

MODELING THE RESPONSE OF POPULATIONS OF COMPETING SPECIES TO CLIMATE CHANGE

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Abstract. Biotic interactions will modulate species' responses to climate change. Many approaches to predicting the impacts of climate change on biodiversity so far have been based purely on a climate envelope approach and have not considered direct and indirect species interactions. Using a long-term observational data set (>30 years) of competing intertidal barnacle species, we built a hierarchy of age-structured two-taxa population models (*Semibalanus balanoides* vs. *Chthamalus montagui* and *C. stellatus* combined as one taxon) to test if the presence of a dominant competitor can mediate climatic influence on the subordinate species. Models were parameterized using data from populations on the south coast of southwest England and verified by hindcasting using independent north coast population data. Recruitment of the dominant competitor, *S. balanoides*, is driven by temperature. The mechanisms of competition explored included simple space preemption and temperature-driven interference competition. The results indicate that interspecific competition between juvenile barnacles is important in regulating chthamalid density but not that of the dominant competitor *S. balanoides*. Simulations were carried out using alternative future climate scenarios to predict barnacle population abundance over the next century. Under all emission scenarios, the cold-water *S. balanoides* is predicted to virtually disappear from southwest England by the 2050s, leading to the competitive release of *Chthamalus* throughout the entire region and thereby substantially increasing its abundance and occupied habitat (by increasing vertical range on the shore). Our results demonstrate that climate change can profoundly affect the abundance and distribution of species through both the direct effects of temperature on survival, and also by altering important negative interactions through shifting competitive balances and essentially removing dominant competitors or predators. Climate change impacts on organisms are unlikely to lead only to straightforward, easily predictable changes in population size and distribution. The complex, indirect effects of climate change need to be taken into account if we are to accurately forecast the long-term effects of global warming.

Key words: age-structured models; *Chthamalus montagui*; climate change; interspecific competition; intertidal barnacles; population modeling; *Semibalanus balanoides*.

INTRODUCTION

The global climate is warming, and much of the rapid warming observed in recent decades is due to human activities (IPCC 2007). Evidence is accumulating that climate change is already affecting the distributions, abundance and phenology of many plants and animals (Walther et al. 2002, Parmesan 2007). Due to the inertia of the atmosphere–ocean system, temperatures will keep on rising over the next few decades, if not longer, regardless of any attempts at mitigation of greenhouse gas emissions (IPCC 2007). We urgently need to forecast just how ecosystems will respond in order to develop adaptation strategies to maintain ecosystem services and conserve biodiversity. There has been a tendency for

investigators to apply the climate envelope model (CEM) to study potential climate effects on species' distributions and biodiversity (e.g., Bakkenes et al. 2002, Erasmus et al. 2002) and even to predict extinction risk from climate change (Thomas et al. 2004). Although successes have been claimed, model validation (as opposed to model verification) is problematic due to a lack of independent test data (Araújo et al. 2005, Araújo and Guisan 2006). Extrapolations of CEMs to predict future distributions of species assume the observed distributions of species are in equilibrium with their current environment and cannot survive outside the defined environmental conditions, which is contradictory to reviewed evidence (Botkin et al. 2007). Further, the role of biotic interactions (both positive and negative) in determining species distributions have generally been neglected and ambiguities concerning their role need to be resolved before integrating in CEMs (Araújo and Guisan 2006).

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It is worth noting that Darwin (1872) was strongly of the opinion that few organisms are directly affected by climate and observed "climate acts in the main part indirectly." It has been hypothesized that ecosystem characteristics are determined by interactions between species such as competition (Connell 1961, Wethey 1984), mutualism (Brooker 2006), and trophic interactions (Goldberg and Barton 1992) rather than by the presence and absence of species (Chapin et al. 2000). The strength and the nature of biological interactions themselves are influenced by climate and will be impacted by climate change. Additionally, population responses may not be determined by species' direct responses (Davis et al. 1998, Bertness et al. 1999, Barker et al. 2005). Climate change impacts will resonate throughout trophic webs and biological communities (Chapin et al. 2000, Edwards and Richardson 2004, Brooker 2006, Harley et al. 2006). Some species will benefit from climate change whereas others will be endangered as physiological stresses, and competitive balances and other biotic interactions are altered (Loya et al. 2001, Aloha et al. 2007, Best et al. 2007). Understanding the mechanisms by which climate and biology interact is important, particularly if we are to forecast biological response to climate change (Brooker et al. 2007). Such understanding can only come from detailed investigations of modulation of ecological interactions by climate (Hallett et al. 2004, Harley et al. 2006).

The purpose of this study was to model the impacts of future climate change on two taxa of competing intertidal barnacles in the United Kingdom (UK): the Arctic-boreal *Semibalanus balanoides*, and the two warm-water chthamalids, *Chthamalus montagui* and *Chthamalus stellatus*. The model and analyses were based on an exceptional data set of the long-term population dynamics of both taxa (Southward and Crisp 1954, Southward 1991, Southward et al. 1995, 2005). Previous investigations have used size-structured matrix population models of *S. balanoides* and *C. montagui* to demonstrate how altered recruitment levels can lead to population extinction; these models were theoretical and not specific to any location (Svensson et al. 2006). We test and extend this idea using a long-term (>30 years) population data set and a modeling approach that considers both the direct effects of climate on survival of recruits of the dominant competitor, thus adult density, and also the subsequent indirect effects on competitive interactions. In our models, recruitment of the dominant competitor is driven directly by temperature using a function fitted to observed population and ocean temperature data from southwest England. Interspecific competition is included as simple space preemption and, in an extension of Svensson's (2006) model, as recruitment-driven interference competition inducing additional mortality in young of the subordinate competitor. Our results demonstrate how competitive interactions can mediate climate influence on population density.

