



The limits to biogeographical distributions: insights from the northward range extension of the marine snail, *Kelletia kelletii* (Forbes, 1852)

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Abstract

Aim The development of accurate models predicting species range shifts in response to climate change requires studies on the population biology of species whose distributional limits are in the process of shifting. We examine the population biology of an example system using the recent northward range expansion of the marine neogastropod *Kelletia kelletii* (Forbes, 1852).

Location This is a marine coastal shelf neogastropod species whose range extends from Isla Asuncion (Baja California, Mexico) to Monterey (CA, USA). Research sites spanned the extent of the range.

Methods We examine abundance distributions and size frequency distributions of *K. kelletii* for evidence of factors determining historic and contemporary distributional patterns. Population studies were supplemented by historic and contemporary hydrographic data, including seawater temperature data from California Cooperative Oceanic Fisheries Investigations (CalCOFI) and National Data Buoy Center (NDBC), and seawater circulation data.

Results The structure of recently established populations varied dramatically from that of historic populations. Markedly low densities and irregular size frequency distributions characterized recently established populations and suggested only occasionally successful recruitment. The point of transition between historic and recently established populations also corresponded to the location of a gradient in seawater temperature and the confluence of two major oceanic currents. The accumulated data suggest that temperature and/or barriers to dispersal could have set both contemporary patterns in population structure as well as the former northern range limit.

Main conclusions Early life stages play a critical role in determining distributional patterns of *K. kelletii*. Dispersal barriers and temperature limitation are two plausible mechanisms that could determine both contemporary and historic distributional patterns. Future studies on this species should attempt to tease apart the relative importance of these factors in maintaining the populations at the northern edge of the range.

Keywords

California, North America, dispersal, global warming, *Kelletia*, range expansion.

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INTRODUCTION

In the coming decades, scientists expect increasing numbers of species invasions and shifts in species range distributions in response to global climate change (Porter *et al.*, 1991; McCarty, 2001; Warren *et al.*, 2001). Indeed, such invasions and range shifts are already occurring; recent evidence suggesting northward or altitudinal range shifts by a variety of species is consistent with the hypothesis that species limits are moving in response to shifting climate (Peters, 1992; Ray *et al.*, 1992; Barry *et al.*, 1995; Parmesan, 1996; Holbrook *et al.*, 1997; Sagarin *et al.*, 1999). The prediction of distributional shifts and the observation of such shifts are often premised on the implicit assumption that physiological limitation by a suite of environmental factors determines where population distributions reach their limit. When the environment changes, the physiological barrier to individual survival and reproduction is moved, and distributional limits shift.

Although this relatively simple view of shifts in species distribution in response to climate change is commonly used as a framework for anticipating change, it is clearly inadequate. It does not account for the number of species whose distributions have been unaltered nor does it account for the unpredictability of invasion success. More recently, emphasis has changed from predicting that distributions will shift and invasions will occur to developing models that predict which species distributions will shift and which characteristics of species make them most likely to invade successfully (Lodge, 1993a; Sakai *et al.*, 2001; Kolar & Lodge, 2001). Central to the success of these efforts is the recognition that species range limits are not generated by the physiological limitations of individuals alone. Rather, shifts in climate affect a suite of ecological, physical and physiological factors that act on population level processes (birth rates, mortality rates, recruitment rates and linkages between populations) to shape the dynamics of species borders (Carter & Prince, 1981; Brown *et al.*, 1996; Lennon *et al.*, 1997; Davis *et al.*, 1998).

The development of accurate predictive models, therefore, requires intensive studies on the population biology of both invasive and native species whose distributional limits are in the process of shifting (Lodge, 1993a, b; Carlton, 2000; Sakai *et al.*, 2000). These detailed studies of population dynamics in newly established populations may provide enlightening natural experiments that indicate which population level processes determine the success or failure of a particular distributional shift or invasion. Comparisons of the structure and dynamics of recently colonized vs. long established populations across a species range might lend further insight into the causal factors (Hutchins, 1947; Lewis *et al.*, 1982; Kendall, 1987; Caughley *et al.*, 1988; Lewis, 1996).

Here we consider the natural experiment of a 'sudden' range extension. We document both temporal and spatial characteristics of shifts in the distribution of the marine neogastropod, *Kelletia kelletii* (Forbes, 1852). In the past few decades, *K. kelletii* substantially extended its range northward past its historic northern limit at Point Concep-

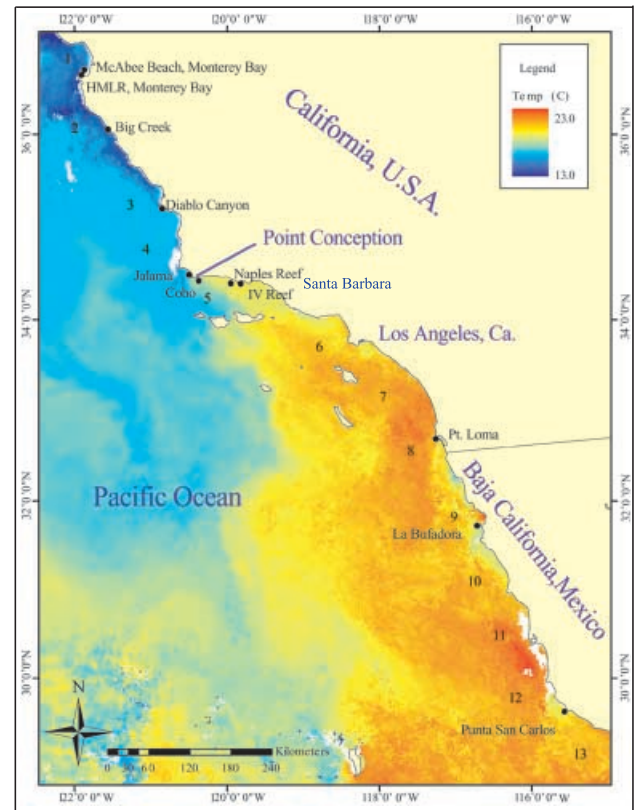


Figure 1 Map of portions of California, USA, and Baja California, Mexico, showing coastal sites surveyed for *Kelletia kelletii* (Forbes, 1852). Mean monthly sea surface temperature data from August 1998 is superimposed. Point Conception was the historic northern range limit for *K. kelletii* and is also a major biogeographical boundary for species across multiple taxa. CalCOFI station locations are indicated by numbers.

