae, often in reefs of <i>Serpulorbis</i>
<i>Lepidochitona bartwegii</i> (Carpenter, 1855)	Chiton	Monterey Bay, California to Abreojos, Baja	Upper mid zone	Common under rockweeds, sometimes in damp crevices
<i>Lottia pelta</i> (Rathke, 1833)	Limpet	Alaska to Bahia del Rosario, Baja	Upper mid zone	Common under rockweeds, sometimes in damp crevices
<i>Mytilus californianus</i> (Conrad, 1837)	Mussel	Southern Baja to Aleutian Islands	Entire intertidal, especially exposed zone	Exposed rocky faces
<i>Nucella ostrina</i> * (Gould, 1852)	Whelk	Alaska to northern Baja	Mid-zone, exposed zone	Amid barnacles and mussels and in small crevices
<i>Pisaster ochraceus</i> (Brandt, 1835)	Sea star	Pta. Baja to Alaska	Mid to low and exposed zone	In tide pools, surge channels and crevices, and near mussel beds
<i>Serpulorbis squamigerus</i> (Carpenter, 1857)	Tube snail	Monterey Bay, California to central Baja	Lower mid zone	On angled, vertical or overhanging rock walls and sides of boulders. Requires water flow, but avoids direct wave action
<i>Strongylocentrotus purpuratus</i> (Stimpson, 1857)	Purple sea urchin	British Columbia to Isla Cedros, Baja	Lower mid-zone and low zone	In tide pools, surge channels and crevices
<i>Tegula funebris</i> (A. Adams 1855)	Turban snail	British Columbia to central Baja	Entire mid-zone	Ubiquitous, except on sand channels
<i>Tetraclita rubescens</i> (Darwin, 1854)	Barnacle	San Francisco, California to Cabo San Lucas, Baja	Mid and lower mid-zone	Tops and sides of angled rocks, under overhangs

*Records may include *N. emarginata* in the southern part of the range, see Methods.

evaluate if substantial differences in sizes of sampling sites were responsible for the observed abundance patterns.

Data analysis

To examine patterns of the density across sites we analysed transect data in two ways: (1) densities were averaged over all transects at the site (hereafter 'average' density) and (2) densities were averaged from quadrats only in the transect with maximal average density at the site (hereafter 'maximum' density). Average density from all transects ignores geographical patterns in the availability of suitable habitat, because densities in prime habitat for the species are averaged with densities from areas where the species did not occur. We use densities from the one transect with highest average density to estimate peak densities, which may bear little resemblance to patterns of total population size at the site.

Our primary goals in this study were to test the abundant centre hypothesis (that species abundances are highest in the centre of their ranges and decline towards the edges) and to determine if other types of abundance distributions (e.g. where abundance is greatest at the range edges) occur in nature. Previous investigators have tested the abundant centre hypothesis using linear regression analysis under the assumption that abundant centre distributions will produce

a negative relationship between abundance and distance from the range centre (Emlen *et al.*, 1986; Curnutt *et al.*, 1996). However, there are problems with the use of linear regression when comparing abundance to a continuous variable such as latitude or range position when sampling is not completely uniform across the range (Pacheco & Henderson, 1996; Scharf *et al.*, 1998). Moreover, linear regression does not characterize the actual shape of the abundance distribution.

To get a better idea of the actual shape of abundance distributions, we compared the cloud of points on density vs. latitude plots to four distribution shapes that represent both an abundant centre distribution and distributions where abundance is highest near one or both of the range edges (Fig. 2). We used a procedure similar to that used by Enquist *et al.* (1995) to find the shape that best fits the data distributions. This approach only examines the bounds on abundances in different parts of the range. Thus, for example, it does not assume that *all* sites near the range centre will be high abundance sites. This acknowledges the probability that even in the most optimal part of a species range there may be some sites with unsuitable habitat or other detrimental factors that reduce local populations.