We applied a two-step approach to determine the mechanisms underlying changes in abundance of competing species in relation to climate change. First, statistical analysis of the data on abundance of the two taxa identified sensitive phases in the life cycle that may drive population variability and interactions between species, and distinguished between direct and indirect effects of environmental change, building on Southward (1967, 1991). Second, population models including climatic influences on survival were developed from the age-structured space preemption approach of Roughgarden et al. (1985) using four hypothesized sets of assumptions based on mechanistic processes involving two forms of competition occurring between recruits: resource competition where competition for space occurs through space preemption by settled individuals and interference competition where the dominant competitor can overgrow and undercut subordinate individuals. The hypothesized sets of assumptions are: (1) resource competition, (2) resource competition plus stock-recruit effects on dominant competitor, (3) interference plus resource competition, and (4) interference plus resource competition plus stock-recruit effects on dominant competitor. We were able to parameterize our models using data from populations on the south coast of southwest England and validate the models by hind-casting using independent north coast population data. Our models only consider interaction and space preemption among juvenile barnacles and do not take account of other processes such as predation or facilitation. Finally, we extended the best fit model using projections of June mean sea surface temperature to 2100 to forecast potential population abundances under four alternative future climate scenarios likely to result from different emission levels of greenhouse gases.

METHODS

Overall approach

First, underlying patterns and processes in the barnacle data set were explored by statistical analyses and environmental drivers of abundance relevant to the biology of intertidal barnacles identified. The results guided development of population models to test the role of interspecific competition in population responses to climate variability. Finally, the most appropriate model was forced with future climate scenarios to forecast barnacle population abundances to 2100.

Intertidal barnacle biology

The restriction of populations of warm water chthamalids in the mid-intertidal by the competitively superior arctic-boreal *S. balanoides* on UK coasts was among the earliest experimentally verified examples of competition for space (Connell 1961). These intertidal barnacles have an adult sessile stage and a pelagic larval stage but show differing reproductive strategies. Individual *S. balanoides* produce one large brood of larvae a

year, with peak settlement time generally occurring in spring (April–May), whereas the chthamalids produce multiple smaller broods later in the warm summer and autumn (Burrows et al. 1992). Competition between these taxa probably takes two forms. First, field observations suggest that *S. balanoides* settlement in the spring occupies bare rock denuded of barnacles by winter storms (Moore and Kitching 1939, Barnes and Powell 1950, Connell 1961) before the later settlement of chthamalids. Secondly, experimental observations indicate that interference competition occurs with the more rapidly growing young *S. balanoides* overgrowing and undercutting young chthamalids. This happens both in northern Europe (Connell 1961, Foster 1971a) and on the northeast coast of the United States (Wetthey 1984) where *S. balanoides* interacts with another chthamalid, *Chthamalus fragilis*.

Barnacles have two larval stages: a planktotrophic nauplius larva, which may remain in the plankton for a number of months and develops into the second stage, a non-feeding cyprid larva. Breeding duration and performance, and larval survival and development are all strongly influenced by water temperature (Crisp 1950, Southward 1976, Burrows 1988, Burrows et al. 1999). Fertilization in *S. balanoides* is inhibited when water temperatures are above 10°C (Barnes 1989) while the onset of breeding in *Chthamalus* in southwest England is initiated when water temperatures reach 10°C (Burrows et al. 1992). At suboptimal water temperatures, larval mortality is high. Threshold water temperatures may also trigger metamorphosis of cyprids (Pineda et al. 2002). Recruitment of common intertidal barnacles to adult populations appears to be driven by larval settlement rates modified by early settlement processes such as thermal stress (Foster 1971b, Gaines and Roughgarden 1985).

Demographic data

The demographic climate forecast model was based on 32 years of survey data. The data were first interrogated to reveal potential causes of variation in the data set. Correlations with key environmental data sets identified which environmental variable was driving interannual variation while application of path analysis revealed the potential underlying mechanism.

Our data set contains density measurements of adult intertidal acorn barnacles from almost 200 sites in southwest England, made generally in the months of April and May between 1955 and 1987. Sites with more than 10 annual counts of adult barnacles were selected for analysis (Appendix A). *Chthamalus montagui* and *C. stellatus* were considered varieties of a single species (Darwin 1851, Pilsbry 1916) until taxonomic revision by Southward (1976). In the UK, these species have comparable breeding seasons, fecundity, and growth rates (Burrows et al. 1992, 1998) therefore they have been grouped together as a single taxon in all years. Statistical analysis revealed that most of the temporal

variance in abundance was common to the whole network of sites (Appendix B). Interannual patterns in abundance of the two taxa (chthamalids and *S. balanoides*) were represented by average values for northern and southern coasts at each of the three shore heights. Only mid-shore yearly means were used in the population models as competitive interactions between chthamalids and *S. balanoides* are strongest in the mid-shore region of overlap (Connell 1961, Foster 1971a).

The correlations between mean mid-shore north and south coast barnacle abundances and mean monthly sea surface temperature (SST) from station E1, 22 nautical miles southwest off Plymouth, and air temperature data from Plymouth (see Southward et al. 2005) were measured using Pearson's correlation coefficient (r). Annual mean barnacle abundances were correlated with each monthly mean SST and each monthly mean air temperature lagged back over a three-year period, from December in the year of observation to January two years previously. To determine the proportion of variance in chthamalid abundance explained purely by SST, purely by *S. balanoides* abundance and that shared between the two explanatory variables, we fitted a generalized least squares (GLS) model with an AR1 autocorrelated error structure to both the north and south coast mid shore data (Appendix B). Different routes for environmental influence on yearly abundance can be considered as multiple causal pathways in a formal path analysis (Petraitis et al. 1996). Path coefficients were calculated for a model with both barnacle species and mean SST in the previous June (the month identified as having the strongest association with abundance; Fig. 1) for the south coast populations (Appendix C).

