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Climate change in the coastal ocean: shifts in pelagic productivity and regionally diverging dynamics of coastal ecosystems

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Climate change has led to intensification and poleward migration of the Southeastern Pacific Anticyclone, forcing diverging regions of increasing, equatorward and decreasing, poleward coastal phytoplankton productivity along the Humboldt Upwelling Ecosystem, and a transition zone around 31° S. Using a 20-year dataset of barnacle larval recruitment and adult abundances, we show that striking increases in larval arrival have occurred since 1999 in the region of higher productivity, while slower but significantly negative trends dominate poleward of 30° S, where years of recruitment failure are now common. Rapid increases in benthic adults result from fast recruitment–stock feedbacks following increased recruitment. Slower population declines in the decreased productivity region may result from aging but still reproducing adults that provide temporary insurance against population collapses. Thus, in this region of the ocean where surface waters have been cooling down, climate change is transforming coastal pelagic and benthic ecosystems through altering primary productivity, which seems to propagate up the food web at rates modulated by stock–recruitment feedbacks and storage effects. Slower effects of downward productivity warn us that poleward stocks may be closer to collapse than current abundances may suggest.

1. Introduction

Among the earliest scientific predictions about the effects of global climate change in the ocean was that coastal upwelling would intensify due to an enhanced thermal sea–land contrast, usually known as the Bakun effect, which has now been demonstrated to occur in most eastern boundary upwelling ecosystems (EBUEs) of the world [1–7]. This, together with the documented intensification and poleward migration of the high-pressure atmospheric systems that control winds and coastal climate in all EBUEs [5,8,9], are probably the most unmistakable signatures of climate change in the coastal ocean. Along the Humboldt Upwelling Ecosystem (HUE), both climate-induced changes are occurring and, like other EBUEs, the intensity and even direction of these changes vary with latitude [6,10]. First, at lower latitudes, north of about 30° S, increased pressure gradients have increased upwelling-favourable winds (figure 1*a*,*b*), leading to well documented surface cooling of the coastal ocean [4,11–13]. Second, while the winter position of the South Pacific Anticyclone (SPA) has remained relatively stable around 29–30° S, the spring–summer position, typically found at about 33–34° S
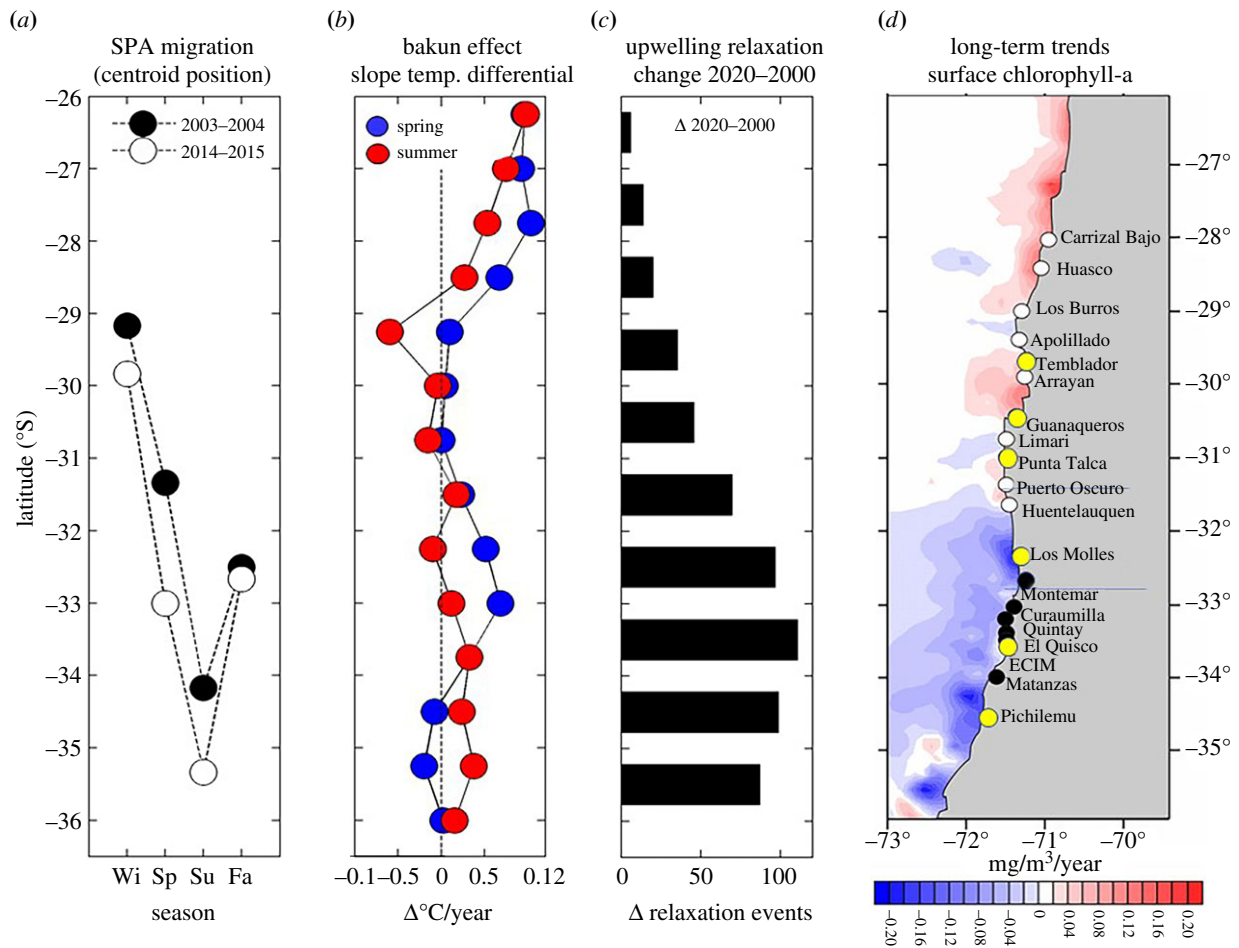
Figure 1. (*a*) Average seasonal latitudinal position of the South Pacific Anticyclone (SPA) maxima for the period 2003–2006 (open circles) and 2014–2015 (black circles). (*b*) Latitudinal trends of long-term (16 years) slopes of the sea-land thermal difference in the surface atmosphere (Bakun effect) for spring (green circles) and summer (red circles) months. (*c*) Difference in the number of events of upwelling relaxation observed during spring–summer months between the seasons 2000–2001 and 2010–2020. Upwelling relaxation events defined as the times when the 6-hourly Offshore Ekman Transport was less than 0 m³ s⁻¹ per 100 m shoreline. (*d*) The long-term linear change in surface chlorophyll-a for the study region, obtained from a 16 year analysis of satellite data according to Weidberg *et al.* [11]. The map shows the location of study sites, with black and yellow dots indicating the long-term larval recruitment monitoring sites used in these analyses, and white circles the additional sites used to examine recruitment event distributions. Yellow circles are the sites where, in addition to larval recruitment, *per capita* barnacle reproductive output was measured. (Online version in colour.)