Densities for each target species were converted to relative abundance (RA) values by dividing densities for each site by the maximum density found at any site within the

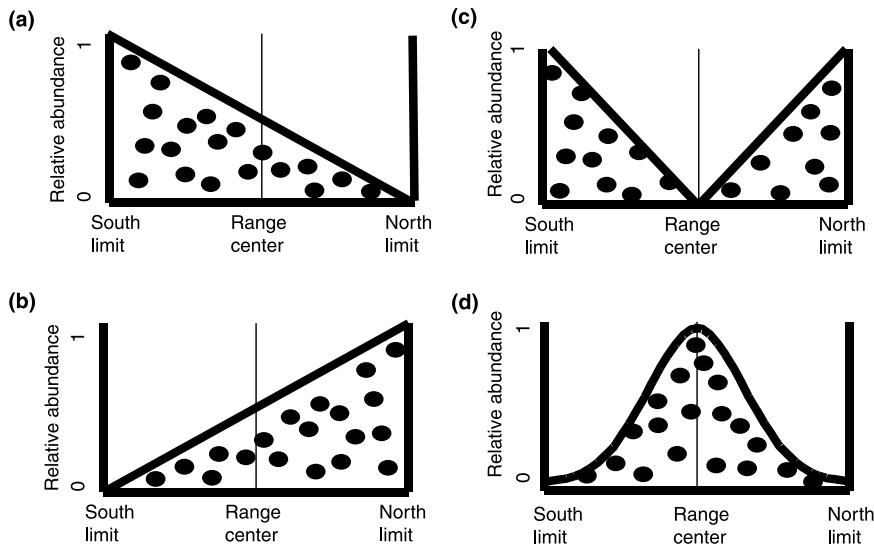


Figure 2 Shapes of distributions compared with observed data using goodness-of-fit tests. Hypothetical data sets that fit within the constraint spaces are illustrated by filled circles. Shapes are referred to in the text as (a) ramped south, (b) ramped north, (c) abundant edge, (d) normal.

geographical range. Range locations were converted to range index (RI) values, which standardize position within the range:

$$RI = 2(L - S)/R \quad (1)$$

where L is the location of the sample in degrees latitude, S is the latitudinal mid-point of the species range and R is the latitudinal extent of the range. The RI can range from -1 to 1 with values near zero indicating that the species was sampled near the centre of its range and values near 1 or -1 indicating the species was sampled near the northern or southern edge of its range, respectively.

Range boundaries were determined based on those reported by Morris *et al.* (1980). In cases where we found species outside their published range, we expanded the range used in the analysis. We did not contract ranges if we did not find a species at sites within the published range. This is a conservative approach that should enhance the likelihood of finding abundant centre distributions if ranges have shifted, because there will be zero values near the range edges included in the analysis. Our results should not be used as evidence of range expansions or contractions as our sample sites were limited, and we did not extensively map range edges.

The expected bound on densities was defined by one of four constraint curves (see Fig. 2). For each site, a constraint value, D_{\max} , was established from the equation for the constraint function. For linear constraint spaces (e.g. Fig. 2a–c) this is simply the equation for a line:

$$D_{\max} = ax + b \quad (2)$$

where a is the slope, x is the position in the range and b is the expected maximum density at the centre of the range. For the normal constraint space (Fig. 2d), we assume the maximum density is 1 at the centre of the range ($x = 0$) and that 99.9% of all individuals occur between $-1 \leq RI \leq 1$. This yields a maximum density constraint curve where:

$$D_{\max}(x) = 1/[\sigma(2\pi^{0.5})] \exp[-0.5(x/\sigma)^2] \quad (3)$$

For each species, a site was considered outside the constraint space if the observed density, RA, exceeded $D_{\max}(x)$ for the location (RI) of the site. For each species, we calculated the sum of squared deviations (SS) for sites that exceeded the constraint boundary to evaluate the fit of observed data to the constraint space. To obtain a probability estimate for the SS value, we used a randomization approach to rearrange all the observed RI and RA values to create repeated random species abundance distributions. We generated 10^5 rearrangements to obtain a probability distribution of SS. Small values of SS suggest that the constraint curve adequately bounds the distribution of abundance. A test was considered significant if more than 95% of the rearranged data sets had higher SS than the original data set (see Enquist *et al.*, 1995).

In summary, the procedure randomizes the observed data, compares the randomized data set to four idealized constraint spaces and then gives us the probability that the randomized data distributions fit any of the four constraint spaces better than the observed data.