tion (CA, USA) (Herrlinger, 1981). In addition to being a headland where major ocean currents collide, Point Conception is also a major biogeographical boundary and coincident range limit for many marine taxa (Newman, 1979; Morris *et al.*, 1980; Doyle, 1985). A 325-km northward extension *K. kelletii* (Fig. 1) to its present limit in Monterey Bay (CA, USA) occurred during a period of both seawater warming (Roemmich, 1992; Barry *et al.*, 1995) and substantial variation in ocean circulation (McGowan *et al.*, 1998).

In this study, we document spatial patterns in contemporary populations within the historical and newly inhabited parts of the range and combine these spatial comparisons with an analysis of temporal changes in physical and biological features. We identify plausible hypotheses that may both explain the contemporary pattern of distribution and account for the rapid shift in this species distribution over the past few decades. We discuss the merits and problems associated with these hypotheses and suggest critical tests for future research.

BACKGROUND AND METHODS

Study organism

The marine neogastropod, *K. kelletii* (Forbes, 1852), is a whelk belonging to the family Buccinidae, and is a generalist predator that feeds on a variety of mobile and sessile invertebrates. The range of *K. kelletii* currently extends from Isla Asuncion (Baja California, Mexico) to Monterey (CA, USA). Individuals generally occupy a vertical distribution from 2 to 70 m in depth (Rosenthal, 1970) on rocky reefs and cobble-sand interfaces in kelp forests.

Rosenthal (1970) reported onset of sexual maturity at *c.* 60 mm in shell length (defined as maximum shell length from the tip of the spire to the tip of the siphonal canal). *Kelletia kelletii* reproduces annually, with egg laying restricted to late spring and summer. The females lay masses of egg capsules on benthic hard substrate in which larvae develop for a period of *c.* 30–34 days. The hatched larvae are pelagic; the length of this life stage is unknown (Rosenthal, 1970; Morris *et al.*, 1980). Larvae are facultative lecithotrophs, with a yolk supply that lasts *c.* 6–10 days, depending on temperature (D. Zacherl, unpubl. data).

The timeline of the range extension of this species into central California (including sites north of Point Conception, see Fig. 1) is fairly well documented (Lonhart, 2001). *Kelletia kelletii* was absent from faunal lists of pre-historic shell middens and Plio-Pleistocene fossil records of sites in central California (Lonhart, 2001). In contrast, this species (*Siphonalia kelletii*) was included on faunal lists at one archaeological (Wallace, 1956) and several palaeontological sites in southern California (Arnold, 1903; Grant & Gale, 1931; Ruth, 1942; Kanakoff & Emerson, 1959). More recently, *K. kelletii* was absent in an extensive review of all molluscs collected in Monterey Bay since 1835 (Smith & Gordon, 1948). Its presence was not recorded in extensive subtidal surveys of the kelp forest at Hopkins Marine Life Refuge (HMLR) in Monterey Bay during the 1970s (Pearse & Lowry, 1974), nor from subtidal surveys further south at Diablo Canyon, conducted during the same time period (J. Blecha, pers. comm.; see Fig. 1 for site locations). An extensive search of the shell collections of California museums yielded only one *K. kelletii* specimen from Monterey Bay during the 1960s and 1970s: an old, heavily fouled adult shell (Los Angeles County Museum specimen 60-23.26) was found on the sandy bottom near HMLR at 37-m depth.

In 1980, Herrlinger (1981) collected three adult specimens (>65 mm shell length) of *K. kelletii* at HMLR in Monterey Bay. It is more likely that *K. kelletii* were present before their detection in 1980, as larvae during the early or late 1970s, but remained undetected for several years until reaching a conspicuous size. This sudden appearance of numerous adult specimens in Monterey in the 1980s corresponds with the appearance of individuals in subtidal and intertidal surveys at Diablo Canyon (J. Blecha, pers. comm.). It is more likely, therefore, that the conditions contributing to this range extension took place sometime in the 1970s or early 1980s. Since that time, reproductive populations have persisted at

several sites in central California (Lonhart, 2001; J. Blecha, pers. comm.; D. Zacherl, pers. obs.).

Methods for examining spatial patterns in population structure

To compare population characteristics of *K. kelletii* in the newly inhabited regions north of Point Conception vs. historically inhabited regions in southern and Baja California, we completed subtidal density and size frequency surveys on SCUBA at eleven sites distributed throughout the snail's range in the summers of 1997, 1999 and 2000 (see Fig. 1 and Table 1 for site names and locations). At each site, we standardized the sampling habitat by surveying only within rocky reef and cobble habitats between 8 and 22 m that were dominated by the giant kelp, *Macrocystis pyrifera* (Linnaeus) Agardh 1820, or the bull kelp, *Nereocystis luetkeana* (Mertens) Postels & Ruprecht 1840. Divers surveyed multiple 50 × 2 m transects and collected whelks along each transect. At the surface, we measured the maximum length (mm) of each whelk from the tip of the spire to the tip of the siphonal canal using dial callipers (precision ±0.1 mm) and then returned the whelks to the reef. To build size frequency histograms, we divided whelks into 10-mm size classes. In 3 years of exhaustive survey work, we collected more than 4000 whelks, but we encountered only two whelks shorter than 20 mm in length. In 1999, in response to the absence of very small whelks in the surveys, we tested whether increased search effort would result in increased detection of small whelks at IV Reef and at Naples Reef. Divers increased their search time on transects and expanded the range of microhabitats sampled within the kelp forest (including overturning cobbles, sifting through patches of sand and searching kelp holdfasts). These more intensive surveys yielded no additional whelks smaller than 20 mm in length and were not included in the survey data presented in this paper. We concluded that smaller whelks remain cryptic or exploit a different habitat from adults, and therefore, do not enter into our census.

