ORIGINAL ARTICLE

Shifts in southern endpoints of distribution in rocky intertidal species along the south-eastern Pacific coast

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ABSTRACT

Aim Despite the pervasive and well-documented effects of global warming on species' ranges in terrestrial taxa and systems, the effect of sea surface warming has been poorly studied in marine systems. Here we analyse changes in the southern endpoints of distribution of rocky intertidal species (gastropods and chitons) along the Chilean coast, and trends in sea surface temperature (SST), using data collected during the last half-century.

Location South-eastern Pacific coast, between 18°20′ S and 42°35′ S.

Methods Past southern endpoints of distribution were obtained for 10 intertidal species from museum collections and literature reviews. Current endpoints are based on field sampling conducted between 1998 and 2000. Changes in the position of southern endpoints were analysed individually for each species, as well as for the entire assemblage of species included in the analysis. SST records encompassing 51–57 years were obtained from five coastal stations located between 18° and 36° S.

Results and main conclusions Most species (eight of 10) did not show expansion of their southern endpoint. The proportion of species expanding, contracting or maintaining their southern limit did not differ from chance expectation. On average, species showed small (1° latitude), non-significant contractions, with low rates of decadal change (0.18° latitude per 10 years). This pattern can be explained by changes in SST, which showed a weak warming trend (and at some sites even cooling) along the Chilean coast during the last 57 years. Our results show that different regional warming trends occur, and suggest that generalizations about poleward shifts in species ranges cannot be made. However, our results support the hypothesis that temperature is a major determinant of species range dynamics.

Keywords

Chile, global change, ocean warming, marine invertebrates, range boundaries, range dynamics.

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INTRODUCTION

Under the current scenario of climate change and global warming, one of the most pervasive changes documented in biological systems is the shift in geographical ranges of terrestrial species (Parmesan, 1996; Parmesan *et al.*, 1999; Thomas & Lennon, 1999). This pattern has also been revealed in studies of marine species (Barry *et al.*, 1995; Southward *et al.*, 1995; Holbrook *et al.*, 1997; Sagarin *et al.*, 1999; Smith *et al.*, 1999; Beaugrand *et al.*, 2002). The vast majority of these

studies have been conducted in the northern hemisphere (Parmesan & Yohe, 2003; Root *et al.*, 2003), although it has been shown that warming rates differ among regions (Cane *et al.*, 1997; Levitus *et al.*, 2000; Gille, 2002). For instance, in recent decades there is evidence that the south-eastern Pacific Ocean is warming at rates two to three times slower than the northern Pacific and Atlantic Oceans (Cane *et al.*, 1997, Shaffer *et al.*, 2000, Montecinos *et al.*, 2003). In recent reviews, Parmesan & Yohe (2003) and Root *et al.* (2003) have documented range shifts corresponding to the direction of

climatic changes. Thus, regional differences in warming trends may have very different impacts on biotas, including the intensity and direction of shifts in species' ranges.

In contrast to terrestrial studies, range shifts in marine species have been addressed by only a handful of studies (Barry *et al.*, 1995; Southward *et al.*, 1995; Holbrook *et al.*, 1997; Sagarin *et al.*, 1999; Smith *et al.*, 1999; Beaugrand *et al.*, 2002). Moreover, range shifts have been indirectly assessed using temporal changes in either assemblage composition or richness (e.g. Holbrook *et al.*, 1997; Beaugrand *et al.*, 2002) or relative abundance of species at local sites (e.g. Barry *et al.*, 1995; Holbrook *et al.*, 1997; Sagarin *et al.*, 1999; Smith *et al.*, 1999). This approach relies strongly on the assumption that species abundances are higher at the centre of their distributions and decrease towards the edges, which is not a general pattern (Sagarin & Gaines, 2002a,b), and that temporal changes in species abundances mirror shifts in species ranges. Therefore, direct methods should be preferred to assess shifts in species ranges (e.g. Parmesan *et al.*, 1999; Warren *et al.*, 2001).