RESULTS

Individual species plots of density by latitude show high site-to-site variation for all species (Figs 3 & 4). Sites of relatively high and low abundance appear in all regions of the species ranges. Abundance distributions fit a variety of shapes, with no single dominant pattern. In analyses using average density, five species showed patterns where density was highest at one or both range edges (e.g. 'ramped', 'abundant edge' shapes), whereas two species showed abundant centre patterns (e.g. 'normal' shapes) and five species showed no significant pattern (Table 3). For analysis of maximum density, six species showed concentration at the edges, one species showed an abundant centre pattern, and five species showed no pattern (Table 4).

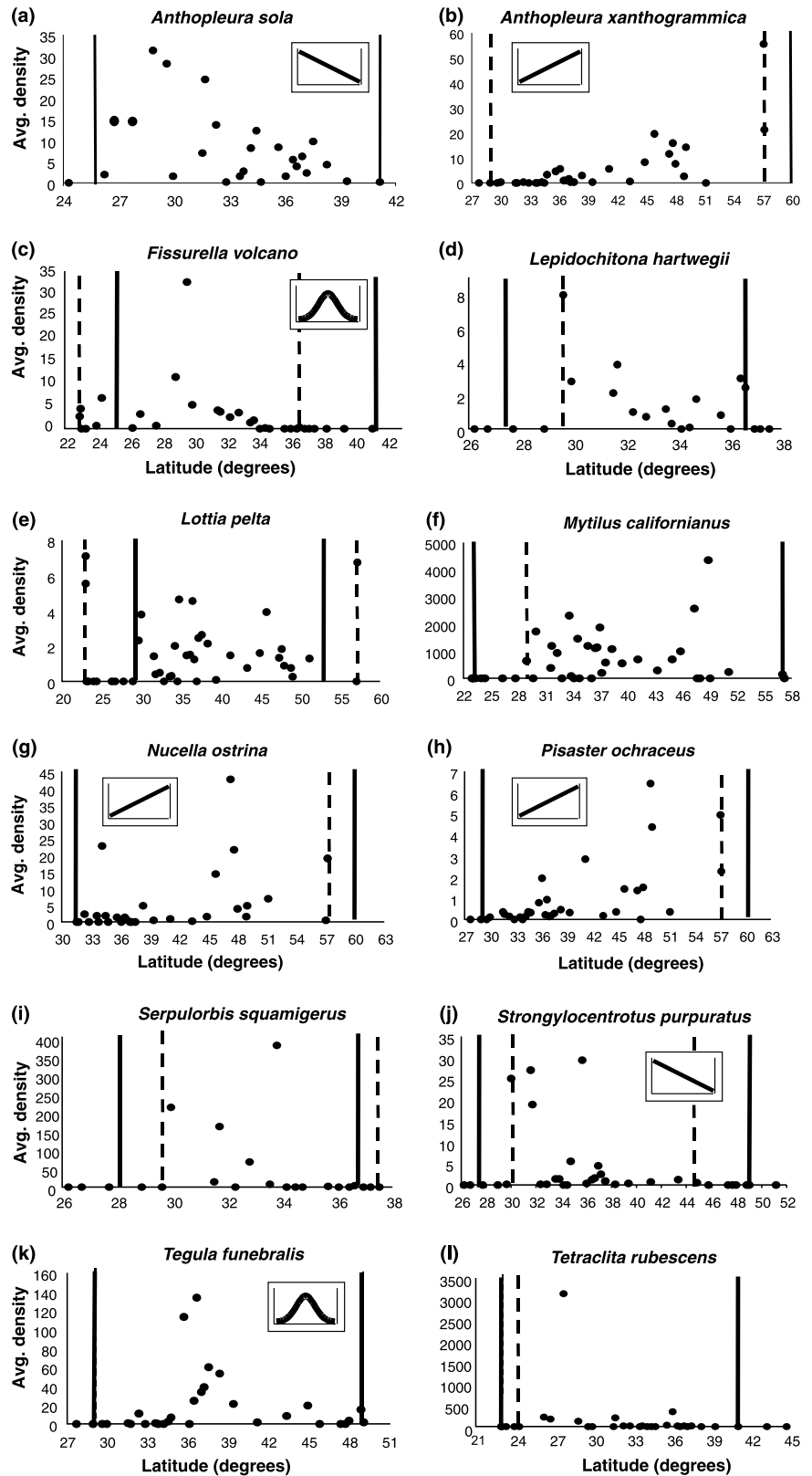


Figure 3 (a–l) Distributions of average densities per m² for the twelve focal species. Solid vertical lines indicate published range limits (see text). Dashed vertical lines indicate range limits encountered in this study. Inset cartoons indicate the shape (from Fig. 2) fit best by the distribution based on goodness-of-fit tests, if significant (see Table 3).

