

DR. SAMUEL CRICKENBERGER (Orcid ID : 0000-0001-9359-8782)

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Annual temperature variation as a time machine to understand the effects of long-term climate change on a poleward range shift

Running head: Temperature variation as a time machine

Sam Crickenberger*+ and David S. Wethey

University of South Carolina, Department of Biological Sciences, Columbia, SC, USA

+Present address: The Swire Institute of Marine Science and School of Biological Sciences, The University of Hong Kong, Hong Kong SAR, China

*Corresponding author: phone:852-2809-2179, email: scricke@gmail.com

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Abstract

Range shifts due to annual variation in temperature are more tractable than range shifts linked to decadal to century long temperature changes due to climate change, providing natural experiments to determine the mechanisms responsible for driving long-term distributional

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shifts. In this study we couple physiologically grounded mechanistic models with biogeographic surveys in two years with high levels of annual temperature variation to disentangle the drivers of a historical range shift driven by climate change. The distribution of the barnacle *Semibalanus balanoides* has shifted 350 km poleward in the past half century along the east coast of the USA. Recruits were present throughout the historical range following the 2015 reproductive season, when temperatures were similar to those in the past century, and absent following the 2016 reproductive season when temperatures were warmer than they have been since 1870, the earliest date for temperature records. Our dispersal dependent mechanistic models of reproductive success were highly accurate and predicted patterns of reproduction success documented in field surveys throughout the historical range in 2015 and 2016. Our mechanistic models of reproductive success not only predicted recruitment dynamics near the range edge, but also predicted interior range fragmentation in a number of years between 1870 and 2016. All recruits monitored within the historical range following the 2015 colonization died before 2016 suggesting juvenile survival was likely the primary driver of the historical range retraction. However, if 2016 is indicative of future temperatures mechanisms of range limitation will shift and reproductive failure will lead to further range retraction in the future. Mechanistic models are necessary for accurately predicting the effects of climate change on ranges of species.

Introduction

Range edges of species are retracting in response to climate change (Parmesan *et al.*, 2003; Chen *et al.*, 2011). Population dynamics at range edges are highly complex, and often it is not a simple case of the inability to survive beyond the current edge, making it challenging to predict the rate and magnitude of these retractions (Hargreaves *et al.*, 2014).

Microhabitats can provide important thermal refugia (Lima *et al.*, 2016; Jurgens & Gaylord, 2018), physiological tolerances can vary throughout life history (Portner *et al.*, 2017), and dispersal can create both direct (Gaylord & Gaines, 2000; Alexander & Edwards, 2010) and indirect barriers through interactions with physiology and habitat availability (Travis & Dytham, 1999; Sorte *et al.*, 2018). The importance of variation in thermal responses throughout life history, and the interactions of this physiological variation with dispersal are important in determining range edges in a wide variety of systems (e.g. mammals: Anderson *et al.*, 2009; birds: Jiguet *et al.*, 2007; lizards: Buckley, 2008; plants: Broennimann *et al.*, 2006; butterflies: Crozier, 2004; fish: Walsh *et al.*, 2015; marine invertebrates: Sanford *et al.*, 2006). In many of these same systems early life history stages represent important population bottlenecks (Sinclair *et al.*, 2016). For example, phenological mismatch between hatching time of birds and food peaks can lead to population declines (Jiguet *et al.*, 2007), cold tolerance of butterfly larvae can play an important role in limiting colonization beyond the range edge (Crozier, 2004), viability of early life stages of fish drive much of the variation in population abundance (Peck *et al.*, 2012), and crab larvae are unable to complete development at locations where adults are able to overwinter (Sanford *et al.*, 2006). Very few studies, however, mechanistically consider how early life history stages and dispersal work interactively to influence range dynamics when predicting how climate change will alter distributions of species.