For sites where fewer than fifty individual whelks were encountered in all transect survey work, we supplemented the size frequency surveys by hand collecting additional whelks outside the surveyed transects. We caught fewer than fifteen whelks at Big Creek in 1997 and therefore did not report a size frequency distribution for that population.

To compare density between regions, we calculated average density per site for 1997, 1999 and 2000 (Table 1), then grouped sites into historic range vs. extended range (south vs. north of Point Conception) and tested for differences between regions for 1997 and 1999 using Welch one-way ANOVA. For 2000, we sampled only four sites, too few for meaningful statistical analysis.

Methods for characterizing temporal and spatial aspects of the physical setting

To characterize the physical setting across the expanded and historical ranges, we examined records of spatial and

Table 1 Summary of sites surveyed, locations and densities [$\# (\text{m}^2)^{-1}$] of *Kelletia kelletii* (Forbes, 1852) measured per year \pm SE. Numbers in parentheses represent number of 50×2 m transects surveyed

Site	Location	1997# (m^2) ⁻¹ \pm SE (n)	1999 # (m^2) ⁻¹ \pm SE (n)	2000 # (m^2) ⁻¹ \pm SE (n)
McAbee Beach	N36 °37.09'W121 °53.82'	na	0.06 \pm 0.02 (8)	0.01 \pm 0.01 (8)
Hopkins Marine Life Refuge	N36 °37.27'W121 °54.10'	0.10 \pm 0.04 (6)	0.02 \pm 0.01 (8)	na
Big Creek	na	0.01 \pm 0.00 (6)	na	na
Diablo Canyon	N35 °12.267'	0.05 \pm 0.02 (4)	0.04 \pm 0.02 (6)	0.06 \pm 0.02 (9)
Jalama	W120 °51.049'N34 °29.468'	0.08 \pm 0.04 (5)	0.07 \pm 0.02 (9)	na
Coho	W120 °29.841'N34 °26.885'	0.48 \pm 0.06 (11)	0.68 \pm 0.08 (6)	na
Naples Reef	W120 °24.110'N34 °25.330'	1.11 \pm 0.08 (7)	1.05 \pm 0.19 (6)	1.11 \pm 0.27 (6)
Isla Vista (IV) Reef	W119 °57.082'N34 °24.281'	0.63 \pm 0.09 (5)	0.43 \pm 0.05 (6)	0.41 \pm 0.03 (6)
Point Loma	W119 °52.051'N32 °41.310'	0.72 \pm 0.11 (5)	0.14 \pm 0.02 (5)	na
La Bufadora	W117 °15.61'N31 °43.410'	0.90 \pm 0.14 (4)	0.37 \pm 0.05 (5)	na
Punta San Carlos	W116 °43.080'N29 °37.034'	0.85 \pm 0.16 (4)	na	na

na, Data not available/no surveys completed.

temporal patterns of coastal ocean temperatures. No single data set for seawater temperatures covered the entire spatial or temporal scales relevant to the shifting biogeographical distribution of *K. kelletii*. We characterized historic surface and subtidal coastal thermal regimes from central Baja California to Monterey Bay (CA) using near-shore California Cooperative Oceanic Fisheries Investigations (CalCOFI) monthly mean time-averaged data for 1950–84 (see Fig. 1 for locations). To characterize more recent year-to-year variation in sea surface temperatures, we used National Data Buoy Center (NDBC) surface temperature data from 1994 to 2000 for coastal sites from San Francisco to Los Angeles. The NDBC data set differs in multiple ways from the CalCOFI data set. First, it covers a different time period (1994–2000 vs. 1950–84 for CalCOFI). Secondly, NDBC data are collected hourly, whereas CalCOFI data are taken sporadically during cruises to particular sites. CalCOFI data are more spatially extensive and include depth profiles. NDBC data include sea surface temperatures only. To investigate long-term trends in sea surface temperature variation, we calculated annual mean shoreline data for Santa Barbara from 1955 to 1994.

We compared sea surface temperature NDBC data with seawater circulation patterns around Point Conception from 1994 to 2000. To characterize patterns of circulation, we drew on extensive drifter and moored instrument studies from the Santa Barbara Channel and Santa Maria Basin (Aquad *et al.*, 1998; Dever *et al.*, 1998; Harms & Winant, 1998; Dorman & Winant, 2000). These studies reveal three primary flow states around Point Conception: equatorward, convergent and poleward. Two moored current meters, just north and south of Point Conception, can be used to distinguish among these alternate flow conditions (E. Dever, pers. comm.). Equatorward flow is characterized by southward currents at the north meter and eastward currents at the south meter. Poleward flow is characterized by northward currents at the north meter and westward currents at the south meter. Convergent circulation is characterized by

southward currents at the north meter and westward currents at the south meter. We compare circulation states using the above method with seawater temperature from the NDBC meteorological buoys.

RESULTS

Patterns in population structure

In 1997, northern coastal populations had significantly lower densities of whelks than coastal populations within the historical part of the range (Welch ANOVA, $F = 60.30$, $P < 0.001$; Fig. 2). Northern populations averaged 0.06 ± 0.02 (1 SE) whelks m^{-2} , whereas southern populations averaged 0.78 ± 0.09 whelks m^{-2} . There was a sharp disjunction in population density at Point Conception, the historic northern range limit for this species. Densities decline sixfold between Coho and Jalama, sites that are separated by fewer than 15 km (see Fig. 1). Surveys in 1999 showed similar patterns. Northern populations, averaging 0.05 ± 0.01 whelks m^{-2} , had significantly lower whelk densities (Welch ANOVA, $F = 9.66$, $P < 0.05$) than southern populations, averaging 0.53 ± 0.16 whelks m^{-2} . Throughout the 4-year study period, the overall biogeographical distribution of density did not change qualitatively – *K. kelletii* was rare throughout the expanded part of its range.