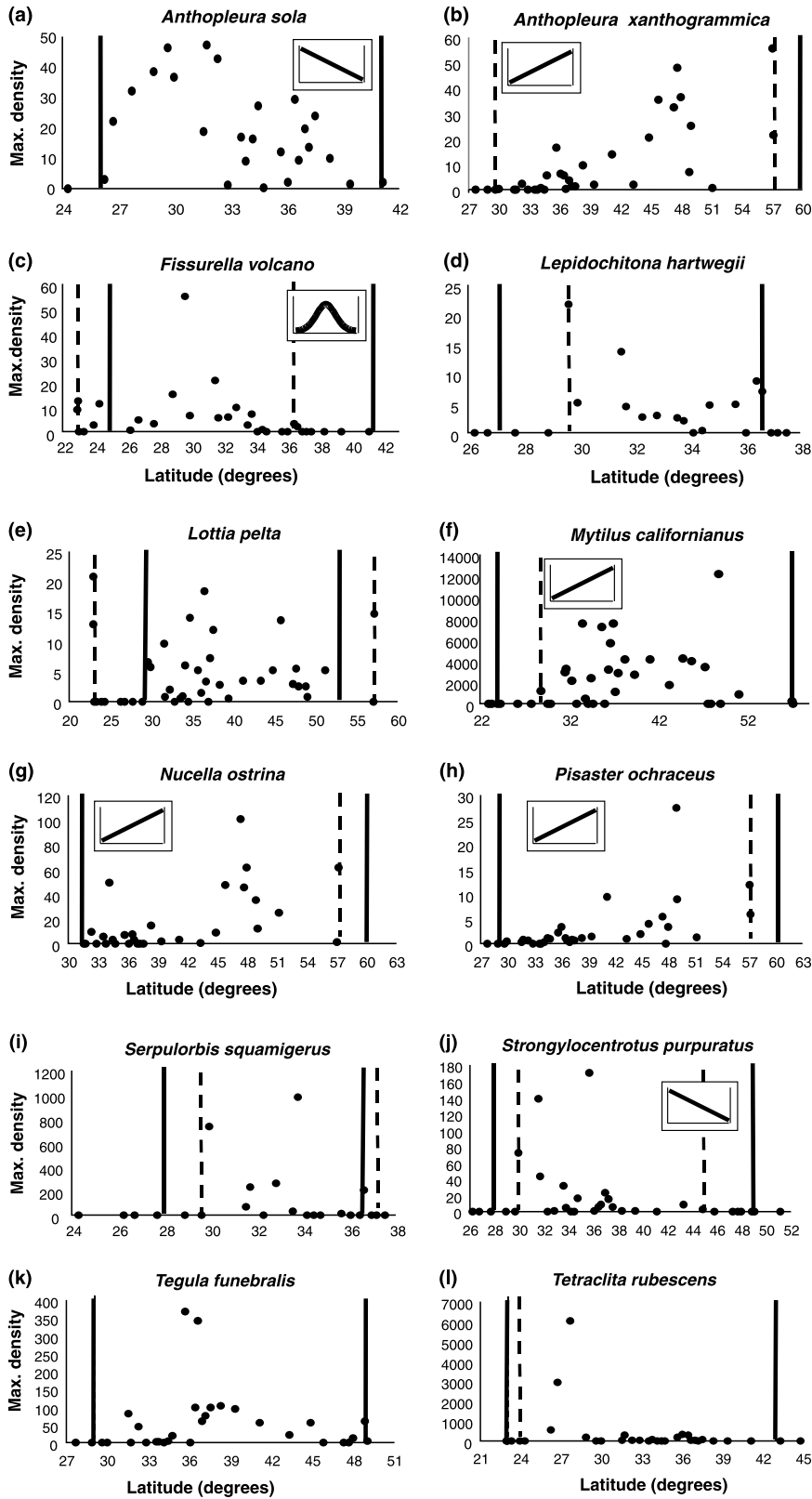


Figure 4 (a–l) Distributions of maximum densities for the twelve focal species. Solid vertical lines indicate published range limits (see text). Dashed vertical lines indicate range limits encountered in this study. Inset cartoons indicate the shape (from Fig. 2) fit best by the distribution based on goodness-of-fit tests, if significant (see Table 4).

Table 3 Best fitting constraint shapes for goodness-of-fit tests for distributions of average density

Species	Shape (<i>P</i>)	<i>P</i> -value
<i>Anthopleura sola</i>	Ramped south*	0.01
<i>A. xanthogrammica</i>	Ramped north	<0.001
<i>Fissurella volcano</i>	Normal	0.01
<i>Lepidochitona hartwegii</i>	Ramped south	0.15
<i>Lottia pelta</i>	Ramped south	0.12
<i>Mytilus californianus</i>	Ramped north	0.07
<i>Nucella ostrina</i>	Ramped north	0.05
<i>Pisaster ochraceus</i>	Ramped north	<0.001
<i>Serpulorbis squamigerus</i>	Ramped south	0.10
<i>Strongylocentrotus purpuratus</i>	Ramped south	0.01
<i>Tegula funebris</i>	Normal	0.01
<i>Tetraclita rubescens</i>	Ramped south	0.23

Shape refers to distribution shapes from Fig. 2. Significant *P*-values (bold) indicate that the distribution of abundance fit the distribution shape more closely than a random distribution in 95% or more of 10⁵ randomization procedures (see Methods).

*'Abundant edge' shape also fit, *P* = 0.04.

Table 4 Best fitting constraint shapes for goodness-of-fit tests for distributions of maximum density

Species	Shape	<i>P</i> -value
<i>Anthopleura sola</i>	Ramped south	0.01
<i>A. xanthogrammica</i>	Ramped north	<0.001
<i>Fissurella volcano</i>	Normal	0.02
<i>Lepidochitona hartwegii</i>	Ramped south	0.21
<i>Lottia pelta</i>	Ramped north	0.32
<i>Mytilus californianus</i>	Ramped north*	0.01