Population models

Age-structured population models were developed to explore assumptions of different processes on population structure. Simple, space-preemptive competition and temperature driven recruitment of *S. balanoides* was included in all models. The additional influences of adult stock effects on recruiting *S. balanoides* and temperature-driven interference competition between juvenile *S. balanoides* and *Chthamalus* on population variability were explored. Models were fitted to the 32-year data test from the south coast of southwest England and validated with the independent (see Appendix B) north coast data set.

Population models used June SST as a dominant influence on the survival of *S. balanoides* recruits. Deterministic age-structured population models were constructed following the approach of Roughgarden et al. (1985). The assumptions of the models were (1) the population is open and recruitment is proportional to free space available (Gaines and Roughgarden 1985) and (2) mortality is age specific and density independent. The models have two steps per year (1 June and 1 December) with recruitment of *S. balanoides* to the adult

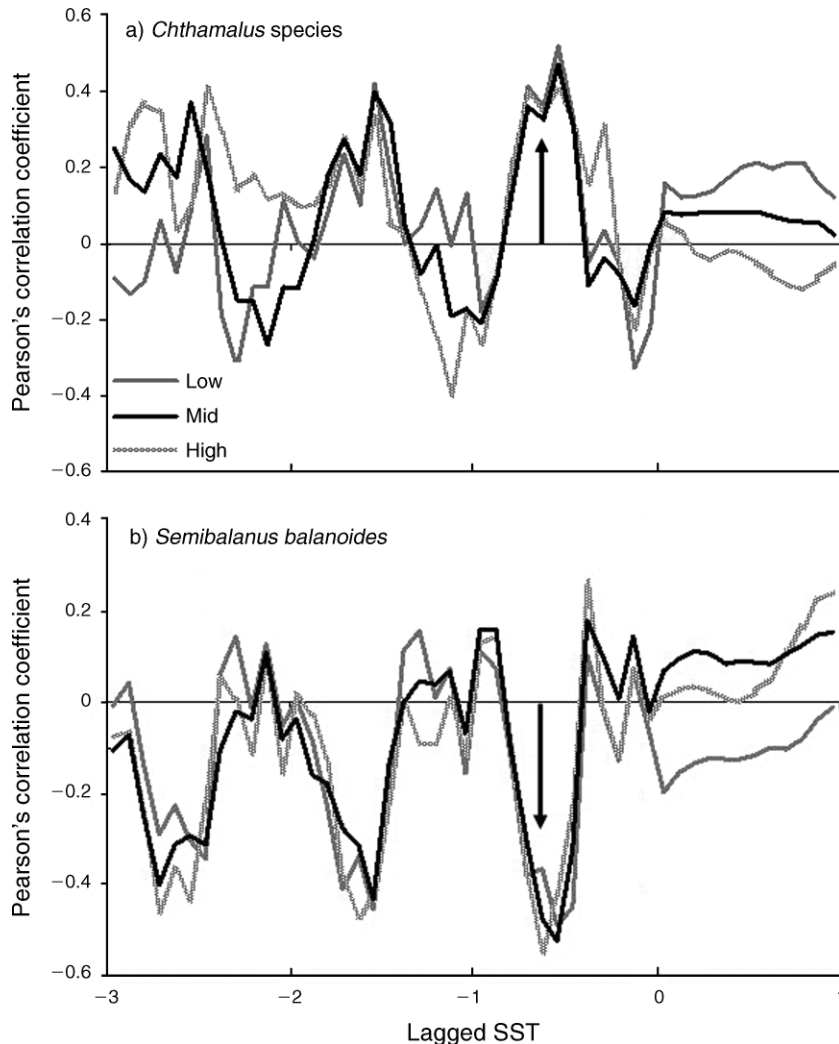


FIG. 1. Pearson's correlation coefficients for adult intertidal barnacle counts for (a) chthamalids and (b) *Semibalanus balanoides*, averaged for south coast sites, against lagged mean monthly sea surface temperature (SST) from station E1, 15 miles off Plymouth, UK (see Southward et al. [2005] for location): 0 = SST in January of year of count, -1 = SST in January previous year, -2 = SST in January two years previous, -0.6 = SST in June of previous year, indicated by arrows.

population in June and of *Chthamalus* species in December. The number of individuals entering each age class six months and above was expressed as

$$n_{x,i+1,t+1} = P_{x,i} n_{x,i,t} \quad (1)$$

where $P_{x,i}$ is the probability of surviving the six months from age class i to age $i + 1$ for species x . The last age class is assumed to be additive. Survival rates, growth rates, and maximum recruitment values were selected after considering the literature (e.g., Burrows 1988) and from our own field work (Appendix D).

June SST may affect the population dynamics of these species in a number of ways. To evaluate and discriminate between these possibilities, we built a hierarchy of increasingly complex models to evaluate the performance of different sets of assumptions about the critical population processes linking these species to climate.

Model 1: resource competition.—Temperature-driven two-taxa models with SST in June influencing *S. balanoides* recruitment in June. Evidence suggests recruitment success of *S. balanoides* determines population abundance in the following years and in southern areas, where thermal stress on *S. balanoides* is high, survivorship of *S. balanoides* recruits and larvae may be determined by SST (Pineda et al. 2002).