The size distributions of *K. kelletii* also differed sharply between historic and recent portions of the range during 1997. Older, larger individuals dominate the size frequency distributions (see Fig. 3) in populations north of Point Conception. By contrast, historic populations had more even size distributions with a significantly higher frequency of juveniles (defined as pre-reproductive size classes under 60 mm in length, Welch ANOVA, $F = 18.21$, $P < 0.01$). South of Point Conception, 39.07% of individuals were juveniles compared with only 0.78% north of Point Conception. The Big Creek population (not included in Fig. 3 because of small sample size) was entirely composed of adults >75 mm in length. This near complete absence of

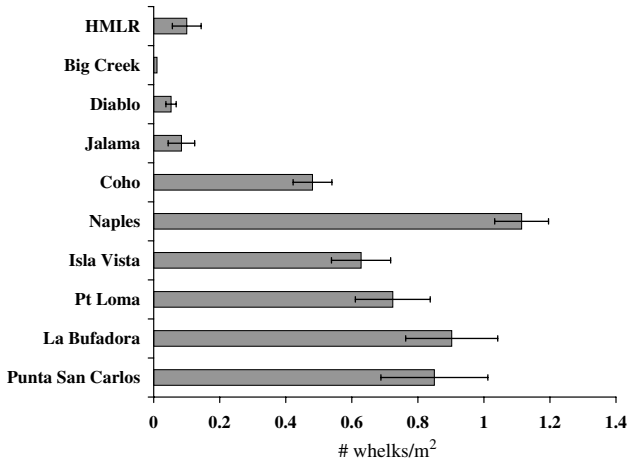


Figure 2 Distribution of mean densities (\pm SE) of *Kelletia kelletii* for 1997. Note the precipitous decline in density between Coho, located just south of Point Conception, and Jalama, located just north of Point Conception.

juvenile whelks throughout the expanded range of *K. kelletii* suggests recruitment failure in recent years. All sites with low snail densities (i.e. north of Point Conception) had skewed size frequency distributions dominated by large individuals in the 1997 surveys.

Unlike the consistent geographical pattern of density through time, the size frequency distributions changed between 1997 and 1999. In 1999, populations north of Point Conception showed recruitment of juvenile size classes that were absent in the 1997 surveys (compare Figs 3 & 4). The 1999 size frequency distributions for populations north of Point Conception suggest an episodic recruitment of juveniles. Whelks in size classes smaller than 50 mm represent new additions to the population. The absence of juveniles in 1997 was seen in the 1999 surveys as a suppression of individuals in size classes from 50 to 70 mm.

Physical setting

The CalCOFI monthly mean time-averaged data for 1950–84 surface waters (Fig. 5) show that surface seawater temperatures drop abruptly at stations north of Point Conception (stations 1–4). The contrast between this cold-water region and warmer water in the Southern California Bight (stations 5–8) persists throughout the year, and the gradient is steepest in the fall. The sharp distinction in ocean temperatures between northern and southern regions breaks down off the coast of Baja California. Surface waters are somewhat cooler along the coast of Baja California (stations 11–13) than in southern California with two stations (9 and 13 in May) having temperatures as cool as those north of Point Conception.

The 20-m temperature records represent a more realistic measure of temperature experienced by *K. kelletii* recruits,

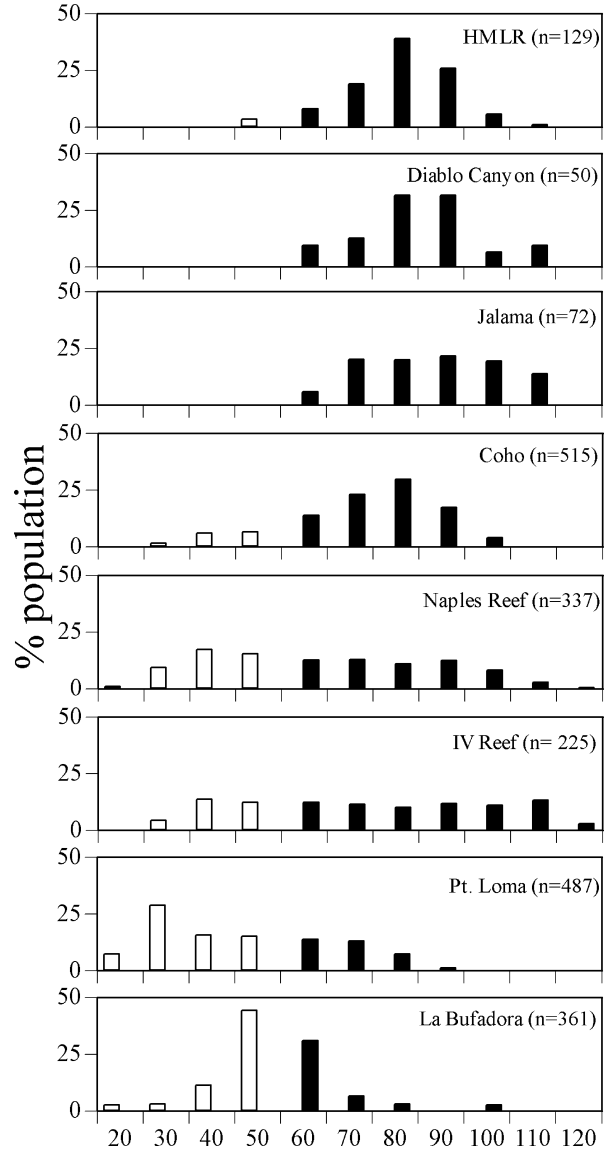


Figure 3 Size frequency distributions from surveys in 1997. White bars represent size classes smaller than 60 mm in length (juvenile size classes). Note the abrupt transition associated with Point Conception, where populations north show an almost complete absence of juvenile size classes.

juveniles and adults because they exploit benthic habitat. The 20-m temperature records show moderate warming occurring only during September–November and again mostly limited to southern Californian sites. Station 9, located near La Bufadora in Baja California, shows a seasonal pattern quite similar to those for stations north of Point Conception throughout the year.