Correlative species distribution models (SDMs) are the most common approach to predicting changes in the distributions of species with climate change (Araújo *et al.*, 2005; Broennimann *et al.*, 2006; Araújo & Peterson, 2012). Correlative SDMs use the current distribution of adults and environmental data to predict the distributions of species. SDMs are then projected into novel environments to predict how distributions of species will be altered by climate change (Araújo *et al.*, 2005; Pearman *et al.*, 2008). While these

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approaches often yield accurate predictions, projections into novel environmental conditions can fail when the mechanism(s) limiting the distribution of species has changed, commonly known as a niche shift (Pearman *et al.*, 2008; Alexander & Edwards, 2010). Niche shifts can be driven by a release from dispersal barriers, rapid evolution, novel biological interactions, or novel climatological conditions (Soberón & Peterson, 2011; Woodin *et al.*, 2013).

Hindcasting, or projecting into past environmental conditions with historical records of the distribution for the target species, prior to predicting future changes in distribution is a good way to prevent inaccurate climate change predictions using SDMs (Araújo *et al.*, 2005; Lima *et al.*, 2007; Hilbish *et al.*, 2012). However, if range limiting mechanisms change through time model validation through hindcasting can still fall short. Mechanistic models based on organismal physiology (Kearney & Porter, 2009), which consider both species interactions (Araújo & Luoto, 2007) and dispersal (Broennimann *et al.*, 2006; Anderson *et al.*, 2009) can avoid these shortcomings of correlative SDMs. Mechanistic understanding of the drivers of range limits throughout life history is necessary to make accurate predictions about how species' distributions will shift with climate change (Southward *et al.*, 1995; Kearney & Porter, 2009; Sinclair *et al.*, 2016).

Shifts in distribution are occurring over decadal to centennial time scales (Parmesan *et al.*, 2003; Chen *et al.*, 2011; Southward, 1967; 1980; 1991; Hawkins *et al.*, 2008; 2009; Poloczanska *et al.*, 2008; Mieszkowska *et al.*, 2014a) making it difficult to determine the underlying mechanisms driving these changes, although associations with temperature fluctuations (Southward, 1967) and large scale oceanographic cycles like the North Atlantic Oscillation and the Atlantic Multidecadal Oscillation have been observed in some cases (Broitman *et al.*, 2008; Mieszkowska *et al.*, 2014b). Biological responses to climatic variation occurs over much shorter time scales (Harley, 2008; Coma *et al.*, 2009). Climatic variation can also cause rapid range shifts (Crisp 1964a; Crickenberger & Moran, 2013; Morley *et al.*,

2016), particularly near range edges where organisms live near their physiological limits for reproduction and survival (Hutchins, 1947; Wethey *et al.*, 2011). The shorter time-scale of climate variation can help inform long-term range dynamics and test the predictive accuracy of mechanistic species distribution models, but these types of comparisons are only possible in well-studied species.

Rocky intertidal invertebrates provide ideal systems for mechanistically testing the importance of multiple population bottlenecks throughout life history because adults are often sessile enabling environmental conditions experienced to be quantified, long distance dispersal can be modeled using hydrodynamic data, long-term remotely sensed data are available to estimate physical constraints on individuals and populations, and similarly long-term biogeographic patterns are well documented. As a result of these advantages, distributional shifts driven by both climate change and climate variation are well documented in marine invertebrate populations (Crisp, 1964a; Lima *et al.*, 2006; Helmuth *et al.*, 2006; Mieszkowska *et al.*, 2006; 2007; 2014a,b; Wethey & Woodin, 2008; Berke *et al.*, 2010; Keith *et al.*, 2011; Wethey *et al.*, 2011). However, it is often less clear which of the number of population bottlenecks throughout the life-histories of marine invertebrates determine their distribution and abundance (Pineda *et al.*, 2009). In many marine invertebrates early life-history stages and adults are decoupled in the habitats they occupy providing a variety of mechanisms that could potentially delimit range boundaries. Typically, adults must survive and reproduce in their benthic habitats to ensure the release of larvae into the plankton (Pechenik, 1990; Pineda *et al.*, 2009). Within the plankton larvae face a number of threats to survival including patchy food availability, phytoplankton mismatch, predation, and transport away from suitable habitat for settlement (Barnes 1956; Connell 1961; Hawkins & Hartnoll, 1982; Pineda *et al.*, 2009). Larval transport is dependent on both planktonic larval duration and the velocity and direction of oceanographic currents (Pineda *et al.*, 2007). Temperatures