In this study, we evaluated the patterns of shifts in the southern endpoints of distribution of intertidal marine species during the last half-century, along the coast of Chile, in the south-eastern Pacific. This system is particularly well suited for this type of analysis given the clear north–south orientation of the coast of Chile and the one-dimensionality of rocky intertidal zones for biogeographical assessments (Sagarin & Gaines, 2002b). We also tested whether the observed changes corresponded with the direction and intensity of climatic changes in the region, which differ from the patterns reported in the northern hemisphere. We hypothesize that comparatively minor changes in the southern endpoints of species distribution should be observed, mirroring the lower warming rates observed in the south-eastern Pacific Ocean during the last half-century (Cane *et al.*, 1997). These analyses allowed us to estimate the real intensity of shifts in southern boundaries, as well the rates at which these shifts have occurred.

MATERIALS AND METHODS

Our study focused on one of the most diverse groups of mobile species inhabiting the rocky intertidal zone: chitons and gastropods. Fifty species were found in the study area, however, we performed our analyses on a group of 10 species, selected according to the following three criteria: (a) the existence of reliable past records of southern endpoints of distribution, (b) all past endpoints were located within the geographical limits of our study region, and (c) the habitat of the studied species is strictly restricted to the rocky intertidal zone.
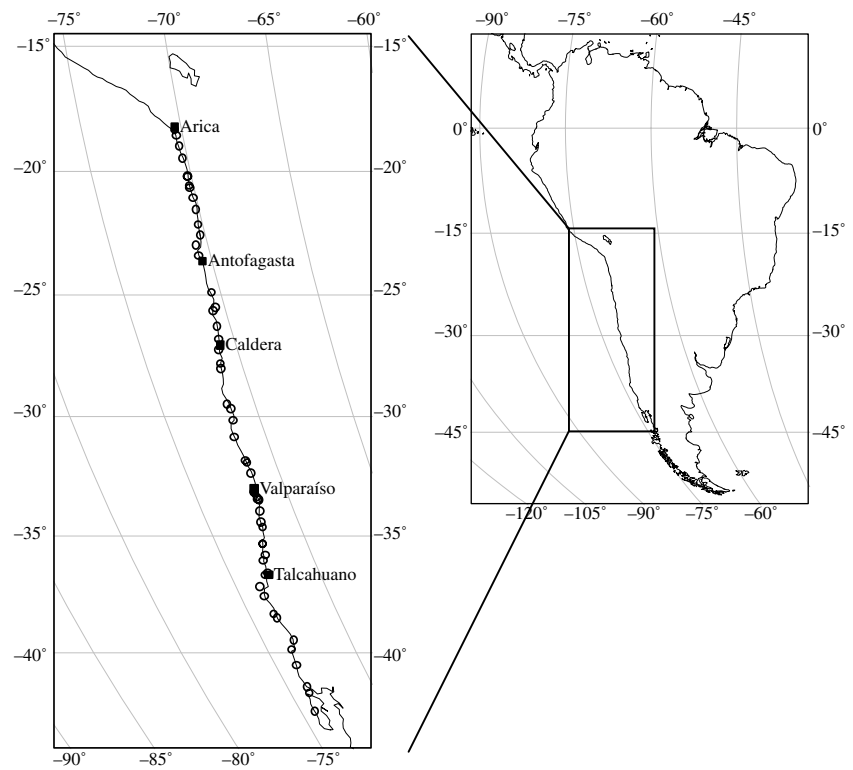
Past southern endpoints of distribution were determined based on: (a) analyses of collections from the Natural History Museum of Los Angeles County (six species), and (b) information from the literature (four species, Table 1). Lonhart & Tupen (2001) recognize several sampling artefacts that may bias range shift analyses: (a) limited spatial and temporal scale of sampling, (b) poorly known taxonomy and ecology of species, and (c) infrequent publication of new range records of species deposited in museum collection. These sampling artefacts do not affect our data. First, since most sources of information are based on extensive field surveys carried out along the Peruvian and Chilean coasts (e.g. see sampling sites in Sebens & Paine, 1977 and McLean, 1984 for most of the museum records used in this study). Second, the taxonomy and ecology of the intertidal species included in our study are well known (e.g. McLean, 1984; Espoz, 2002; Reid, 2002). Third, the explicit use of extensive museum data for six species circumvents any bias related to non-published information on new range data. In addition, the two sources of information used in this paper (museum and literature records) do not introduce any bias (see Results). Therefore, we are confident about the quality of the benchmark data used in this study.