The NDBC data (Fig. 6) show spatial and temporal variations in surface temperatures for sites from Monterey (CA) southward to Los Angeles (CA) from 1994 to 2000. Note the

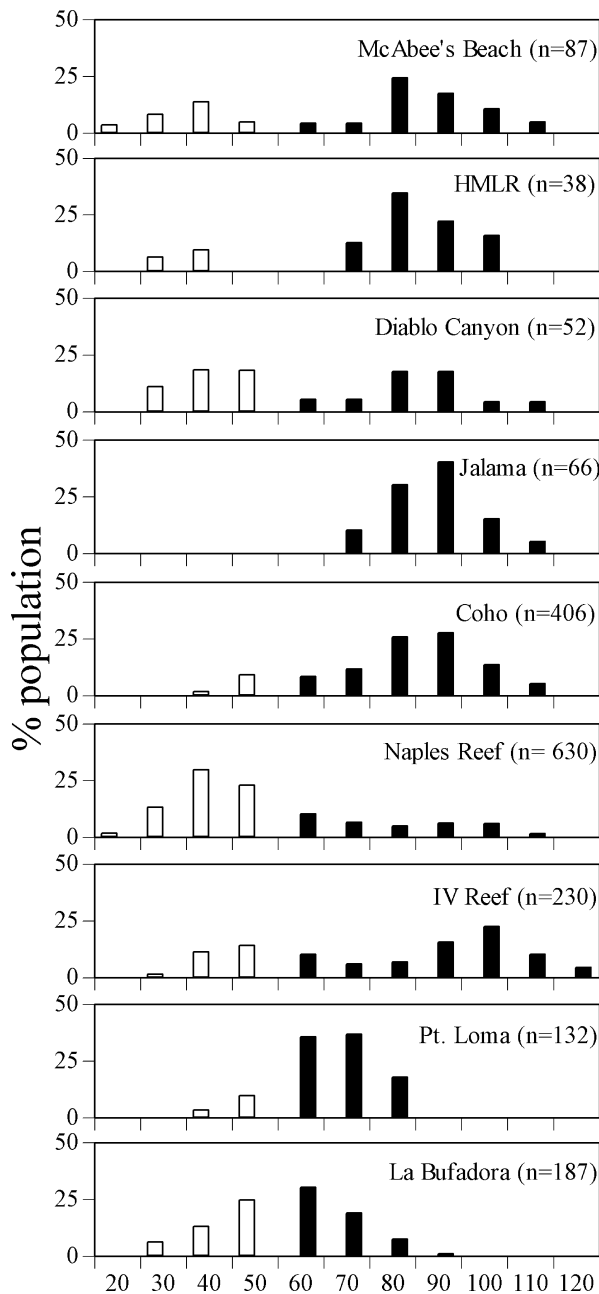


Figure 4 Size frequency distributions from surveys in 1999. Note the appearance of juvenile size classes north of Point Conception, and the notable lack of individuals in size classes in the 50–70-mm range.

marked warming that occurs each year in southern California (sites south of Point Conception in Fig. 6) during June–October. No data are available for surface waters in Baja California for these years, but extrapolating from historic data (see Fig. 5, compare stations 5–9 with 10–14), we can expect that surface waters remain cooler year-round in Baja California compared with southern California. Sea-

water temperatures were particularly warm in 1997 during the El Niño phase of an El Niño Southern Oscillation (ENSO) event, exceeding 18 °C extending as far north as Monterey from June–November.

We compared circulation states with seawater temperatures from 1994 to 2000. Monthly-averaged circulation states are shown as coloured arrows and bars in Fig. 6; blue downward arrows indicate equatorward flow around Point Conception, red upward arrows show poleward flow and green bars indicate convergence. Some regular patterns emerged. Most poleward flow events occurred during November–February. As an exception, note the mass of red upward arrows in late 1997, indicating persistent poleward flow from July–November. Equatorward flow dominated during March–June. July–October generally showed either convergent flow or equatorward flow, and warming sea water extends throughout the region south of Point Conception. The exceptional persistent poleward flow during 1997 occurred in synchrony with the surface water warming that extended well north of Point Conception (see Fig. 6).

The historic shoreline seawater data from Santa Barbara (Fig. 7) show substantial year-to-year variation in shoreline seawater temperatures, with a clear warming trend starting in the mid-1970s. Average annual mean shoreline temperatures rose 1.0 °C over a 40-year time period. Comparable warming trends have previously been reported at Hopkins Marine Station in Monterey (CA) with a 0.75 °C increase in annual mean shoreline temperature in the past 60 years (Barry *et al.*, 1995).

DISCUSSION

The recent range extension by *K. kelletii* offers an opportunity to document differences in the structure and dynamics of recently established populations vs. historic populations.

Caughley *et al.* (1988) propose that by looking at how features of populations (like density or growth rate) differ in edge populations vs. central populations, one can infer causation for range limitation. Our data may indeed provide evidence suggestive of a mechanism driving the former range limit at Point Conception. Lewis *et al.* (1982); Kendall (1987) and Hutchins (1947) use age or size frequency distribution patterns for populations on the edge of a range to narrow the range of factors that could be limiting species distributions. They argue that if populations at the edge of the range are biased towards small size classes or young ages, it implies that survivorship rates are lower at the edge of the range. Edge populations may even be ephemeral and suffer frequent local extinctions. Higher mortality in fringe populations is the mechanism setting the range limit. Alternatively, if the peripheral populations have an irregular size structure with sporadic waves of discrete cohorts, or if they are biased towards older size classes, then the failure of young to recruit very likely plays a more important role in limiting the edge of the range. Such infrequent recruitment at range margins could be caused by a number of factors, including low adult