<i>Nucella ostrina</i>	Ramped north	0.04
<i>Pisaster ochraceus</i>	Ramped north	<0.002
<i>Serpulorbis squamigerus</i>	Ramped south	0.14
<i>Strongylocentrotus purpuratus</i>	Ramped south	0.02
<i>Tegula funebris</i>	Normal	0.07
<i>Tetraclita rubescens</i>	Ramped south	0.07

Shape refers to distribution shapes from Fig. 2. Significant *P*-values (bold) indicate that the distribution of abundance fit the distribution shape more closely than a random distribution in 95% or more of 10⁵ randomization procedures (see Methods).

*'Normal' shape also fit, *P* = 0.05.

Regardless of the overall distribution, sites of high abundance are found near the range edges in many species. We divided each species range into five sections of equal latitude and examined the rank density for each site within the section. For nine of the twelve species, range edge sections had densities ranking among the top 20% of sites (Tables 5 & 6). This occurred despite the fact that for some wide-ranging species, the number of study sites was low in the northern range edge. Some species, including *Lottia pelta* and *A. xanthogrammica*, showed highest densities right at the range edge.

The patterns we observed were not merely because of differences in habitat availability among sites. Linear regressions of average and maximum species density vs.

the total area of the intertidal site produced no significant relationships. Regressions of average and maximum species density vs. total area of available habitat at each site showed a significant relationship only for the chiton *Lepidochitona hartwegii* (average *Lepidochitona* density vs. total area: $R^2 = 0.70$, $P < 0.01$; maximum *Lepidochitona* density vs. total area: $R^2 = 0.65$, $P < 0.01$).