at the end of the 1990s, moved south to 35–36° S by the end of the 2010s (figure 1*a*), and this migration apparently accelerated since about 2007 [4,9,11,14,15]. Consequently, the spring–summer upwelling-favourable winds have weakened between 30° S and 35° S and led to increased frequency of upwelling relaxation events in spring–summer months (figure 1*c*). Upwelling winds have strengthened poleward from that latitude, producing sharp cooling of the water column at a point around 36° [9,16], an effect that apparently extends as far south as 43° S [15,17]. Since spring–summer upwelling winds bring up to surface the cold nutrient-rich waters that make EBUEs the most productive large marine ecosystems of the planet, affording a large fraction of all fish, invertebrate and algal biomass landed by the world's fisheries, it is of great interest to define whether changes in HUE are increasing or decreasing primary productivity of the coastal ocean, and especially whether such changes are cascading up to pelagic and benthic food webs.

Recent analyses of surface chlorophyll-a have demonstrated that climate-induced changes in upwelling winds are indeed causing significant long-term changes in productivity along the HUE [11,14]. These studies define two domains in phytoplankton productivity trends: (i) a relatively narrow coastal

band of increasing phytoplankton biomass equatorward of 30–31° S (figure 1*d*), which is positively associated with wind intensification produced by the Bakun effect. And (ii) an extensive region of decreasing phytoplankton productivity poleward of 31–32° S and that extends south to at least 35° S (figure 1*d*), which is apparently associated with decreasing upwelling winds due to SPA poleward migration [11]. A transitional region separates these productivity domains. Assessing the consequences of climate change on other trophic levels of marine ecosystems, which cannot be observed through satellite imagery, is undermined by the dearth of long-term and spatially extensive data. For regions of the world where such datasets exist [18,19], insight into the complexity of regional-scale climate forcing on natural ecosystems has been invaluable, highlighting the importance of considering climate effects on larval pelagic stages, and warning about single-location studies that can sometimes provide misleading conclusions about the impact of climate forcing [19,20].

The majority of marine invertebrates and fishes, including harvested and non-harvested species, possess life cycles that include pelagic, usually plankton-feeding larval stages that develop in the water column for variable periods of time [21,22]. Replenishment and persistence of coastal populations

is therefore critically dependent on biophysical conditions for larval development and future recruitment to adult habitat [23,24]. Phytoplankton productivity affects adult larval output, larval development and survival, while coastal circulation modulates dispersal and transport to adult habitat, thus modifying the supply of young and the productivity of populations [25–27]. The linkages between large-scale variation in hydrographic conditions, surface water productivity and recruitment of invertebrates have been studied in the Northern [18–20,28] and, to a lesser extent, Southern Hemisphere [29–31]. Along the northeastern Pacific, large-scale ocean-climate oscillations alter upwelling regimes and primary productivity (e.g. North Pacific Gyre Oscillation, Pacific Decadal Oscillation) and leave identifiable signals on larval recruitment of intertidal barnacles and/or mussels [18,20], and subtidal sea urchins [19]. These studies show that long-term climate variation can be heterogeneous over space, partly because of the complexity of local species interactions, and partly because adult-recruitment feedbacks vary over large spatial scales that cannot be discerned from local studies [32,33]. Thus, climate change cannot only lead to geographical range shifts in species distribution, a predominant focus of climate change research [34,35], but it can alter the vital rates that control population dynamics, persistence and overall productivity of harvested and non-harvested populations.

Here, we take advantage of a database in the HUE region, comprised 19–21 years of monthly larval arrival of two rocky shore barnacle species at multiple coastal sites spanning the two domains of increasing and decreasing phytoplankton productivity [36–38]. We assess whether reported regional-scale changes in phytoplankton are mirrored by changes in larval arrival rates, and whether these in turn are altering benthic adult populations. Finally, we examine whether positive and negative changes are occurring at a similar pace across the two productivity domains.

2. Methods

(a) Study sites and data collection
The study was conducted at eleven primary sites located along 29–34° S on the central-northern coast of Chile (figure 1d), for which we have between 19 and 21 years of monthly larval recruitment rates of the two common intertidal barnacles, *Jehlius cirratus* and *Notochthamalus scabrosus*. These sites are a subset of 19 sites fully exposed to prevailing waves, where we have monitored monthly barnacle recruitment over multiple years (figure 1d; electronic supplementary material, table S1). Larval recruitment was quantified using 10 × 10 cm Plexiglas plates covered with SafetyWalk (3 M), an anti-slip surface that ensures homogeneity of conditions across sites [31].