Current southern limits were obtained based on an extensive field survey carried out between 1998 and 2000 on rocky

Table 1 Changes in southern endpoints of distribution of rocky intertidal species inhabiting the south-eastern Pacific Ocean. Baseline year is the year in which the past limit was determined. The present endpoint corresponds to the period 1998–2000

Taxa	Species	Baseline year	Past endpoint	Present endpoint	Interpretation of the southern endpoint dynamic
Polyplacophora	*Acanthopleura echinata* (Barnes)	1949*	36°27′	36°40′	No change
	Chiton granosus Frembly	1958*	42°00′	42°58′	No change
	Enoplochiton niger (Barnes)	1949*	33°02′	29°41′	Contraction
Gastropoda	*Fissurella costata* Lesson	1962†	41°52′	41°47′	No change
	Fissurella crassa Lamarck	1962†	41°52′	38°30′	Contraction
	Fissurella limbata Sowerby	1975†	39°23′	40°33′	No change
	Scurria viridula (Lamarck)	1962†	29°55′	31°51′	Expansion
	Echinoittorina peruviana (Lamarck)	1962†	42°00′	37°10′	Contraction
	Thais haematoma (Linnaeus)	1947‡	33°02′	25°32′	Contraction
	Lottia orbignyi (Dall)	1975†	39°26′	42°35′	Expansion

Either expansions or contractions in southern endpoints were concluded if the absolute latitudinal difference between present and past endpoints was higher that the spatial resolution of our sampling (see Methods). Baseline sources: *Dell (1971); †Natural History Museum of Los Angeles County; ‡Clench (1947 in Marincovich, 1973).

Figure 1 Map of the study area showing the 53 rocky intertidal sites (open circles) sampled to determine the present southern endpoints of distribution of the 10 analysed species. The locations of the five stations where historical records of SST were obtained are also indicated (black squares) (see also Table 2).

intertidal shores along the Chilean coast. Fifty-three wave exposed sites were sampled between 18°20′ S and 42°35′ S (Fig. 1), covering a latitudinal extension of more than 2600 km (average distance between adjacent sites was 0.44° latitude, SD = 0.33° latitude). Across this region, the variation in longitude is only 3°51′, so the distance between two sites along the coast is mostly due to changes in latitude. Therefore, latitudinal changes alone could likely explain most of the variation in range shifts. All sites were visited once, and one or two platforms were sampled at each site, to obtain current southern endpoints of species. In order to provide a good representation of the rocky intertidal zone, we sampled across different tidal levels and microhabitats, which included: low, mid- and high zones of intertidal platforms (between 0 and 45° of inclination), mid- and high zones of vertical walls (≥ 75° of inclination), boulders (between 20 and 50 cm of diameter), and tidal pools (between 50 and 300 cm maximum diameter). Some microhabitats were not present at all sites (i.e. tidal pools, and boulders), however, the species used for analyses were not restricted to either of these habitats. Therefore, habitat availability should not bias our results. At each site, we performed 100–150 min of search time across all microhabitats present. This level of sampling effort is enough to register all species within each site (Rivadeneira et al., 2002). Rates of changes in endpoints were correlated with the proportion of microhabitats occupied by each species in order to assess whether habitat-specialist and generalist species show different range dynamics.