DISCUSSION

The distributional data from this suite of Pacific Coast intertidal invertebrates were congruent with a wide range of distributional shapes. Most notably, the abundant centre pattern was more the exception than the rule. Although we cannot use this small sample as a blanket rejection of the abundant centre hypothesis, it is clear that abundance distributions are more diverse than suggested by the abundant centre hypothesis.

Although our selected group of species represents a wide range of intertidal invertebrate life-history strategies, we would need to test terrestrial species to assess the generality of our results. It might also be argued that some aspect of intertidal species in general makes them less likely than terrestrial species to show abundant centre patterns. There is, however, no feature common among intertidal species that would suggest a mechanism to create this bias. For example, a pelagic larval phase, which occurs in most intertidal invertebrates, might be considered *more* likely to result in abundant centre patterns under Grinnell's (1922) and Cain's (1944) hypothesis of individuals dispersing outward from an optimal point. In fact, dispersive larval may theoretically result in a wide range of distribution shapes, as we discuss below. Here, we discuss how our studies might be refined methodologically and how our results might be combined with other geographically scaled data sets to help answer long-standing and timely ecological questions of the causes of range boundaries and responses of species to climate change.

METHODOLOGICAL ISSUES

Although our surveys were far from exhaustive, it is unlikely that sampling more sites would result in finding more abundant centre patterns, particularly for species already showing one of the 'abundant edge' patterns. The sites where we found maximal densities of species tended to show extremely high cover. For example, seastars (*P. ochraceus*) at the north end of their range tend to form continuous mats just below the mussel bed, resulting in very high densities. To change the observed 'ramped north' pattern in seastars to an abundant centre pattern, sites would have to be found near the centre of the range where densities greatly exceed densities in these mats, which is highly improbable.

Because our surveys are essentially a 'snapshot' of density at a particular time it is uncertain whether the distribution patterns are representative of long-term patterns. Continued monitoring of these sites would test both the robustness of the patterns we found and provide information on how

Table 5 Number of sites ranking in top 20% for average density for each species in five zones of equal latitudinal extent within the range

Species	South edge	Southern	Central	Northern	North edge
<i>Anthopleura sola</i>	3 (4)	2 (4)	0 (7)	0 (7)	0 (3)
<i>A. xanthogrammica</i>	0 (11)	0 (10)	3 (4)	2 (5)	2 (2)
<i>Fissurella volcano</i>	2 (6)	0 (3)	3 (3)	0 (6)	0 (7)
<i>Lepidochitona hartwegii</i>	0 (1)	1 (2)	1 (4)	0 (5)	1 (4)
<i>Lottia pelta</i>	2 (11)	3 (13)	1 (8)	1 (7)	1 (8)
<i>Mytilus californianus</i>	0 (11)	5 (14)	1 (7)	2 (7)	0 (3)
<i>Nucella ostrina</i>	1 (14)	0 (3)	3 (6)	1 (3)	1 (2)
<i>Pisaster ochraceus</i>	1 (12)	1 (8)	0 (6)	2 (3)	2 (2)
<i>Serpulorbis squamigerus</i>	0 (2)	2 (3)	1 (3)	1 (4)	0 (7)
<i>Strongylocentrotus purpuratus</i>	3 (6)	2 (9)	1 (6)	0 (3)	0 (6)
<i>Tegula funebris</i>	0 (6)	3 (10)	3 (4)	0 (3)	0 (6)
<i>Tetraclita rubescens</i>	1 (7)	3 (5)	1 (6)	1 (9)	0 (4)

Numbers in parentheses indicate number of sites sampled for each species in each zone.