Model 2: resource competition plus stock-recruit effects on dominant competitor.—This model is as model 1 but with the addition of adult stock size influencing recruitment of *S. balanoides*. Settlement and recruitment of *S. balanoides* has been shown to vary positively with adult density except at very high adult densities, whereas for *C. montagui* the relationship is much weaker (Kent et al. 2003). It has been long known that *S. balanoides* cyprids are gregarious in settlement, attracted chemical-

ly to adult and juvenile conspecifics (Knight-Jones and Crisp 1953, Crisp 1961). Application of a stock–recruit function explores the influence of this process on recruitment rates and thus adult stock abundance.

Model 3: interference competition.—This model is as model 1 but with the addition of young *S. balanoides* competing directly with young chthamalids. Field experiments have demonstrated that, where these species compete for space, *S. balanoides* overgrows young chthamalids and is generally the dominant competitor (Connell 1961, Wethey 1984).

Model 4: interference competition plus stock-recruit effects on dominant competitor.—This model is as model 2 but with the addition of June SST also influencing competition between young *S. balanoides* and young chthamalids.

Recruitment, R , was defined as the number of settlers alive at the end of the settlement season, taken as 1 June for *S. balanoides* and 1 December for *Chthamalus* species. Recruitment rate per unit free space, S , for *Chthamalus* species was assumed to be constant between years and was set at 40 recruits per square centimeter of free space ($R = S \times F$). For *S. balanoides*, recruitment R was expressed as

$$R = S \times F \times G \quad (2)$$

where F is total free space and G is the gregariousness function that scales recruitment rates by the occupancy of area by adult *S. balanoides* at the time of recruitment in June. G was set to 1 for models 1 and 3. For *S. balanoides* recruitment in June, S is a temperature-dependent function:

$$S = S_{\max} f(t, T_{\text{crit}}, c) \quad (3)$$

where S_{\max} is the maximum recruitment rate per unit free space at cool temperatures, set at a constant of 30 recruits per square centimeter, f is a cumulative Gaussian function, t is the SST in June, T_{crit} is the SST at which recruitment is 50% maximum, and c represents the rate of decline of recruitment per unit free space with increasing SST. Variables for parameters T_{crit} and c were set by optimizing the fit between predictions and historical data.

The function used to represent gregariousness in recruitment was

$$G = \frac{P_{\text{SB}}}{b + P_{\text{SB}}} \quad (4)$$

where P_{SB} is the proportion of total area occupied by adult *S. balanoides* and b is the half-saturation constant for gregariousness. For models 1 and 3, b was set to 0 so G becomes 1 and there is no gregariousness in recruitment. If b is small, G rapidly reaches an asymptote of 1 with increasing P_{SB} ; while with increasing b , G shows a more linear increase with P_{SB} . Values of b were fitted by optimization in models 2 and 4.

Survival from the 6-month to the 12-month age class in *Chthamalus* species, effective in December, was made dependent on the population density of newly settled *S. balanoides* in the previous June for models 3 and 4:

$$N_{12} = N_6 M_{6,12} f(N_{\text{SB6}}, N_{\text{SBcrit}}, e) \quad (5)$$

where N_{12} is the number of 12-month-old *Chthamalus* sp. in the population in December; N_6 is the number of 6-month-old *Chthamalus* sp. in the population in June; $M_{6,12}$ is the mortality rate moving between age classes 6 and 12 months in the absence of competition; f is a cumulative Gaussian function; N_{SB6} is the number of *S. balanoides* recruited in June; N_{SBcrit} is the density of *S. balanoides* recruited in June that produces half the maximum survival rate $M_{6,12}$; and e is the rate of decline in survival of *Chthamalus* species with increasing *S. balanoides* recruitment. N_{SBcrit} and e were fitted by optimization.

Historical mean June SST were taken from the MBA data set for E1 (Maddock and Swann 1977, Southward et al. 2005) from 1903 to 1987. For missing years, 1910–1920 and 1939–1946 inclusive, a mean June SST data set from 1903 to present day was extracted from the Global Ocean Surface Temperature Atlas Plus (45°–50° N, 5°–0° W; GOSTAPlus, British Atmospheric Data Centre) and regression analysis used to scale these to the E1 data set.

Time series of barnacle abundance from mid-shore on the south coast were used both as an input and as a test for the models, while north coast time series were used to validate the fitting procedure and the relative performance of the models. The north coast time series, from unconnected populations sharing similar environmental forcing (Appendix B), is thus a good independent test of model performance. Models were fitted by minimizing the total deviance for time series of *S. balanoides* and combined *Chthamalus* species (Appendix E). The *S. balanoides* temperature-dependant recruitment function (model 1) was fitted first (model 1) and held constant for models 2–4. Subsequent models used the same method to find best-fit parameter values for the *S. balanoides* gregariousness function (Eq. 4; b : models 2 and 4) and the interspecific competition function (Eq. 5, SB_{crit} , e : models 3 and 4). The robustness of these parameter values was estimated by running 1000 bootstrap simulations for each model. The 95% confidence limits for fitted parameter values (Appendix E; Table E.1) and for predictions were calculated.

The deviance of each model was compared to that produced by a ‘mean model’, in which the predicted value for each taxon in each year was the mean for the 33-year period. Akaike’s information criterion (AIC), which considers model fit and the number of variable parameters, gave a numerical index of model performance. The Akaike weights, which convert the AIC values into probabilities that each of the four models is the best available, were used to select the most appropriate model.