At 13 of the 19 study sites, field surveys of adult abundance over multiple years (minimum of 5 and maximum 9 different years (figure 1d and electronic supplementary material, table S1) were conducted in the high intertidal zone, where species reach maximum abundance [39]. Surveys were not regularly spaced over time. Visual estimates of cover were conducted using ten 50 × 50 cm quadrats with a 10 × 10 cm sub-grid following the method described in [40]. Since in several field surveys the two barnacle species were not separated, we pooled them together for analyses. At 12 of the 13 study sites, the number of barnacle individuals and their per cent cover were measured in ten 10 × 10 cm quadrats, allowing us to convert cover to density of individuals. At six sites across the region, we quantified *per capita* reproductive

output of intertidal adults as egg (larval) mass per body mass in spring–summer 2012 and again in 2013 (figure 1c and electronic supplementary material, table S1).

Surface chlorophyll-a data were obtained from moderate resolution imaging spectroradiometer (MODIS). Estimated upwelling transport data were obtained from the Pacific Fisheries Environmental Laboratory (PFEL) Live Access Server. See electronic supplementary material and [11] for details.

(b) Data analysis
Since the number of days between plates deployment and retrieval varied through time, rates were standardized by the number of days in the field, expressed as individuals per $100 \, \text{cm}^2 \, \text{d}^{-1}$, and we eliminated collectors that were exposed for less than 15 or more than 45 days. To analyse long-term larval recruitment trends at the 11 primary sites using traditional parametric analysis, we first used linear interpolation to standardize our data as larval arrival rates for each month and then calculated yearly anomalies across the entire time series. Positive(negative) significant correlations between anomalies and time are evidence of long-term positive(negative) long-term trends. In addition, since long-term temporal trends rarely occur at constant rate, we used non-parametric generalized additive model (GAM) regressions to fit linear trends and smoothing functions of time (years) and month of the year (seasonality), using cubic spline smoothing and the backfitting procedure, with 4 degrees of freedom [41] on log-transformed recruitment density (electronic supplementary material).

The hypothesis of positive long-term trends in larval arrival rates in the northern domain, where primary productivity is increasing, versus the southern domain, where primary productivity is decreasing [11], was tested with a Wald–Wolfowitz runs test [42] against the prediction that long-term positive and negative trends occur at random, separately for each barnacle species. Since results supported this pattern, we conducted both GAM and LOWESS (locally weighted scatterplot smoothing) to better define the equatorward, southward and a transition zone between 31° S and 32° S (figure 1d). We then conducted the same GAM analyses described above but pooling all sites within these geographical regions. Since defining the central zone is necessarily difficult and we had few sites in that region, we conducted separate analyses including or not including the sites at the edges. Since discrete classification of sites to regions does not take into account the spatially uneven site distribution and interactions that may occur among sites in yearly trends, we conducted non-parametric spline smoothing fitting both time and space using the latitudinal position of the study sites (electronic supplementary material).

To determine whether a model containing heterogeneous long-term trends across the study domain (trends changing among the regions) provided significantly better fit to the data than a model with a single uniform long-term trend, we used generalized linear mixed model (GLMM) selection approach to fit three mixed nested models (see electronic supplementary material).

To further examine the nature of the changes in larval recruitment occurring since the late 1990s, we divided the time series into two periods, before and after 2007. We chose this year as the breaking point for two reasons. First, independent studies have reported that SPA poleward migration accelerated starting in 2007 [9], and *in situ* measurements of chlorophyll-a at a site in central Chile changed rather abruptly at the end of this year [11]. Second, our results show non-uniform time trends in both barnacle species, with discontinuities around 2007. Nonetheless, we assessed the robustness of our results using multiple years (2006–2010) as breaking point of the time series. We calculated changes in mean Studentized larval recruitment rates before and after the breaking point for the two regions, the frequency and duration of

recruitment failure years, and the distribution of positive (non-zero) recruitment events observed on all plates at all 19 study sites (see electronic supplementary material).

To determine whether adult barnacle intertidal abundances have changed significantly over the time span of the recruitment studies, we fitted ordinary least squares (OLS) linear regressions on log-transformed cover data for each site. The sparsity of surveyed years over this timespan (electronic supplementary material, table S1) rendered temporal GAM analyses uninformative. We then examined the spatial structure of linear trends in population abundance using both GAM and LOESS smoothing, as described above for recruitment, using all 13 sites for which we have a minimum of 5 years of intertidal surveys (electronic supplementary material, table S1).

To determine whether long-term changes in larval recruitment are similar between the regions of increased and decreased phytoplankton productivity, we consider the effect that recruitment has on adult populations, and future larval production, i.e. the relationship between stock (S, adult population size) and larval recruitment (R). We first calculated the absolute changes in recruitment rates and in adult abundances per unit change in chlorophyll-a per year in the northern and southern regions. Second, we examined how yearly recruitment rate altered adult abundance the year after. These barnacles reproduce within the first year after settlement, therefore a year time-lag seems appropriate. We used a Cushing power recruitment–stock relationship and simple linear regressions for both regions (electronic supplementary material). The slopes of the recruitment–stock Cushing relationships were compared between northern and southern regions using the generalized linear model (GLM): $\log(S) = \text{Region} + \log(R) + \text{Region} \times \log(R)$ and the log-link function.