The significance level of changes in southern endpoints were analysed separately for: (a) each individual species, and (b) the whole set of species studied. In order to evaluate single species changes in the southern endpoint of distribution, the distance between sample sites was used as a null expectation. This distance reflects the precision or level of sampling error for which changes can be assessed. Changes in endpoints were considered significant if they were greater than the 99th percentile of the distance between adjacent sites (i.e. greater than 1°29′). To analyse the change in the southern endpoints of the whole set of species studied, the proportion of species showing expansions, contractions and no changes in their southern endpoints was compared against a random expectation, using a chi-square test. The mean overall change in southern endpoints was assessed by comparing the past and current southern endpoints, using a paired t-test. Although the use of a snapshot approach to assess shifts in species' ranges at rocky intertidal (Barry et al., 1995) has been validated (Sagarin et al., 1999), we considered that short-term (e.g. inter-annual) dynamics could still bias our conclusions. In order to shed light on this problem, we evaluated changes in the southern endpoints of distribution for two species (Enoplochiton niger and Scurria viridula) after re-sampling ten sites along the central coast of Chile, between 29° and 34° S, during the austral summer of 2001. These species were selected because their southern endpoints fall within the re-sampled region.

Since past endpoints were determined in different years within the twentieth century (the period of past records ranges between 25 and 51 years ago; see Table 1), there was no common benchmark to allow a simultaneous across-species comparison with the current data. The lack of a common benchmark should not introduce any important bias into our

analyses since the intensity of latitudinal changes (irrespective of the sign) was not correlated with the year of the past record ($r = 0.28$, $P = 0.43$, $n = 10$). Nevertheless, we standardized changes in endpoint distribution by the time elapsed between the past and current assessments. Standardized changes were expressed in degrees of latitude per 10 years, which can be considered the rate at which changes in endpoints have occurred.

In order to test whether species shifts are coupled with changes in ocean temperature, trends in the variation of sea surface temperature (hereafter SST) along the Chilean coast were analysed. Mean annual SST data were obtained from an hydrographic atlas (SHOA, 1996) for five coastal stations (Fig. 1). Overall warming or cooling trends were determined for each station based on the value of the slope of OLS regression between SST and time (years).

RESULTS AND DISCUSSION

Of the 10 species analysed, six (60%) presented significant changes in their southern limit, whereas four species (40%) exhibited no significant shifts (Table 1). Of the six species showing significant changes, only two expanded their southern limit (*Lottia orbignyi* and *Scurria viridula*), while the four remaining species exhibited significant range contractions. The proportion of species showing contraction, expansion or no change did not differ from a chance expectation ($\chi^2 = 0.80$, d.f. $= 2$, $P = 0.67$). Shifts in endpoints varied between expansions of c. 4° latitude to contractions of c. 8° latitude. The average contraction in the southern endpoint was small (1°12′ latitude) and non-significant (paired t-test, $t = 1.12$, d.f $= 9$, $P = 0.29$). The rate of change in the southern limit varied between −1.41 and 1.26° latitude per 10 years, but most species (70%) showed absolute rates slower than 1° latitude per 10 years (Fig. 2). The mean rate of change was c. −0.18° latitude per 10 years and did not differ from the random expectation of zero (one-sample test, $P = 0.523$). The source of information concerning past endpoint (Table 1) did not bias our results since the mean rate of change in species southern endpoints of distribution did not differ between data collected from the museum or from the literature (t-test, $t = 2.30$, d.f. $= 8$, $P = 0.41$). Inter-annual variability in southern endpoints between 1998 and 2001 was not significant for *S. viridula* (0°30′ latitude) and *E. niger* (1°20′ latitude), with both values falling within our level of spatial resolution. Furthermore, inter-annual variability of SST, which indicates the intensity of ENSO events, is much lower around mid-latitudes in comparison with northern areas of the south-eastern Pacific (Montecinos *et al.*, 2003). These pieces of evidence suggest that the snapshot protocol does not bias our conclusions.