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during the process of larval transport can influence both the length of larval development and the larval competency period, which is the period of time when larvae are capable of larval settlement and metamorphosis (Jackson & Strathmann, 1981). Therefore, temperature can influence how long larvae can remain viable in the plankton, or in other words their capacity for dispersal (Marsh *et al.*, 2001; Pineda *et al.*, 2007).

Here we use the barnacle *Semibalanus balanoides* as a model system to mechanistically model the importance of multiple population bottlenecks and dispersal on a range retraction driven by climate change because it is a well-studied marine invertebrate in terms of both its physiology and historical distribution (Darwin, 1854; Pilsbry, 1916; McDougall, 1943; Southward & Crisp, 1954; Crisp & Southward, 1958; Wells *et al.*, 1960; Mohammed, 1961; Barnes, 1963; Tighe-Ford, 1967; Crisp & Patel, 1969; Jones *et al.*, 2012; Rognstad & Hilbish, 2014). Reproduction, larval duration, and adult survival are all dependent on temperature in *S. balanoides*. Similar to other barnacles, *S. balanoides* is fertilized internally and then broods its embryos prior to release of stage I nauplii (Anderson, 1994). Larvae then develop through five more naupliar stages prior to metamorphosis to a non-feeding cyprid stage. Reported lengths of larval development to the cyprid stage vary from nine to 48 days depending on temperature (Barnes & Barnes, 1958; Harms, 1984). Cyprids can remain competent to settle for up to 30 days at 10°C, and the length of their competency period is dependent on the availability of stored energetic reserves because cyprids are unable to feed prior to metamorphosis to a juvenile barnacle (Lucas *et al.*, 1979). In the western Atlantic fertilization occurs between late October and November (Barnes, 1958; Barnes & Barnes, 1976; Yuen & Hoch, 2010). Following fertilization embryos develop within the mantle cavity prior to being released into the plankton as early as December (Fish, 1925; Barnes, 1956; Crisp, 1964b; Barnes & Barnes, 1976; J. Pineda pers. comm.). Fertilization is reduced at temperatures $\geq 16^{\circ}\text{C}$ in *S. balanoides* (Crickenberger &

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Wethey, 2017) and reproductive output is reduced when embryos are brooded at temperatures above 10°C (Barnes, 1963; Crisp & Patel, 1969; Drévès, 2001; Rognstad & Hilbish, 2014; Abernot-Le Gac *et al.*, 2016). Temperatures in the late fall and winter approach these thresholds at the historical southern limit of *S. balanoides* near Cape Hatteras North Carolina (Crickenberger & Wethey, 2017).

Historical records of biogeographic distribution dating back to the late 1800s place *S. balanoides* between Greenland (66.6°N) and Delaware Bay (38.8°N) in the western Atlantic (Darwin, 1854). Prior to the 1960s *S. balanoides* was restricted to shorelines north of Delaware Bay likely due to the lack of hard substrate further south (Barnes, 1958). Following the installation of hard substrates, such as groynes, jetties, seawalls, and piers, on more southern shorelines its range expanded to Cape Hatteras North Carolina (35°N; Wells *et al.*, 1960). A few individuals were found further south in Beaufort North Carolina in 1961 (34.7°N; Mohammad, 1961) where a study in the early 1940s did not find the barnacle when looking for it (McDougall, 1943). Various hypotheses have been proposed to explain the geographic distribution of the species. Hutchins (1947) suggested winter temperatures limited reproduction of *S. balanoides* to locations north of Cape Hatteras. Both summer and winter temperatures are highly divergent on either side of this major marine biogeographic barrier leading Wells *et al.* (1960) to also suggest *S. balanoides* had reached its thermal limits to reproduction and survival. More recent surveys of the southern range limit of *S. balanoides* found the range had retracted from Cape Hatteras to Lewes Delaware (Jones *et al.*, 2012). Additionally, they provided experimental evidence, and evidence from models based on field measurements of survival and temperature (e.g. Foster, 1969), that adult mortality was primarily responsible for the long-term range retraction, though reproductive failure may also play a role (Jones *et al.*, 2012). Here we coupled physiologically grounded dispersal dependent mechanistic models of multiple life history stages with biogeographic