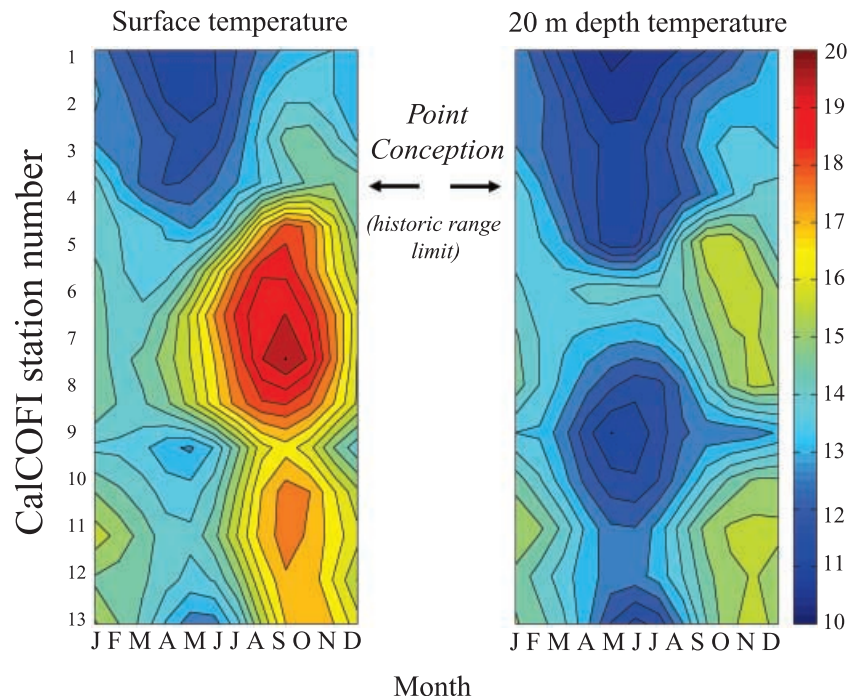


Figure 5 Monthly mean seawater temperature profiles at the surface and at 20-m depth for CalCOFI stations from 1950 to 1984. Month is identified along the x-axis, while station number is indicated along the y-axis. See Fig. 1 for station locations.

fecundity, irregular delivery of larvae, or low juvenile survival. Any feature that varies temporally and targets settlement or recruitment success could cause irregular size structure or a bias towards older size classes. *Kelletia kelletii* populations north of Point Conception exhibit just such a pattern; size frequency distributions in the northern region suggest occasional pulses of recruitment (Fig. 4). The differences in structure between populations in the extended vs. historical ranges of *K. kelletii* focus attention on the critical role of young life stages in setting geographical distribution patterns.

The spatial concordance between population density and recruitment success suggests that these patterns are coupled. The abrupt shifts in density and size structure that co-occur between populations at Coho and Jalama focus attention on changes that occur at Point Conception. One feature dominates this region – the collision of the southward flowing, cold-water California Current (ranging roughly from 9 to 14 °C in central CA), with the warm-water Southern California Gyre (roughly 12–17 °C in the Santa Barbara Channel – see Figs 5 & 6). The sharp transition between these two water masses suggests two potential mechanisms, possibly acting in concert, causing the abrupt changes in *K. kelletii* populations. In one scenario, physical gradients affect larval or juvenile success. In the second scenario, changes in coastal currents alter geographical patterns of larval settlement. Although definitive tests of these potential explanations await more detailed studies of larval and early juvenile stages, we can gain some insight into each explanation in the light of oceanographic and biological data from the region.

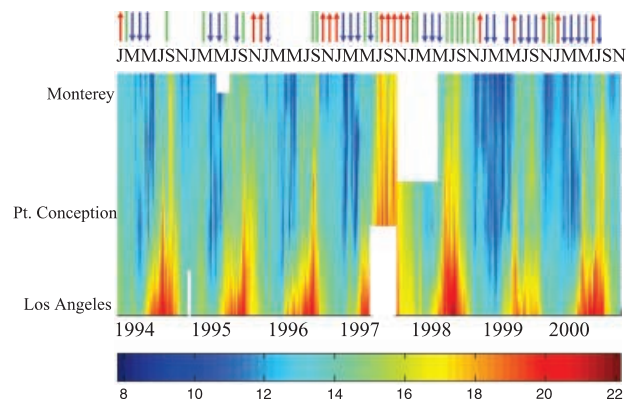


Figure 6 Sea surface temperatures for NDBC buoy stations from San Francisco south of Los Angeles (Catalina buoy) from 1994 to 2000. Note the exceptional warming that occurred north of Point Conception during 1997. Monthly-averaged circulation states are indicated as coloured arrows and bars; blue downward arrows indicate equatorward flow around Point Conception, red upward arrows show poleward flow, and green bars indicate convergence.

Here we provide a brief overview of the two scenarios, followed by more detailed examinations of each later in the discussion. Under the first scenario, the dramatic shift in *K. kelletii* demographics at Point Conception may arise from a temperature gradient that typically limits the success of young north of Point Conception. Populations in the expanded part of the range now persist because this thermal limit to recruitment occasionally breaks down. Under the second scenario, populations north of Point Conception typically receive few larval settlers, perhaps

because of the lack of upstream sources of larvae in a typically southward flowing current system. Populations now persist north of Point Conception because circulation patterns sporadically change in ways that link these northern populations with either local or more southern sources of larvae.

Examining spatial and temporal patterns in contemporary population structure highlights the importance of early life stages in setting *K. kelletii* distribution patterns and suggests the above two plausible hypotheses. Can the appearance of juvenile size classes that occurred north of Point Conception between 1997 and 1999 be linked with specific thermal and/or circulation events?

Merits of the physical gradient hypothesis

In the first mechanism, the sharp gradient in surface temperature (averaging about 3 °C) occurring at Point Conception could limit the recruitment success of *K. kelletii* in the expanded part of the range. Such climatic regulation of species distributions is commonly invoked to explain patterns of both terrestrial and marine species distributions (Valentine & Jablonski, 1993; Barry *et al.*, 1995; Brown, 1995; Parmesan, 1996; Roy *et al.*, 1996; Brown & Lomolino, 1998). Consistent with this hypothetical explanation, Roy *et al.* (1996) attributed historical range shifts by marine molluscs in the fossil record along the continental shelf of southern California to changes in ocean temperatures. If temperature plays a role in the demographic transition today, it could have played an equally important role in setting the prior northern limit of *K. kelletii*. The range extension to Monterey in recent decades could have occurred in anomalously warm water years (see Fig. 6), or as a result of recent warming trends in shoreline surface seawater temperatures (see Fig. 7). Further support for this mechanism includes a study (Barry *et al.*, 1995) that attributed a shift in dominance to southern CA shoreline species in Monterey to the 0.75 °C annual mean shoreline temperature increase over the past 55 years.