3. Results

The magnitudes of larval recruitment from the plankton varied largely among years and, especially, among sites, but were very similar between species (electronic supplementary material, table S2). Contrasting trends across the study region were visually apparent, with generally positive anomalies towards the end of the time series at equatorward sites, and generally negative anomalies at poleward sites (electronic supplementary material, figures S1 and S2), leading to significantly positive and negative linear correlations between monthly anomalies and time (electronic supplementary material, figure S3). Long-term linear trends supported the diverging pattern across the HUE, with equatorward sites showing significantly increasing rates and poleward sites significantly negative rates of larval recruitment for both species (figure 2a). This spatial pattern was significantly different from random spatial ordering (Wald–Wolforitz $p = 0.0183$), and the smoothing on linear long-term trends helped define two distinctive regions: equatorward of 31°S and poleward of 32°S, with a transition region in between (electronic supplementary material, figure S4). A more precise definition of the transition region is difficult due to low spatial coverage in that coastal section and, probably, because geographical position may fluctuate from year to year.

Pooling sites within these broad regions and fitting non-parametric GAM revealed the strikingly different trends among regions and that rates of change have not occurred at a constant pace (figure 3a–f; electronic supplementary material, table S3). The steep increasing larval arrival rates in the northern region presented an inflection around 2007–2010 for both species (figure 3a,d). Decreasing larval arrival rates in the poleward region have been fairly constant for

N. scabrosus (figure 3c) and more variable for J. cirratus (figure 3f), suggesting the potential existence of a multi-year cycle (greater than 20 year) for this species, which cannot be resolved with our data. No significant long-term trends or interannual variation were observed at sites within the transitional zone for both species (figure 3b,e; electronic supplementary material, table S1). These regional changes in larval replenishment rates corresponded well with long-term changes in surface chlorophyll-a observed over the past 16 years (figure 1d). Changing the latitudinal position of the transition zone did not significantly alter the patterns observed in the equatorward and poleward regions (electronic supplementary material, figures S5 and S6). Non-parametric fits to monthly data (non-adjusted) showed the variation in seasonality among regions and stronger seasonal fluctuations in J. cirratus (electronic supplementary material, figure S7). To avoid the potential artefact of pooling sites, we used latitude and time (years) as continuous, interactive smoothing variables (figure 3g,h). Results more clearly show that at the beginning of the time series, larval arrival rates were higher at poleward sites up to about 31–32°S, especially in J. cirratus. Around 2007 there was a rapid increase in larval arrival rates that affected the equatorward region and has persisted since, while, simultaneously, a decrease has been observed at the poleward end for both species (figure 3g,h). Larval recruitment within the transition zone seems variable over time, with several years of favourable trends followed by years of adverse trends. The GLMM showed that the model containing an interaction between latitude and long-term trends was better supported by the data than a model with a single long-term trend across the region (table 1).

Summary statistics showed that in the northern region mean standardized larval recruitment per day increased nearly 1.2 s.d. units between the period 1999–2006 compared to 2010–2019 (electronic supplementary material, figure S8a). In the southern region, the decrease has been around 0.4 s.d. units over the same period (electronic supplementary material, figure S8b). Temporal changes have not only altered mean larval arrival. Years of recruitment failure were common and comparatively long at northern sites in the early 2000s, and relatively uncommon and brief at southern sites, a pattern that reversed over the past decade (electronic supplementary material, figure S8c,d). Large positive (non-zero) recruitment events were completely absent (N. scabrosus) or nearly absent (J. cirratus) at the equatorward region at the beginning of the time series, while they were common in the poleward region, leading to a 4.5–15.6-fold increase in numbers of settling larvae per $100\,cm^2\,d^{-1}$ (electronic supplementary material, figure S9a,c). Extreme recruitment events (greater than 350 individuals per $100\,cm^2\,d^{-1}$), which were common in the poleward region before 2007, have not been observed after 2007, leading to a 2.5–2.7-fold decrease (electronic supplementary material, figure S9b,d).