We think that the low proportion of species exhibiting an increase in the southern limit can be explained by the relatively weak warming trends of SST along the Chilean coast during the last 57 years (Table 2, and see Cane *et al.*, 1997). Warming rates during the last half-century varied between −0.0079 and 0.0085 °C year^{-1}, indicating that SST has increased, on
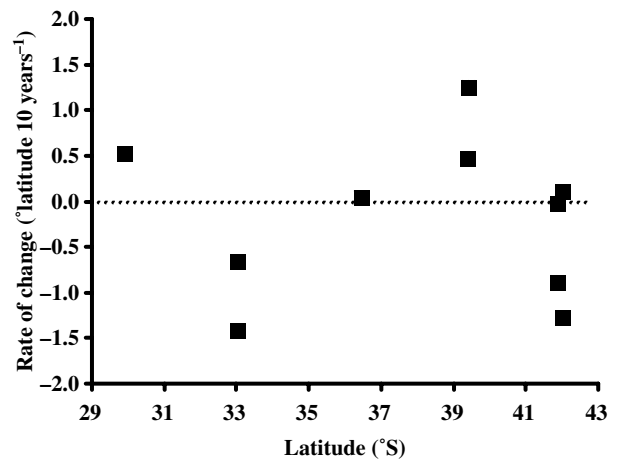
Figure 2 Rate of change (degrees of latitude per 10 years) in the southern endpoint of distribution for 10 rocky intertidal mollusc species along the Chilean coast, according to the past latitudinal distribution reported during the last half-century. Negative values indicate a contraction of the southern endpoint. The dotted line indicates no net change.

average, c. 0.43 °C over the last 50 years. These warming rates are comparable with those reported for subsurface waters in northern and southern Chile (Shaffer *et al.*, 2000), and for the entire Southern Ocean (Gille, 2002). Furthermore, at two coastal stations in Chile a reverse trend is evident, where a cooling of surface waters was observed (see Table 2, and Montecinos *et al.*, 2003). SST warming along the south-eastern Pacific coast has been on average two to three times lower than in regions where significant expansions in species' ranges have been reported, or inferred (north-eastern Pacific: Barry *et al.*, 1995; Holbrook *et al.*, 1997; Sagarin *et al.*, 1999; north-eastern Atlantic, Southward *et al.*, 1995; Beaugrand *et al.*, 2002). The warming rate reported by Sagarin *et al.* (1999) at a coastal station in California of 0.0125 °C year^{-1} is greater than the rates observed across all the stations analysed along the Chilean coast. Moreover, warming rates observed at all Chilean stations were not significant, in contrast to observations made by Sagarin *et al.* (1999), and SST trends may not be monotonic over time (Yáñez *et al.*, 2001).

The link between SST changes and shifts in species endpoints relies on the basic assumption that species ranges are largely determined by physiological constraints imposed by temperature. In fact, northern limits of distribution of marine prosobranch gastropods in the north-eastern Pacific seem to be controlled by the species' cooling resistance (Pörtner, 2001). Furthermore, evidence suggests that species across the globe have shown range shifts coherent with the direction of climate change (Parmesan & Yohe, 2003; Root *et al.*, 2003). However, range dynamics of marine species might not be driven by a single factor, such as sea temperature. Recently, Gaylord & Gaines (2000) suggested that species ranges can be determined solely by the effect of flow on larval transport (i.e. ignoring the effect of temperature gradients). Probably the interaction of several factors, including ocean currents, temperature, as well

Table 2 Changes in mean annual sea surface temperature (SST) at five coastal stations along the Chilean coast during the last half-century. Data for the period between 1945 and 1995 were extracted from SHOA (1996). Recent records (1996–2002) were provided by CENDOC-SHOA

Latitude	Station	Period of time	Years with observations	Rate of warming (°C year^{-1})	P-values
18°15′S	Arica	1951–2002	42	0.0085	0.233
23°39′S	Antofagasta	1946–2002	51	0.0051	0.267
27°04′S	Caldera	1951–2002	44	−0.0079	0.282
33°02′S	Valparaíso	1945–2002	44	0.0043	0.17
36°40′S	Talcahuano	1951–2002	37	−0.0018	0.706