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surveys to examine the role of early life history stages in driving the range of *Semibalanus balanoides* 350 km poleward.

Materials and methods

Distributional surveys

From 22 to 25 March 2015 a total of 7 sites between Manomet Massachusetts and Oregon Inlet North Carolina were surveyed for the presence of *Semibalanus balanoides* recruits (Fig. 1; Table 1). When recruits were present at a site four to six photographs with a scale in each photo were taken in the area of maximum abundance using an iPhone 5s. In each photograph we counted the number of cyprids, uncalcified pink recruits, and calcified white recruits. Recruits become calcified 5 d after settlement (e.g. Wethey, 1985). Following this initial survey a total of 15 sites within the area of range expansion were surveyed for the presence of adult *S. balanoides* and recruits between 06 April and 10 May 2015 (Fig. 1; Table 1). Surveys were repeated between 31 March and 09 May 2016 at all the same sites (Fig. 1; Table 1). Similar to other studies on rocky intertidal biogeography, each site was surveyed for the presence of adults and recruits for 30 min. If *S. balanoides* was not found during the 30 min survey it was considered absent (Crisp & Southward, 1958; Jones *et al.*, 2012). When adults or recruits were found, six photographic quadrats were taken in the zone of maximum abundance using a Nikon Coolpix AW100 or Olympus TG-4 camera attached to a camera framer with a 10 × 10 cm base (Jones *et al.*, 2010; Wethey *et al.*, 2011; Jones *et al.*, 2012). Densities of adults and recruits in photographs were quantified using ImageJ (Schneider *et al.*, 2012).

Reproductive success modeling

We modeled reproductive success to predict the number of recruits per 100 cm² using temperatures during the timing of fertilization (Barnes, 1958; Barnes & Barnes, 1976; Yuen & Hoch, 2010) and brooding (Fish, 1925; Barnes, 1956; Crisp, 1964b; Barnes & Barnes, 1976; J. Pineda pers. comm.) along the east coast of the USA, which are November and December respectively. We used the relationship between temperature and fertilization in Crickenberger & Wethey (2017) to model fertilization success and mapped this relationship using average November monthly sea surface temperatures (SST) between 1870 and 2016 from 1°×1° monthly Hadley SST data (HADISST, 2016; Rayner *et al.*, 2003; 2005). Then we used the relationship between recruitment and winter temperature during brooding from the 33-year time series in Abernot-Le Gac *et al.* (2016), and mapped this relationship using average December monthly SSTs between 1870 and 2016 from the 1°×1° monthly Hadley SST data to model how temperatures during brooding impacted recruitment success. We then multiplied predictions from the fertilization and recruitment maps to predict the geographic distribution of recruits per 100 cm² between 1870 and 2016 (see Crickenberger & Wethey, 2017 for more details). Additionally, we projected our fertilization and recruitment success models onto 0.05°×0.05° OSTIA SST data (OSTIA, 2016; Donlon *et al.*, 2011) for 2014 and 2015 to provide better spatial resolution in the years preceding our surveys of the southern range limit of *S. balanoides*. Poloczanska and others (2008) found June SST was the best predictor of *S. balanoides* abundance, and a good predictor of recruitment because recruitment is a major determinate of *S. balanoides* population abundance in subsequent years. Admittedly, June SSTs may capture the direct influence of temperature on larval and recruit survival because settlement time in the UK is typically between April and May, or may be a proxy for breeding success and larval survival because June SSTs were strongly correlated with SSTs and air temperatures in the preceding months (Poloczanska *et al.*, 2008).