Seasonality in larval arrival also varied across the region. Two larval settlement peaks were observed in the equatorward region in both species (figure 4a,d; see also electronic supplementary material, figure S7), while a single late summer peak was observed in the poleward region (figure 4c,f). No significant seasonality was observed in the central region (figure 4b,f). Seasonality of chlorophyll-a also varied greatly among regions, with two productivity peaks in the northern region, and single spring peak in central
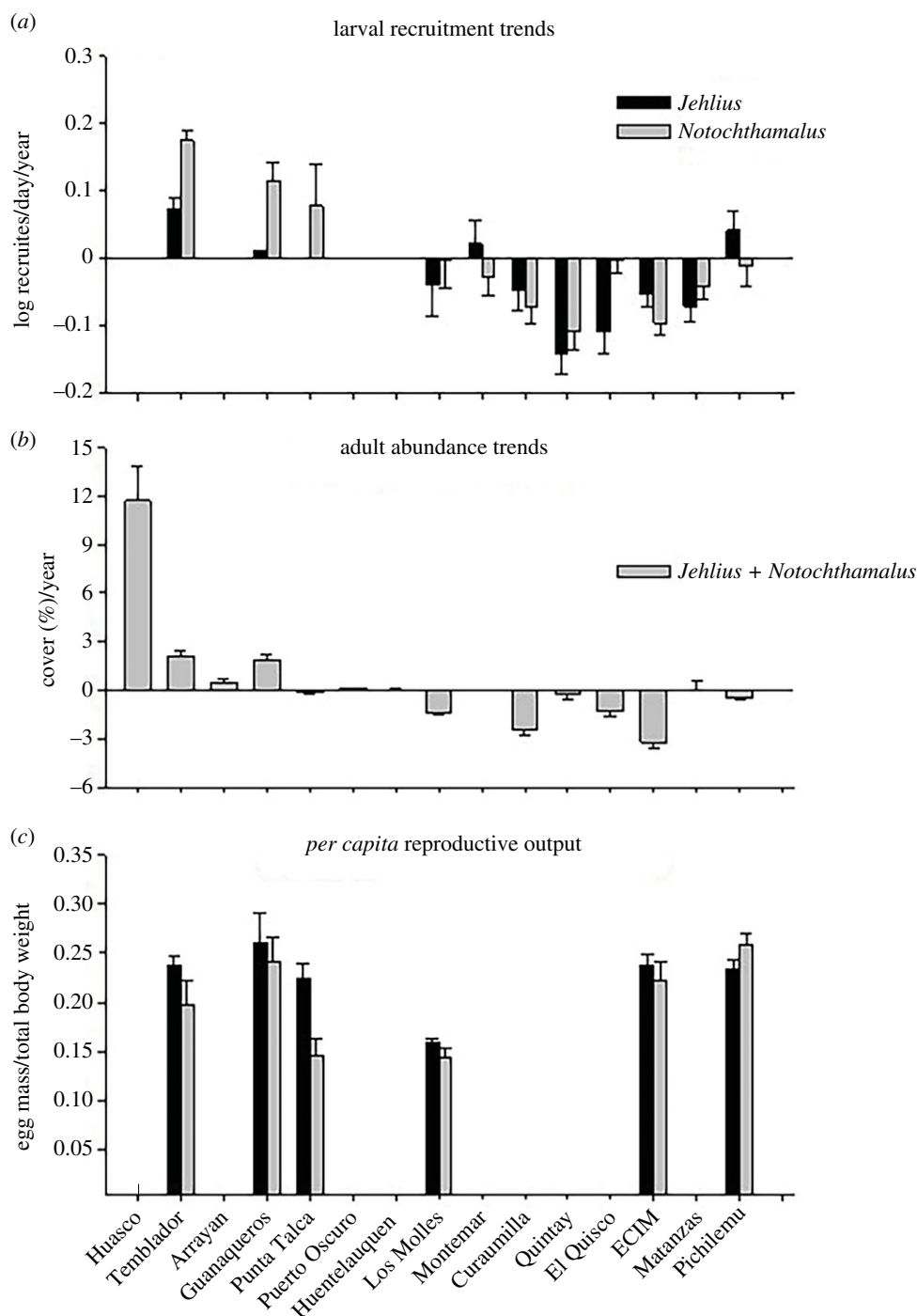
Figure 2. (a) Long-term linear trends in larval recruitment rates (recruits/day/year) over the past two decades at monitoring sites ordered from north to south (figure 1d) for the two barnacle species, *Notochthamalus scabrosus* and *Jehlius cirratus*. Linear slopes fitted on log-transformed data. (b) Long-term linear trends in intertidal chthamalid barnacle abundance measured as per cent cover for the study sites ordered from north to south (figure 1d). Both barnacle species pooled. (c) *Per capita* reproductive output of intertidal adult individuals collected in 2012 and 2013 of both barnacle species.

and southern regions (figure 4g,i). Chlorophyll-a peaks in northern and southern regions occurred about two months before peak larval recruitment. Besides the broad similarity in seasonal patterns, a strong positive association was observed between the long-term mean larval arrival rate at a site, and the long-term 16 year mean chlorophyll-a recorded at two satellite pixels orthogonal to shoreline orientation 4 km offshore of the study site (electronic supplementary material, figure S10).

Significant long-term changes in intertidal adult abundances of both barnacle species have also occurred across the region (electronic supplementary material, figure S11), with generally positive and significant linear trends at

equatorward sites, no significant changes in the transition region, and significantly negative linear slopes at poleward sites (figure 2b). The magnitudes of the changes in adult abundance have also been slightly larger at equatorward sites than the magnitude of reductions at poleward sites. By contrast, *per capita* reproductive output, measured as egg mass over individual body mass, did not show geographical trends in the study region (figure 2c), at least not for the 2 years for which we have information.