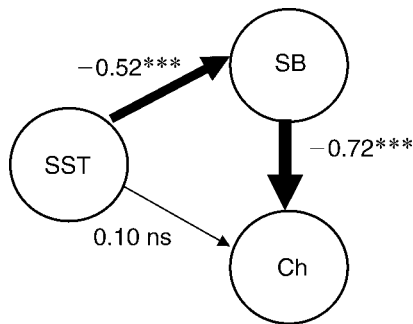


FIG. 2. Results of path analysis for testing causal relationship between abundance of intertidal barnacles, *Semibalanus balanoides* (SB) and *Chthamalus* spp. (*Chthamalus montagui* plus *C. stellatus*; Ch), and mean sea surface temperature in June the previous year (SST). Data are from average numbers at mid-shore levels (low, mid, and high) from over 30 years of data (Southward and Crisp 1954, Southward 1991, Southward et al. 1995, 2005) from sites around southwest England (see Appendix A). The path for mean June SST directly influencing *Chthamalus* spp. is not significant, but the paths for mean June SST influencing *S. balanoides* and for *S. balanoides* influencing *Chthamalus* spp. are significant, indicating that the effect of mean June SST on *Chthamalus* spp. is mediated by the presence of *S. balanoides*. Most of the population of *S. balanoides* will be individuals settled in the previous year so the relationship between mean June SST in the previous year and adult counts of *S. balanoides* indicates that mean June SST is acting on or is a proxy for environmental influence on juvenile stages.

*** $P < 0.001$; ns, not significant.

Population changes under projected climate change scenarios

We used projections for UK climate under four alternative greenhouse gas emission scenarios: low, medium-low, medium-high, and high, from the UK-CIP02 future scenarios prepared for the UK Climate Impacts Programme (UKCIP; Hulme et al. 2002). Projections were available for three future time slices: the 2020s, the 2050s, and the 2080s. Stochastic yearly series for mean June SST to 2100 were produced for each emission scenario by assuming a linear increase between mid points of the time slices. Although extreme events are projected to become more common in most climate forecasting exercises, for simplicity it was assumed that variability about the lines were both similar to that seen in the historic data for the baseline time series and normally distributed. The model identified as most appropriate to simulate population dynamics (model 3) was used with mean June SST future projections. 1000 simulations were run for each for the future emission scenarios.

RESULTS

Demographic data

The strongest significant associations between annual barnacle abundance and monthly measurements of sea and air temperature were found with mean SST in the previous June for both taxa (Fig. 1). The associations were negative for *S. balanoides* and positive for

Chthamalus species; this suggests that a warm spring favors *Chthamalus* species survival from juveniles settled two years previously to new adults in the year of observation. The results explain the two-year time lag in adult chthamalid numbers noted by Southward (1991) in response to fluctuating sea surface temperature; June is the end of the settlement season for *S. balanoides*. June SSTs are probably a proxy for a suite of environmental influences on larval and early settlement life stages. Mean June SSTs in the E1 data set are strongly correlated with mean SSTs in the preceding spring months, when *S. balanoides* larvae are in the water column, (R^2 range from 0.72 [February] and 0.97 [May]). Strong correlations are also found with mean monthly air temperatures in May ($R^2 = 0.65$) and June ($R^2 = 0.61$), when recently metamorphosed juveniles are vulnerable to desiccation stress.

Significant path coefficients described the influence of SST directly on *S. balanoides* (Fig. 2; Appendix C). For *Chthamalus* species, path analysis suggested the effect of June SST is mediated by the presence of *S. balanoides*. The pure effect of June SST on midshore *Chthamalus* abundance, where *S. balanoides* dominates, was very small: less than 1% of the total variance in abundance of this species (see Appendix B). Most of the variability in *Chthamalus* was thus explained by variation in the abundance of its superior competitor.

Population models

The fitted function for south coast *S. balanoides* recruitment against mean June SST (Fig. 3) declined above 11.5°C and approached zero above 14.5°C. Warm June SSTs may directly influence survival of new settlers of *S. balanoides*, or be a proxy for processes such as reduced breeding success or larval survival during warmer springs. Counts of juvenile *S. balanoides* per unit free space were not available for the model period (1955–1987). It was possible, however, to project likely numbers of recruits from counts of adults one year later,

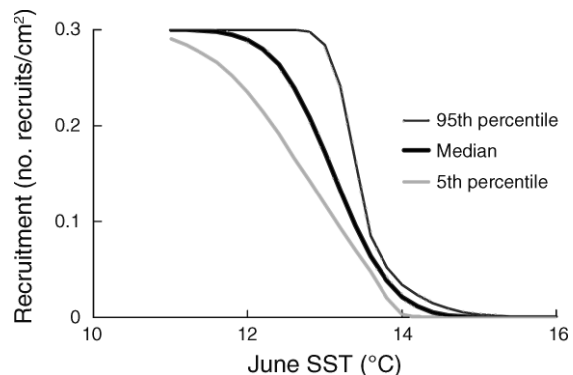


FIG. 3. Fitted function for recruitment of *Semibalanus balanoides* into free space vs. mean June sea surface temperature using south coast data. Lines show fifth percentile, median (black), and 95th percentile of predictions using parameter values (T_{crit} , b) from 1000 bootstrap simulations.