Warming rate was calculated as the slope between mean annual SST and time (years). P-values indicate the significance levels of warming rates estimated from regression slopes.

as type and length of planktonic development determine species range limits; thus, species with a longer planktonic phase should be more affected by changes in ocean flows. Indeed, two species showing the largest endpoint changes (*Echinolittorina peruviana* and *Thais haematoma*) have planktotrophic larvae that spend several weeks in the water column, in comparison with the remaining species, which possess lecithotrophic larvae that spend only a few days in the plankton. The great contraction in the range endpoint of the former species might indicate a northward intensification of coastal currents, but a larger data set of species and/or instrumental evidence is needed to test this idea. Another factor to consider for intertidal species is the geographical and inter-annual variability in the timing of summer low tides, which can make the prediction of range shifts in intertidal species more complex, since air temperature should also be considered (Helmuth *et al.*, 2002). Ongoing research (G.R. Finke, unpublished data) indicates that latitudinal variation in the cumulative mid-summer day exposure to air observed at intertidal sites along the south-eastern Pacific is not as intense as that observed in the north-eastern Pacific. Nevertheless, the same study (G.R. Finke, unpublished data) also reveals that overall cumulative mid-summer day exposure to air is much higher in the south-eastern Pacific in comparison with the north-eastern Pacific, emphasizing the importance of considering air conditions (i.e. temperature trends) to explain species' range dynamics in our system. For instance, a cooling trend of air temperature has been recorded during the last century between 38° S and 41° S, despite the fact that air temperature has warmed up in southern South America during last century (Rosenblüth *et al.*, 1997). Among the species considered in this study, the gastropod *Echinolittorina peruviana* inhabits the high intertidal zone and is clearly affected by changes in air temperature (Soto & Bozinovic, 1998; Rojas *et al.*, 2000). Thus, the marked cooling of air temperature around the former southern limit of distribution of *E. peruviana* might also account for its large endpoint contraction.

The complexity of the interacting factors affecting species distribution can include human exploitation, or the ecology of the species. For instance, the positive relationship between the rate of change in southern endpoints and the proportion of intertidal microhabitats occupied by each species ($r = 0.636$, $P = 0.048$, $n = 10$) suggests that species with specific habitat requirements might be more prone to experience contractions

in their range boundaries, whereas habitat-generalist species may tend to expand their ranges. Range expansions observed in generalist species might be explained by a wider tolerance to environmental conditions, whereas range contractions observed in specialist species might also be affected by some form of habitat deterioration (Warren *et al.*, 2001; Hill & Fox, 2003) or complex species interactions (Davies *et al.*, 1998). Conversely, despite the fact that harvesting by humans is a major factor affecting the structure of rocky intertidal communities along the Chilean coast (Moreno *et al.*, 1984; Castilla, 1999), it does not seem to play a significant role in causing shifts in species ranges. Exploited species (i.e. *Fissurella* spp., see Table 1) showed rates of change similar to non-exploited species (t-test, $t = -0.07$, d.f. $= 8$, $P = 0.939$). Moreover, the relative abundance and distribution of harvested species are similar to those of non-harvested ones (M.M. Rivadeneira *et al.*, unpublished data), suggesting that exploited species are not facing higher extinction risk at regional scales. Again, these hypotheses need further testing, using a larger set of species.

The intensity of global warming and the responses of species to ensuing changes may vary among regions, and this variability could open a window of opportunity for assessing the effect of temperature on endpoints of species' distributions. Furthermore, other factors (e.g. habitat breadth, ocean currents, warming trends in air temperature) are likely to interact with ocean warming, and may be responsible for differences in the direction and intensity of boundary changes between species. We think that it is necessary to refine and intensify assessments, and learn from the variability in temperature changes among regions to make strong predictions about the effect of temperature on species' distributions.

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BIOSKETCHES

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