A number of observations on contemporary patterns in demographics suggest that this simple physical gradient mechanism could only act during a short window of time in the life history of this species. For example, at cold-water upwelling sites in north-central Baja California, subtidal seawater temperatures are typically as cold as those north of Point Conception (Fig. 5). Yet, these sites have some of the highest densities of *K. kelletii* and recruitment is consistently strong (Figs 2–4). Culturing experiments in the lab at temperatures comparable with those north of Point Conception (10–12 °C) suggest that *K. kelletii* adults mate and produce viable egg capsules at these colder temperatures, and the hatched larvae can survive, feed and grow in culture (D. Zacherl, unpubl. data). Competent larvae ready to settle and early post-settlement juveniles are the only stages that remain to be examined for their performance under these colder temperatures.

Parts of the life cycle of *K. kelletii* remain poorly studied (especially larvae in the field and early settlers on the reef),

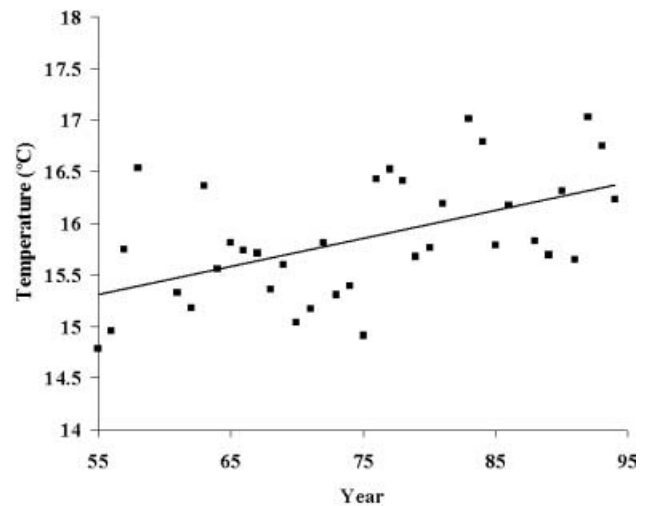


Figure 7 Shoreline seawater temperature variation for Santa Barbara, CA, for 1955–95, including linear regression line ($y = 0.0273x + 13.809$). Each point represents the annual mean shoreline temperature calculated from daily measurements.

which certainly compromises any definitive conclusions about the underlying causes of its distribution. Nonetheless, the hypothesis that temperature directly or indirectly plays a defining role in setting current distributional patterns or played the defining role in setting the range boundary of *K. kelletii* in the recent past can only be reconciled if temperature acts on the survivorship of dispersing larvae or early settlers while they are in shallow surface waters. The surface waters are the only place where substantial thermal gradients that match both the historic and contemporary distributional shifts exist. The recruitment pulses recorded in the 1999 surveys are consistent with the notion that small size classes of whelks should begin to appear in surveys 1–2 years following a substantial warming event (1997–98 El Niño, see Fig. 6) that would favour high survivorship of dispersing larvae and early settlers.

Merits of the limited settlement hypothesis

Under the second hypothetical mechanism, northern populations of *K. kelletii* lack juvenile size classes because they rarely receive settlers. Rather than focusing on the poor success of young once they arrive at a site north of Point Conception, this hypothesis posits that the absence of young occurs because few arrive. The adult size classes that are found at peripheral sites represent the occasional settlement events that occur under anomalous current conditions. Cowen (1985) invoked a similar hypothesis to explain the dominance of the age class distribution of the sheephead (*Semicossyphus pulcher*) by a small number of cohorts in the northern portion of its range. In the Channel Islands of southern California, sheephead only recruit during current reversals associated with the El Niño phase of ENSO. In other years, those populations at the northern edge of the species range appear to lack an 'upstream' source of larvae.

Harms & Winant (1998) characterized the near-surface circulation in the Santa Barbara Channel just south and east of Point Conception. Their data suggest seasonal differences in circulatory patterns. During the summer from July–August, when *K. kelletii* releases planktonic larvae, the mean current direction at a buoy stationed just north of Point Conception shows average flow southward. Along-shore flows in the adjacent Santa Barbara Channel are westward towards the point. The collision of currents results in convergent flow and presents a potential barrier to transport of larvae towards the north of Point Conception. Occasional northward flow reversals can occur during summer months (Harms & Winant, 1998, L. Washburn, unpubl. data), which could transport larvae to the north (for example, see Fig. 6, 1999 and 2000 during May–June). The spatial extent of northward transport during these brief reversals, however, is unclear. The more likely mechanism of dispersal to the site north of Point Conception is due to circulation changes associated with the El Niño phase of ENSO events, such as those that occurred during 1997–98. Northward movement of larvae and adults of many southern species can be common during such events (Cowen, 1985; Lenarz *et al.*, 1995; Lonhart & Tupen, 2001). Under this scenario, *K. kelletii*'s invasion north of Point Conception could have occurred in response to a particularly intense El Niño, or to the increased frequency of ENSO events. The sporadic cohort success subsequently seen in our 1999 census in the expanded section of the range is consistent with populations being maintained by such anomalous settlement during years of altered circulation (see Fig. 6, persistent poleward flow during the summer months of the 1997 El Niño event when larvae were entering the dispersal phase), just as sheephead populations in southern California depend entirely on recruitment during El Niño years (Cowen, 1985).