Differences in magnitude of positive versus negative changes in larval recruitment rates and adult abundances per unit change in primary productivity were different between regions (figure 5a,b). Positive significant recruitment–stock
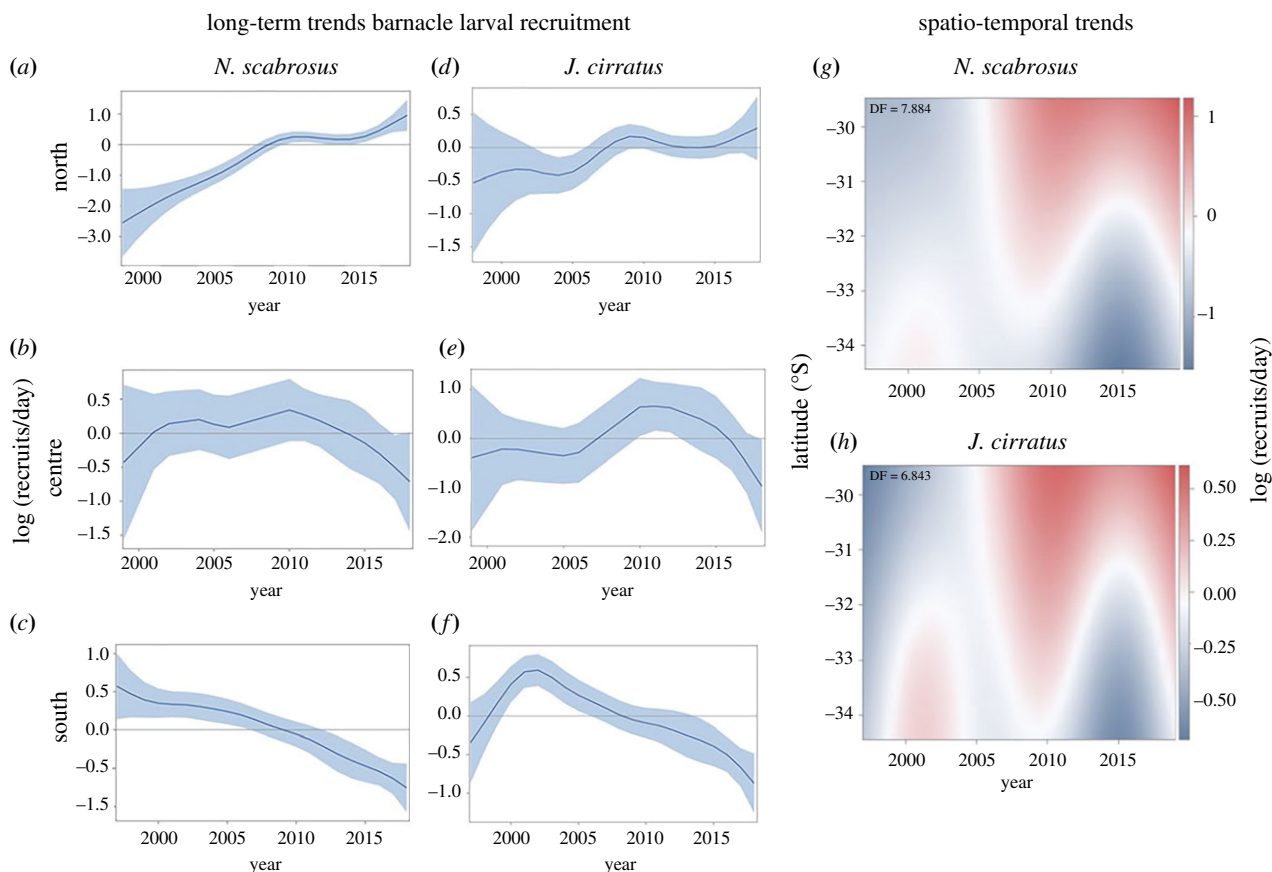
long-term trends barnacle larval recruitment

spatio-temporal trends

Figure 3. (*a–f*) Results from general additive model (GAM) regressions of larval arrival rates (log recruits/day) over time (years) for all long-term monitoring sites pooled within the equatorward (*a,d*), central (*b,e*) and poleward (*c,f*) portions of the study region. The line shows the best GAM fit and the shaded band is the 95% CI. Separate analyses were conducted for the barnacle *Notochthamalus scabrosus* (*a–c*) and *Jehlius cirratus* (*d–f*). (*g,h*) Results of thin-plate space–time GAM regressions of deseasoned larval arrival rates (log recruits/day) using latitudinal position of sites (*y*-axis, figure 1*d*) and time (*x*-axis). Separate analyses conducted for the two species. The colour scale (log recruits/day) is shown on the right of each panel. (Online version in colour.)

Table 1. Results of generalized linear mixed model (GLMM) on monthly barnacle recruitment rate of *Notochthamalus scabrosus* and *Jehlius cirratus*, fitted on residuals after removing seasonal trends using general additive models (GAM) on log-transformed data (log recruits/day, *r*). Models fitted either (*a*) a single fixed linear year (*Y*) trend and random site variation (γ, unstructured across space), (*b*) a fixed unique yearly trend across the study domain, with regionally structured mean effects (*G*) and random site variation, or (*c*) a yearly trend that varied across the three Regions defined in the text (*Y* × *G* interaction). Three information criteria (AIC, AICC and BCI) are presented with models ordered from smallest to largest.

model	species	AIC	AICC	BIC
(*c*) $r = Y + G + Y \times G + \gamma(G)$	*Notochthamalus*	6035.13	6035.13	6035.92
	Jehlius	9623.37	9621.37	9623.77
(*a*) $r = Y + \gamma(G)$	*Notochthamalus*	6187.44	6189.44	6189.44
	Jehlius	9693.47	9695.47	9695.47
(*b*) $r = Y + R + \gamma(G)$	*Notochthamalus*	6342.32	6343.12	6336.32
	Jehlius	9703.00	9701.00	9703.40

relationships were observed in both regions (figure 5*c*), but the slope characterizing the relationship was significantly steeper at equatorward sites than at poleward sites (GLM, interaction between region and recruitment the previous year was significant, Wald-$\chi^2 = 6.25$, $p = 0.0125$).

4. Discussion

While geographical displacements in species distribution are common and have been a primary focus of ecological climate