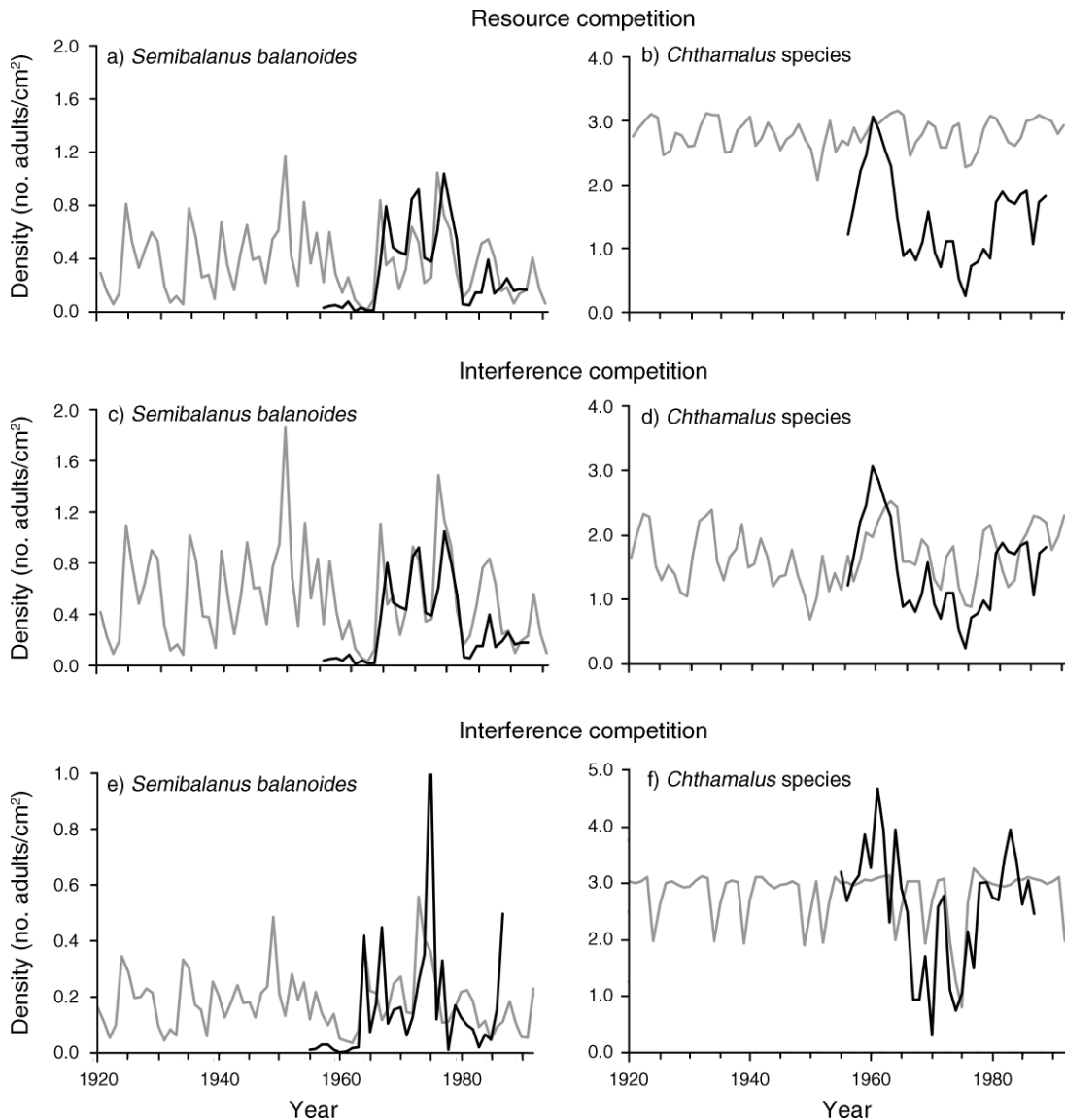


FIG. 4. Output from 1920 to 1991 for two-taxa barnacle (*Semibalanus balanoides* and *Chthamalus* species) population models fitted to (a–d) south coast data and (e, f) north coast data. Predictions from the model with mean June sea surface temperature driving *S. balanoides* recruitment and resource competition for space between juvenile *S. balanoides* and *Chthamalus* species are shown in panels (a) and (b), while model predictions, with temperature-dependent *S. balanoides* recruitment and interference competition between juvenile *S. balanoides* and *Chthamalus* species, are shown in panels (c)–(f). Without any competition, *Chthamalus* spp. reach a steady maximum within a few years. The black line is from historical data, and the gray line is from model data.

the likelihood of survival to adulthood and the average projected free space in June from the model. Projected values of recruits per unit free space followed the model function well. Model 1, where mean June SST drives *S. balanoides* recruitment, reproduced variability in the observed *S. balanoides* time series (Fig. 4a; deviance, 58% of the mean model) but not in the *Chthamalus* time series (Fig. 4b; deviance, 234% of the mean model). Free space in December varied between 12% and 44% with an average of 33% (Fig. 4c). Model 2 performed similarly well for *S. balanoides* and poorly for the *Chthamalus*

series. However, models 3 and 4, which both include a function for competition between juvenile *S. balanoides* and juvenile *Chthamalus*, reproduced much of the variability seen in the *Chthamalus* time series (Fig. 4d; Appendix E: Table E2; deviance, 82% of the mean model). AIC values showed that model 3 was the best-performing model, with mean June SST driving *S. balanoides* recruitment and interspecific competition between juveniles. Akaike weights gave a 52% probability that model 3 was the best of the available set of models (Appendix E: Table E1).

Repeating the above model-fitting process for time series of averaged abundance at north coast sites produced very similar measures of model performance to those for models fit to south coast data (Appendix E, compare Table E1 to Table E2). *S. balanoides* recruitment showed a similar decline with mean June SST when incorporating this function into model 1. The best-performing model was again model 3 (Fig. 4e, f; Appendix E: Table E2), combining temperature-dependent recruitment of *S. balanoides* with interspecific competition driving survival of *Chthamalus* species. Model 3 had the lowest AIC value and Akaike weights giving a likelihood of 56% of being the best of the four models for the north coast mid-shore time series.