In our models we used temperatures for the months when the processes of fertilization and brooding happen on the east coast of the USA to directly capture the effect of temperature on each of these processes.

For the two years when we measured field recruitment, 2015 and 2016, we additionally accounted for the influences of dispersal and adult density in our predictions of recruitment success. To account for dispersal, we considered the predicted connectivity (see Methods below) and predicted reproductive success at each source population where adults were present. To account for adult density we multiplied adult density by reproductive success at each source population before accounting for dispersal. One was added to adult density at all sites to adjust for very low densities at some sites. In total there were four models of reproductive success: 1) Brooding, 2) Brooding + Fertilization, 3) Brooding + Fertilization + Dispersal, 4) Brooding + Fertilization + Dispersal + Adult Density.

Fate of settlers

To track the survival of settlers within the region of range expansion six permanent 10 × 10 cm quadrats were established between 06 and 11 April 2015 on both north and south facing rocks at Oregon Inlet North Carolina (35.7715°N, 75.5284°W), Rudee Inlet Virginia (36.8304°N, 75.9671°W) and Lewes Delaware (38.7911°N, 75.1584°W). Quadrats were photographed every one to two months. At each sampling interval thermochron iButton dataloggers (Maxim Semiconductor, Dallas, Texas, USA) were deployed to measure temperature and attached next to quadrats using the two part marine epoxy Z-Spar Splash Zone Compound A-788 (Kop-Coat Marine Group, Rockaway, New Jersey, USA). Survival of barnacles within the quadrats was modeled using minimum daily temperatures from

Button temperature records and laboratory experiments examining the relationships between temperature and survival (Foster, 1969; Jones *et al.*, 2012; Mislan *et al.*, 2014).

Dispersal modeling

We modeled competency-dependent dispersal with the Ichthyop Lagrangian transport simulator (version 3.3, Lett *et al.*, 2008) using the Naval Oceanographic Office Regional Navy Coastal Ocean Model (NCOM, Martin *et al.*, 2009; NCOM, 2017). The NCOM model has a $1/30^\circ$ grid (~ 3 km) and velocity fields and temperatures are available at 3 h intervals. At each site where recruits were found in our field surveys between 06 April and 10 May 2015 we modeled dispersal in reverse to determine potential origins of these recruits by tracking the dispersal trajectories of 1,000 particles backwards in time from each site. Potential larval recruitment dates from February 15 to May 31 were used in the simulations. At midnight GMT on each recruitment date, 1000 passive particles (larvae) were released in a 5 km diameter circle centered on the recruitment location. Their locations were projected backwards in time for 60 days, using a 5 min time step and Euler's method for integration in Ichthyop, using the mean velocity fields from the top 10 m of the water column. Geographic positions of all particles and the mean temperature in the top 10 m of the water column at each particle location were saved every 30 min.

Barnacle larvae grow through multiple naupliar stages, and then metamorphose into a non-feeding cyprid larval stage. We modeled growth of nauplii as a function of temperature, using data from Harms (1984)

$$\text{Length}(t + dt) = \text{Length}(t) + (0.021 + 0.00375 \times T(\text{lon}, \text{lat}, t)) \times dt$$

(Eq. 1)

where the model time step dt was 5 min, and $T(\text{lon}, \text{lat}, t)$ was the water temperature in °C at the particle location (lon, lat) at time t . We assumed larvae at hatching were 0.3 mm long, and the transition from nauplius to cyprid occurred at 1.3 mm.