change studies [34,35], the vital population rates that allow species to persist, grow and, in some cases, maintain fisheries, are also expected to be altered as a consequence of climate-induced changes in primary production [43,44] and circulation patterns [2] and have been less documented. Indeed, among the many climate-stresses affecting the global oceans, changes in primary production are probably the most pervasive, potentially imperilling trophic amplification in food webs and threatening food production and global fisheries [44–46]. Our results show that both increasing and decreasing changes in pelagic phytoplankton productivity,
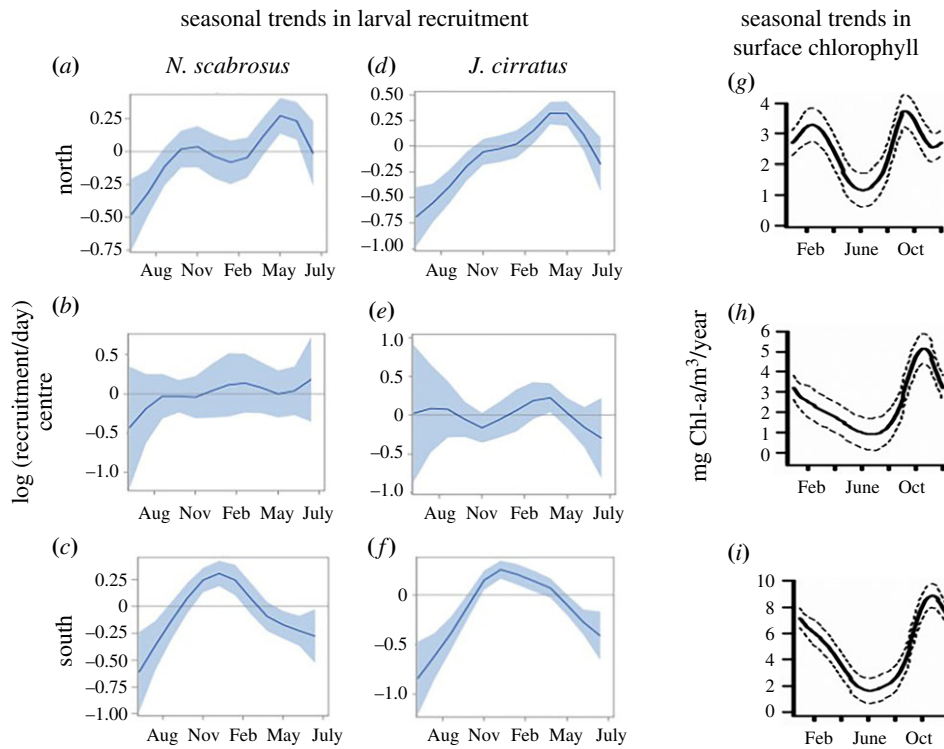
Figure 4. Seasonal component of larval recruitment rates (log recruits/day) obtained from non-parametric GAM models across the entire barnacle recruitment time series for sites in the equatorward (north, *a,d*), centre (*b,e*) and poleward (south, *c,f*) regions. Separate analyses were conducted for the two barnacle species. (*g–i*) Seasonality in surface chlorophyll-a using the same GAM method, but for the 16 year satellite data described in [11]. (Online version in colour.)
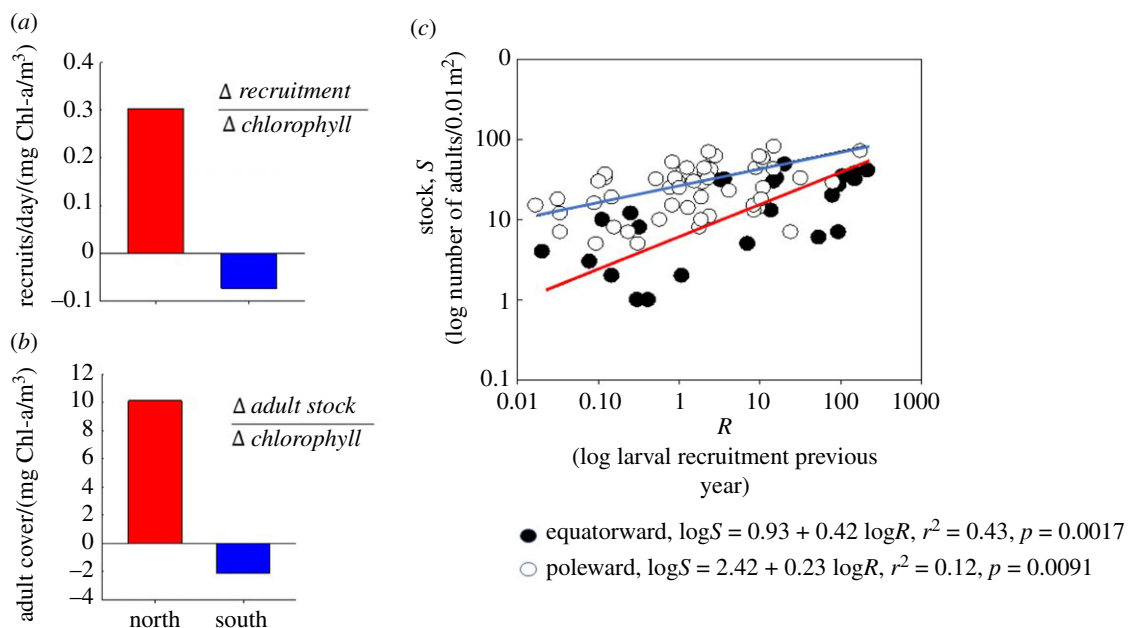

Figure 5. Rate of change per year in (*a*) barnacle larval recruitment (both species pooled) and (*b*) intertidal barnacle adult abundance (both species pooled), per unit of yearly change in chlorophyll-a at the equatorward (northern, red bars) and poleward (southern, blue bars) regions. (*c*) The recruitment–stock (barnacle abundance) relationship for sites in the poleward (open circles, blue line) and equatorward (black circles, red line) regions. Statistics from OLS linear fits on log–log data are shown at the bottom of the panel. (Online version in colour.)

forced by SPA poleward migration and intensification [11], are associated with geographical changes in larval replenishment of benthic populations of two common barnacle species. The hypothesis that such changes result from bottom-up propagation of phytoplankton productivity is also in agreement with the similarity in seasonal trends between phytoplankton and larval recruitment across the regions, the tight correlations between long-term mean phytoplankton concentration and long-term mean larval recruitment at study sites, and by the

fact that adult *per capita* reproductive output does not show regional-scale structure. We also show that increasing/decreasing rates of larval arrival have already impacted adult population abundance in positive/negative ways through recruitment–stock feedbacks, albeit at very different rates.