*Population changes under predicted
climate change scenarios*

Under all four future greenhouse gas emission scenarios, the abundance of *S. balanoides* decreased while the abundance of *Chthamalus* species increased (Fig. 5). This change was much more rapid at the high than the low emissions scenario. The models suggest that *S. balanoides* may be locally extinct in southwest England by 2050 under the high-greenhouse-gas emission scenario and by 2080 under the low-emission scenario.

DISCUSSION

Modeling approaches have previously demonstrated that community responses to climatic change can depend on interspecific interactions and dispersal ability, but such models are rarely parameterized and validated with observed responses to climate change (Svensson et al. 2005, 2006, Brooker et al. 2007). The novelty of our model is that it was parameterized using a long time series and validated with an independent data set, allowing a detailed exploration of modulation of ecological interactions by climate. Warming SST had predictable negative effects on *S. balanoides*. However, as *S. balanoides* is the dominant competitor, warming climate had striking positive effects on the subdominant *Chthamalus*. These results indicate that climate can have opposing effects on two co-occurring species resulting in community-level shifts in dominance. Such shifts have been observed on tropical coral reefs after bleaching events and have been attributed in part to differential survival of coral species (Loya et al. 2001). Given the inherent complexity of ecosystems, climate change impacts on populations and communities will be more elaborate than simple declines in climate-sensitive species and therefore challenging to predict. Our model is based on a well understood example of competition between two taxa and required detailed investigation to define underlying mechanisms. As other biotic interactions are considered, the number of potential mechanisms through which climate can influence a species will increase dramatically.

Both long-term climate variables and short-term weather have been shown to influence biotic interactions and thus species' abundances and distributions (Barker et al. 2005). Large-scale climatic indices, such as the North Atlantic Oscillation and El Niño, or seasonal indices, consistently appear to be good predictors of ecological processes, often outperforming measures of local climate or weather (Hallett et al. 2004) which may explain the success of climate envelope models in predicting present day species distributions. However, the relative success of large scale climate variables may be a reflection of the low accuracy by which the complex associations between ecological and physiological processes and the environment are captured by measurements of local weather (Hallett et al. 2004, Helmuth et al. 2005); the mis-match between biological observations and environmental data is well known. In our model, mean June SST is a proxy for the suite of environmental influences on the success of the early life stages, such as success of larval development through match with appropriate food species (Barnes 1956).

Intertidal animals exist in a highly stressful habitat, being exposed to potentially large fluctuations in temperature between emersion and submersion (Helmuth et al. 2002, 2006). Rock temperatures can be high during aerial exposure on summer days and even in western Scotland where air temperatures do not routinely exceed 20°C in the summer, rock surface temperatures of 38°C and 42°C have been recorded at mid and high shore height, respectively, during the summer (M. Burrows, *unpublished data*). These temperatures are lethal to *S. balanoides* if exposure is prolonged (Southward 1958, Foster 1969). The likelihood of mortality of an individual during aerial exposure will be modulated by interacting factors such as cloud cover, spray from waves, rainfall, the presence of neighbors and other organisms, body condition and the timing of low tide (Bertness et al. 1999, Wethey 2002, Helmuth et al. 2006). Sea temperatures influence the most sensitive life stages, such as the quality and survival of larvae (Barnes 1956, Marshall and Keough 2004, Emler and Sadro 2006), which may explain why sea surface temperatures outperformed air temperatures in our analysis. Further, analysis of the large-scale distributions and abundances of over 40 intertidal species from over 600 sites around the UK with mean monthly climate variables including solar radiation, precipitation, and measures of sea and air temperature found overwhelmingly that mean monthly sea temperature of the coldest and/or warmest month together with an index of wave exposure provided the strongest correlates (Mieszkowska et al. 2005). Regulation of intertidal populations by the marine environmental conditions is not surprising considering intertidal organisms, with a few exceptions, are marine in origin and many rely on water currents for food supply, gaseous exchange and propagule and larval dispersal. Changes in recruitment and juvenile survival, rather than migration and

transport are proposed to regulate intertidal barnacle populations, although larval supply is necessary (Pineda et al. 2002, Power et al. 2006). The relative importance of environmental stressors can vary markedly both spatially and temporally as can the physiological capacity of an organism to adapt to stress (Helmuth et al. 2005). More-detailed studies at an individual scale will provide further understanding of how such processes scale up to large-scale expansion and retreat (Helmuth et al. 2002, 2006).

June SSTs off the south coast of southwest England are projected to warm between 1.2° and 1.8°C by the 2050s and 1.7–3.2°C by the 2080s (Hulme et al. 2002). Our models indicate that *S. balanoides* will virtually disappear from this region by 2050, while the abundance of chthamalids, released from competition with *S. balanoides* and favored by the warmer sea temperatures, should increase. Range extensions and increases in abundance, probably linked to recent warming, have been recorded for both *Chthamalus* species in northern England and Scotland compared to data from the 1950s, while *S. balanoides* is now less abundant in southwest England than it was during the cool climatic periods of the 1960s and 1970s (Mieszkowska et al. 2005). Recently, there have been a number of failure years for *S. balanoides* in southwest England where little or no recruitment has occurred (Mieszkowska et al. 2005). It is likely that successful recruitment of *S. balanoides* will become an increasingly rare event, progressing to local extinction through a period of less and less frequent re-invasions of *S. balanoides* from cooler waters. *S. balanoides* has already been virtually eliminated from its outlying enclave in the cold rias of northwest Spain so its disappearance from southwest England and from the north Biscayan coast of France may now be unavoidable. The consequences for the marine ecosystem are more difficult to predict, but it should be expected the pelagic food web would be altered if *S. balanoides* larvae are replaced by chthamalid larvae in the pelagic realm (Hiscock et al. 2004). Larvae of *S. balanoides* can dominate the plankton in coastal waters of southwest England during spring (Muxagata et al. 2004) when the larvae of cold water species of fish are feeding. At this time, barnacle larvae may account for as much secondary production as calanoid copepods, the largest component of zooplankton biomass in these temperate coastal waters (Hirst et al. 1999, Muxagata et al. 2004). Alteration of the magnitude and timing of seasonal peak of components of the plankton may have significant impacts on higher trophic levels (Edwards and Richardson 2004, Hays et al. 2005). Changes in intertidal barnacle populations attributed to warming may thus provide an early warning system for comparable changes in demersal and pelagic species in coastal waters (Southward 1991, Southward et al. 2005).