The limited dispersal hypothesis could imply that sites north of Point Conception could have been quite satisfactory for *K. kelletii* populations in the past, but they were simply unexploited. There are a growing number of empirical and theoretical studies that suggest that limited dispersal may play an important role setting range limits for marine species (Yamada, 1977; Cowen, 1985; Doyle, 1985; Davis *et al.*, 1998; Gaylord & Gaines, 2000). This idea has received less attention in the biogeography literature, where a much heavier emphasis is placed on niche dimensions, such as climate or physiological limitation and setting range limits (Brown, 1995; Roy *et al.*, 1996; Brown & Lomolino, 1998). But for biogeographical breaks in marine environments, major temperature shifts often co-occur with the collision of major oceanic currents, making both physiological and dispersal limitations potential mechanisms for range limitation that are confounded in space. Wares *et al.* (2001) present distribution and genetic data for species range limits along the CA coast indicating the biogeographical break at Point Conception that acts as a one-way range limit, more profoundly affecting southern species at their northern limit than northern species at their southern limit (also see Horn & Allen, 1978; Murray & Littler, 1981; Doyle, 1985). This pattern matches the pre-

dicted pattern if prevailing current regimes act to set up a barrier to northward dispersal at Point Conception – preventing regular northward transport but permitting southward transport. Further, the range limit at Point Conception affects species differentially depending on life-history features. Species with dispersing larvae are more likely to have a northern range limit at Point Conception than species with direct development (S.D. Gaines, unpubl. manuscript). Recent modelling work by Gaylord & Gaines (2000) demonstrates that species in systems with flow regimes similar to those near Point Conception can be limited in distribution simply by restrictions on dispersal. This growing body of evidence suggests that the role of dispersal as a mechanism setting range limits needs much more attention.

Warming and poleward flow: mechanisms to combine or separate?

For *K. kelletii*, the key location both today and in the past is Point Conception, where a major temperature shift co-occurs with the collision of oceanic currents, making both physiological and dispersal limitations potential mechanisms that are confounded in space. One possibility is that both mechanisms act in concert. For the range extension, the species had to surmount the dispersal barrier, but the recent rise in surface seawater temperatures made settlement and early juvenile survivorship more viable. The door to dispersal may have been open occasionally in the past, but recent environmental changes make the habitat north of Point Conception more exploitable, and make recruitment success in contemporary populations more likely. This combination requires the simultaneous relaxation of both mechanisms explored in this discussion.

Determining the relative importance of these confounded variables depends on the ability to separate them. It is not at all clear from the available data whether these two mechanisms, in fact, always act in concert. In the past, detailed information about circulation patterns was not as easily available as it is today, precluding the option to link past recruitment events to past physical events. In the future, it may be possible to decouple these mechanisms.

There are other avenues for exploring the importance of these two mechanisms. Identifying larval sources through natural or induced tagging, particularly for peripheral populations north of Point Conception, could allow us to directly test the role that dispersal plays in setting *K. kelletii*'s northern distributional patterns. Finding temperature limitations (at 10–12 °C) for settlement success or in early post-settlement juvenile performance would help corroborate the temperature mechanism.

Why now?

Clearly, anomalous hydrographic conditions (such as ENSO events and their associated warming of the surface waters and changes in circulation) occurred before the past few decades, and yet this species established detectable populations north of Point Conception only in the last few decades. The easiest

explanation links the change in distributional limit to the recent rise in sea surface temperatures. We propose three additional hypotheses that might help explain why now:

1. This species undergoes periodic extensions and contractions of range, but past extensions were undetected and were short lived. Sax & Brown (2000) assert that exotic species frequently establish themselves, even after repeated failures to do so in the past. Small founder populations are more susceptible to such demographic pitfalls as skewed sex ratios, variations in age structure and environmental stochasticity. *Kelletia kellestii* might have established small populations in the past, but they died out before detection due to the increased extinction risk associated with small populations. Also, large portions of the central CA coast are relatively difficult for ecologists to explore, particularly on SCUBA. Increases in diving activity over the past decades, and populations that serendipitously avoided the demographic pitfalls associated with small population size for many decades, have increased the likelihood for detection.
2. A combination of two events was required for invasion success. First, the species had to surmount the initial dispersal barrier, and secondly, it needed to establish a new upstream 'source' population that could effectively be self-perpetuating by the presence of some sort of retention feature (see Gaylord & Gaines, 2000). For *K. kellestii*, establishment of populations north of Point Conception may be relatively easy, but maintaining those populations remains the challenge. An upwelling shadow retention feature in Monterey Bay (Graham & Largier, 1997) might enable persistence of populations at McAbee Beach and HMLR. These populations might also provide larvae to downstream sites. This explanation implies that sites like Diablo Canyon might sometimes receive larvae from the north, sometimes from the south. It does not explain, however, the apparent synchrony in recruitment success among all northern populations.
3. A decadal scale regime shift coupled with more frequent and intense El Niño events since the early 1970s increased the occurrence of potential northward dispersal events. Beginning sometime in the late 1970s, the mean temperature and salinity shifted towards a warming regime over a large area of the California Current (McGowan et al., 1998). Interdecadal climatic oscillations like this, alternating between warm and cool oceanic regimes, might provide the conditions for establishing extralimital populations, especially for long dispersing species. It is not clear if the regime shift is closely related to El Niño, but ENSO events have also increased in frequency and severity during the last 20 years (McPhaden, 1999). The combination of these two events might have provided exceptional conditions for northward range extension.

CONCLUSION

The challenge for scientists in the near future is to develop accurate predictive models about which species ranges are

more likely to shift in response to global climate change. The development of these models first requires the detailed study of invasive and native species whose distributional limits are in the process of shifting. Here we introduce an ideal system for continued study – the species *K. kellestii* whose range limit has recently shifted, and we begin to document factors that might play a role in its eventual success or failure as an invasive species.

Spatial comparisons of contemporary populations across the extended range of *K. kellestii* focused our attention on the critical role of early life stages in determining distributional patterns. We used that clue, coupled with an analysis of historical changes in temperature and consideration of near-shore ocean circulation patterns to examine the plausibility of barriers to dispersal and/or temperature determining both contemporary patterns in population structure as well as the historic range limit. Future studies on this species should attempt to tease apart the relative importance of these factors in maintaining the populations at the northern edge of the range.

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