Table 6 Number of sites ranking in top 20% for maximum density for each species in five zones of equal latitudinal extent within the range

Species	South edge	Southern	Central	Northern	North edge
<i>Anthopleura sola</i>	1 (4)	3 (4)	1 (7)	0 (7)	0 (3)
<i>A. xanthogrammica</i>	0 (11)	0 (10)	2 (4)	3 (5)	2 (2)
<i>Fissurella volcano</i>	2 (6)	1 (3)	1 (3)	1 (6)	0 (7)
<i>Lepidochitona hartwegii</i>	0 (1)	1 (2)	1 (4)	0 (5)	1 (4)
<i>Lottia pelta</i>	2 (11)	3 (13)	1 (8)	1 (7)	1 (8)
<i>Mytilus californianus</i>	0 (11)	3 (14)	3 (7)	2 (7)	0 (3)
<i>Nucella ostrina</i>	1 (14)	0 (3)	4 (6)	0 (3)	1 (2)
<i>Pisaster ochraceus</i>	0 (12)	1 (8)	1 (6)	2 (3)	2 (2)
<i>Serpulorbis squamigerus</i>	0 (2)	2 (3)	1 (3)	1 (4)	0 (7)
<i>Strongylocentrotus purpuratus</i>	3 (6)	2 (9)	1 (6)	0 (3)	0 (6)
<i>Tegula funebris</i>	0 (6)	3 (10)	3 (4)	0 (3)	0 (6)
<i>Tetraclita rubescens</i>	1 (7)	2 (5)	1 (6)	2 (9)	0 (4)

Numbers in parentheses indicate total number of sites sampled for each species in each zone.

species distributions respond to climatic change (see below). Nonetheless, large non-random density changes would have to occur to significantly alter the conclusions of this study. Life-history and ecological traits suggest that such population changes are not likely. For example, long-lived species such as the anemones would have to show rapid population changes in some sites, but not others. Even species that showed dramatic changes in population at a single site during the twentieth century seem to have retained their overall abundance distributions. For example, *Serpulorbis squamigerus* has increased significantly in central California since 1980 (Sagarin *et al.*, 1999), but its highest densities continue to be in southern California, as was the case before its northward spread (Hadfield, 1966; C. Baxter, pers. comm.).

Over such large geographical ranges, it is possible that some of our species contain cryptic sister species. Indeed we learned of the whelk *N. ostrina*, the cryptic sister species to *N. emarginata* (Marko, 1998) after we began research on the distribution of *N. emarginata*. It could be argued that several partially overlapping normal-shaped distributions of abundance (e.g. Fig. 2d) among a taxonomic group with many

cryptic species could result in a relatively flat distribution of abundance overall. However, this mechanism could not explain the very high densities we observed near or at the edges of nine of the twelve species ranges. Nonetheless, elucidation of the presence and relative size of cryptic species populations across species ranges would be a worthwhile addition to the data we present here to clarify our understanding of the role of evolution in shaping distributions of species abundance.

Patterns and processes

Predictions of species responses to climate change suggest that ranges should shift poleward with climate warming (e.g. Fields *et al.*, 1993). Although the usefulness of this simplistic hypothesis has been debated in the literature (e.g. see Davis *et al.*, 1998; Hodkinson, 1999), this hypothesis has been supported by observations of biotic responses to post-glacial warming (Davis, 1989) and by the results of studies of species responses to more recent climate warming (McCarty, 2001). If the hypothesis of shifting ranges is correct, we should see changes in individual species densities at a single

site that reflect the shape of the geographical distribution of abundance. For example, a site just northward of the range of a species with a 'ramped north' distribution would see a rapid increase in this species population, whereas it would see only a gradual increase in population due to a shift in a species with an abundant centre distribution.

Central to the issue of predicting species responses to climate change is an understanding of what sets range boundaries. Biogeographers have increasingly accepted the idea that a multitude of factors such as physiology, predation and dispersal limitations are responsible for setting range limits. The diversity of distributional patterns shown here lends support to this idea.

Ramped distributions (e.g. 'ramped north' and 'ramped south' distributions), as we have shown for several species, falsify the generality of the abundant centre hypothesis, but they do not rule out the role of physiological factors in setting range boundaries. Smooth environmental gradients may result in species abundance distributions that drop off suddenly without an apparent loss of available habitat. Carter & Prince (1981) used an epidemic model to show that small changes in physiological performance can lead to large changes in the probability of individuals 'infecting' new areas, which could lead to thresholds between high population areas and zero population areas at range edges. Welch *et al.* (1998) showed that sockeye salmon are very sensitive to specific environmental conditions, leading to sharp gradients in abundance of fish without steep climatological gradients.