Theory indicates that changes in primary productivity can have large effects on stock–recruitment relationships through the alteration of effective recruitment [47]. Moreover, as predicted from coupled physical and size-based food web

models for global fish production [48], decreasing trends in productivity are associated with negative trends in filter feeder populations higher in the food web, and that regions of increasing productivity are associated with positive trends in abundance, overcoming other potential sources of population control common in complex communities [48]. However, we show that positive responses to increased primary productivity have been faster than the negative impact of decreased productivity, both in absolute terms, as well as per unit change in chlorophyll-a. The slopes relating recruitment–stock are steeper within the northern region, suggesting that increased productivity leads to increased larval recruitment and increased reproductive stocks across a large section of the coast. Since northern populations were largely recruitment-limited, at least up to 2003 [37], and since barnacles reproduce within a year after settlement, a few large settlement events could boost local populations and increase total larval output. The slower response to decreased productivity may be explained by storage effect of adult stages that can live several years and still reproduce [39]. The abundant barnacle populations found in the southern region up to the late 2000s [37], can apparently overcome the now frequent years of recruitment failure and, temporarily, avert population collapses. While such storage effects buffer populations against local extinctions, if recruitment failure is driven by long-term climate variation, such effects are only postponing the inevitable population collapses that will be synergized by the regional-scale recruitment–stock feedbacks.

Other climate-induced processes may affect larval recruitment and adults and cannot be ruled out as the underlying cause of regional-scale larval recruitment trends, or as part of the among site variation in the response of larvae to decreased or increased food availability. A leading process is related to changes in wind regimes that modulate coastal upwelling circulation and frequency or relative influence of other anomalies and physical forcing processes that change at about 30–31° S [38,49], and which in turn affect onshore larval transport. The discontinuity in patterns of invertebrate recruitment, macroalgal productivity and population genetic structure found around 30° S has been primarily attributed to shifts in upwelling regimes [37,38]. Thus, changes in upwelling must be altering coastal circulation patterns and net larval onshore transport, probably in complex ways modulated by topography [33]. However, the evidence at hand suggests that long-term changes in larval arrival are occurring despite changes in upwelling circulation and the expected increase/decreased in onshore transport. First, over the past two decades estimated mean Offshore Ekman Transport in spring–summer months, when larvae are developing in the plankton, has been steadily decreasing at latitudes south of about 31° S and remained steady or increased at northern latitudes (electronic supplementary material, figure S12). These changes in wind stress are associated with a sharp increase in the number of upwelling relaxation events observed south of 31° S (figure 1c), which is expected to provide more opportunities for onshore larval transport to competent larvae that can be carried offshore in the upwelling Ekman layer during upwelling intensification. In other words, increased frequency and duration of relaxations would be expected to lead to increased, not decreased recruitment. Thus, although onshore recruitment through the canonical upwelling relaxation process [50] has proven to be more complex than initially envisioned [51,52], changes in larval transport alone do not provide a parsimonious explanation to observed patterns. Second, a numerical ocean circulation model for the same coastal region of our study [53], forced with increased upwelling-favourable winds under different climate change scenarios, predicted that altered upwelling circulation, without changes in productivity, would lead to decreased onshore larval recruitment for species with widely different larval development times [53]. Thus, recruitment would decrease, not increase, at northern sites.

Other climate-related mechanisms could also account for the observed patterns. Alteration of sea surface temperature and, in the case of intertidal organisms, air temperatures can directly affect adult physiological performance, leading to geographical displacements along gradients of climate change velocity [35]. Our surveys of *per capita* reproductive output do not show geographical variability in adults between northern and southern regions, i.e. observed regional changes in larval recruitment cannot be attributed to direct effects of climate change on adults. It should also be noted that these two barnacle species are distributed along most of the southeastern Pacific and, therefore, observed recruitment patterns are not related to changes in range distribution.

Finally, the identification of long-term climate change signals as distinct from multiannual climate oscillations is always limited by the duration of the biological time series. Multiannual oscillations such as the Pacific Decadal Oscillation or North Pacific Gyre Oscillation have been identified in onshore invertebrate larval recruitment at places in the northeastern Pacific [18,20]. Our analyses, which span a similar temporal period to that of Iles *et al.* [20] do not support the existence of regular cycles in our region, but we cannot rule them out, especially in the poleward end of the region where there is weak evidence of a cycle with over 15 year periodicity (figure 1f). In the case reported here, the strength of the connection with longer-term climate changes lies primarily on the geographical shifts in direction of biological changes, which are difficult to explain as resulting from climate oscillations.

In conclusion, rates of positive and negative population changes have occurred, apparently induced by bottom-up productivity effects and modulated by recruitment–stock dynamics, linking pelagic and benthic ecosystems. As suggested by model results, similar bottom-up effects should be affecting most species with plankton-feeding larvae, including fished species [46,48]. This implies that along large section of HUE productivity of fish stocks should increase, and fisheries effort should be displaced equatorward, contrasting with the opposite prediction based on upwelling-driven transport and oxycline position in the northern HUE [54]. Unfortunately, reliable long-term spatial data for coastal fisheries in Chile are nonexistent. But in agreement with this broad prediction, recent analyses of long-term changes in Small Pelagic Fisheries biomass along Chile–Peru showed strong latitudinal variation in density-dependent versus climate regulation of stock biomass between central-southern versus northern Chile [55], with stronger fisheries effects south of 30° S. While adaptation to these climate-driven changes may suggest a northward displacement of the fishing grounds for movable stocks, an urgent reduction of fishing pressure in the poleward region is advisable, as stocks may be much closer to population collapse than current abundances may suggest.

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