In the terrestrial environment, studies of the effect of climate change have found a higher proportion of species extending their high latitude boundaries pole-

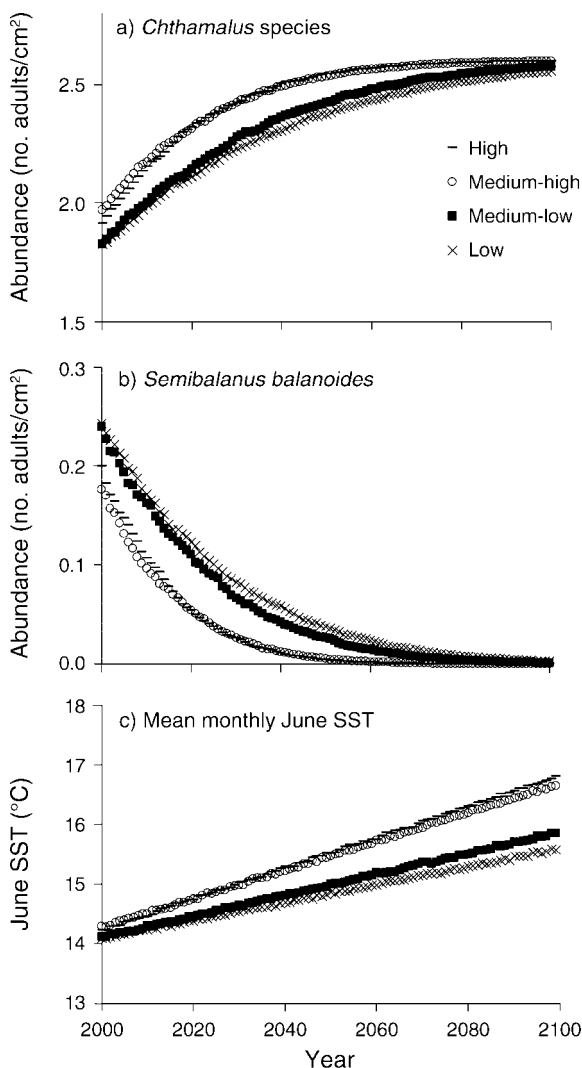


FIG. 5. Mean output of 5000 simulations from 2000 to 2100 for two-taxa barnacle population models fitted to south coast data with temperature-dependent *S. balanoides* recruitment and competition between juvenile *S. balanoides* and *Chthamalus* species under four greenhouse gas emission scenarios: low, medium-low, medium-high, and high (see Hulme et al. 2002). Variability about future mean June sea surface temperature projections is stochastic. (a) Mean abundance of *Chthamalus* species, (b) mean abundance of *Semibalanus balanoides*, and (c) mean monthly June sea surface temperature.

wards than retracting their low latitude boundaries (Parmesan et al. 1999, Thomas and Lennon 1999). Provided populations are connected and events occur within the life spans of species, northern species (or southern species in Southern Hemisphere) may be able to persist for longer than might be expected at low latitude range edges (Svensson et al. 2005). Other model studies have considered recruitment as an entirely stochastic process (Svensson et al. 2005, 2006), we considered recruitment as entirely deterministic. However, inclusion of stochasticity in our recruitment

function may predict that *S. balanoides* persists longer in southwest England as temperatures warm. Species with high competitive ability, such as *S. balanoides*, coupled with occasional recruitment events, enables persistence of these species in fluctuating environments (e.g., *Patella vulgata* compared with *Patella depressa* [Bonaventura et al. 2002]). This has happened off southwest England where cod, *Gadus morhua*, increased in abundance during the cold period from 1963 to 1985 and then maintained a population during a subsequent warm spell (Genner et al. 2004, Southward et al. 2005).

Using a tractable system, we have shown how environmental forcing can be modulated by competitive interactions. Only when a function for interference competition was included in our population models, was much of the variability in the historical barnacle time series reproduced. The challenge now is to build spatially-explicit models linking metapopulation dynamics of species and incorporating connectivity. Our approach highlights the value of a combination of field experiments, long-term observations and modeling in furthering understanding of population responses to climatic variation. Community responses to a changing climate are likely to be complex and difficult to predict, even for relatively well-studied systems such as the rocky intertidal (Bertness et al. 1999). As climate change affects the distributions and abundances of species, changes in biodiversity will occur with novel communities and biotic interactions arising. However, specific models of changing populations will provide crucial insight into how localized extinctions could scale up to large-scale retreat, the underlying mechanisms by which species advance and the long-term persistence of populations under threat from climate change.

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APPENDIX A

Location of study sites (*Ecological Archives* E089-181-A1).

APPENDIX B

Statistical analysis (ANOVA) of 33-year time series of barnacle abundance (*Ecological Archives* E089-181-A2).

APPENDIX C

Path analysis of the influence of sea surface temperature on adult intertidal barnacle abundance (*Ecological Archives* E089-181-A3).

APPENDIX D

Input parameters for barnacle population models (*Ecological Archives* E089-181-A4).

APPENDIX E

Output from barnacle population models (*Ecological Archives* E089-181-A5).