Nonetheless, all the distributions we document may point to causal factors for range limits that are completely independent of physiology or ecological relationships. Recent modelling of marine larvae in flow fields that simulate mechanisms of larval transport along the Pacific coast suggests that species may reach equilibrium abundance distributions that match all of the distributional patterns we examined (as well as uniform distributions) solely through the effects of flow dynamics on dispersal of larvae (Gaylord & Gaines, 2000). Even for terrestrial species that do not have an obligate dispersal phase, simple reaction-diffusion models can result in a range of equilibrium distributions, including abundant centres and abundant edges (Bever & Flather, 1999).

Future directions

The potential for conflicting hypotheses suggests that additional information is needed to draw conclusions about the causes of range limits and how ranges will respond to climate change. Caughley *et al.* (1988) proposed a predictive framework for determining the causes of range boundaries based on the geographical distributions of a species density, physiological 'well-being' and reproductive rate. The potential for different causal factors to produce similar patterns in these three variables limits the practicality of Caughley *et al.*'s framework, but the idea of combining multiple data sets on multiple variables to test hypotheses about range limits is attractive and viable. We suggest three basic areas of

research that, when combined with species abundance distributions and data on such physical variables as temperature, currents and upwelling patterns, should allow us to test specific hypotheses about the causes of species ranges and range limits and responses of these ranges to climatic change.

First, more temporal data are needed to complement the spatial data. We have found that even the scant information we have obtained about changes in an intertidal community at HMS between 1930 and 1996 (Sagarin *et al.*, 1999), combined with new spatial data we present here provides important insight into patterns of change at HMS. For example, we know from field guides and naturalists' records that the tube snail, *S. squamigerus*, which showed a significant increase in abundance between 1930 and 1996 at HMS, was uncommon in Monterey Bay until the mid-1980s (Morris *et al.*, 1980; C. Baxter, pers. comm.). By the early 1990s, however, it was one of the dominant intertidal invertebrates in some areas. This limited temporal record meshes well with the spatial pattern of *Serpulorbis* that we observed. Although it reaches its highest densities towards the centre of its range, *Serpulorbis* did not show a 'normal' distributional pattern because it also has very high abundances near its northern and southern edges. It can be argued that the relatively rapid rise of *Serpulorbis* populations and its steep-sided abundance distribution may be related. Better still, we can test this relationship by observing sites at the northern edge or outside the northern limit of *Serpulorbis* distribution through time. We expect that if warming trends continue, more northerly sites in Santa Cruz and Moss Beach, California, which now have small scattered populations of this species should show rapid increases in *Serpulorbis* densities.

A second area of study that will complement the continued sampling of spatial distributions of abundance is an investigation of population demographics for intertidal invertebrate species. Because most species have an obligate dispersal phase, a logical focus of these studies should be the settlement patterns of new recruits to the population. Areas of low abundance, for example, may be sites that receive few larval settlers. Alternatively, areas of low adult abundance with high settlement might suggest strong post-settlement mortality, either through predation or physiological stress. Species that do not have a dispersive larval phase, such as many of the whelks, make an excellent comparative system for these studies.

Finally, sound investigations of each species physiology will be necessary to properly interpret species abundance distributions. If, for example, we can show that ramped distributions occur with little change in physiological state throughout the range, then other mechanisms causing range limits and species distributions are suggested. Although several studies have compared physical environmental conditions at a species range limits to empirically determined physiological thresholds for species (e.g. Root, 1988), or focused on demographic patterns of species in one region of the range (e.g. Frank, 1975; Lewis, 1986), few studies have documented the physiological state of organisms at field sites

throughout the species range. Combinations of investigations on physiological, demographic and distributional variables can be used to test alternative hypotheses regarding the causes of species range boundaries and species responses to climate change.

The data we have presented here represent an important first step in a broad scale understanding of the distributions of coastal marine species. Although the variety of distributional patterns observed is frustrating in light of attempts to find 'general laws' of ecology, closer inspection suggests opportunities for testing a multitude of hypotheses through comparisons of different types of species in different parts of the range. Moreover, distributional data will become increasingly useful when combined with the results of large-scale demographic and physiological studies currently being conducted along the Pacific Coast of North America.

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BIOSKETCHES

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