Cyprid larvae kept for up to 30 d at 10°C can settle and metamorphose successfully (Lucas *et al.*, 1979). Since cyprids do not feed, this duration of competence to settle and metamorphose is related to the temperature-dependent rate of metabolism of the stored lipid in the larva. We modelled the effect of temperature on the duration of cyprid competence to settle and metamorphose successfully using the same function used to model larval growth (Eq 1). Cyprids do not grow, but we used modelled growth as a proxy for competence, by determining the size that a hypothetical growing cyprid would be after 30 d at 10°C ($LC_{\text{max}}=3.2$ mm). At lower temperatures cyprids remain competent longer, and at higher temperatures cyprids remain competent for shorter times, using the time to reach LC_{max} as the upper limit for competence as a function of temperature. To set bounds on recruitment, we assumed that cyprids settling on a particular date could be any age between a cyprid newly metamorphosed from nauplius stage VI, and a cyprid at its temporal limit for competence (equivalent to 30 d at 10°C). Working backwards from these points, we calculated the number of days along the specific trajectory that it would take a larva to grow from egg hatching to the youngest or oldest possible cyprid stages. This calculation allowed us to calculate the potential starting locations of larvae, as all coastal points less than 2.5 km away from the particle between the earliest and latest possible larval release dates. We repeated this process for the same potential larval recruitment dates using NCOM data from 2014, 2015 and 2016.

Data analysis

Predictive accuracy of the reproductive success models was assessed by comparing predicted recruitment to observed recruitment using data from our 2015 and 2016 surveys. To calculate model accuracy and bias (Finley, 1884; Liu *et al.*, 2011) we considered predictions less than 1 individual per 100 cm² equivalent to zero recruitment when using Hadley SST (HADISST, 2016; Rayner *et al.*, 2003; 2005) and predictions less than 10 equivalent to zero recruitment for OSTIA SST data (OSTIA, 2016; Donlon *et al.*, 2011). Model accuracy ranges from 0 to 1 with 1 being a perfect score. A perfect score for model bias is 1 with values less than 1 indicating underprediction and values greater than 1 indicating overprediction. Area Under the Curve (AUC) scores were calculated to compare predictive accuracy of each reproductive success model over a range of thresholds (AUC values of 0.5 indicate the model predictions are no better than random, 1 is a perfect score). AUC scores were compared with one-tailed DeLong tests, using the R package pROC (Robin *et al.*, 2011). Log-log linear regressions were used to assess the ability of the reproductive success models to accurately predict the magnitude of recruitment. Realized connectivity was calculated as the product of estimated connectivity and adult density in 2015 and 2016. All analyses were run in R (R 3.1.0, R Core Team, 2014).

Results

Distributional surveys

In the March 2015 surveys cyprids and pink uncalcified recruits were found at all sites surveyed except for Manomet Massachusetts. Calcified recruits were present at all sites except for Ocean City Maryland, Guilford Connecticut and Manomet Massachusetts (Fig. 2, Fig. 3). During the 2015 surveys conducted in April and May all sites had recruits present,

while adults were present at Duck Pier North Carolina, Rudee Inlet Virginia, Kitopeke Virginia, Cape Charles Virginia, Chincoteague Virginia, Ocean City Maryland, Indian River Inlet Delaware and Lewes Delaware (Fig. 3). During the 2016 surveys recruits were present at six of 15 sites and limited to sites on the Delmarva Peninsula (peninsula between Chesapeake Bay and Atlantic Ocean, see Fig. 1). Adults were present in 2016 at Jennette's Pier North Carolina, Duck Pier North Carolina, Rudee Inlet Virginia, Chincoteague Virginia, Ocean City Maryland, Indian River Inlet Delaware and Lewes Delaware (Fig. 3).

Reproductive success modeling

Reproduction was predicted to be possible just north of the historical range limit near Cape Hatteras North Carolina (35.5°N) between 1870 and 2014 with a poleward shift in 2015. In the spring of 2016 the southern extent of recruitment closely matched the predicted southern limit to reproductive success (Fig. 3, Fig. 4). Predictions of reproductive success based on Hadley SST (1° x 1°, ~100 km) were further north than those using OSTIA SST (0.05°x0.05°, ~5 km) due to the difference in spatial scale of the two different SST datasets and the lack of consideration of larval dispersal, which improved model predictions (Fig. 3, Fig. 4, Table 2). In 1948, 1986, 1999, 2001, and 2015 reproductive failure was predicted within the interior of the range of *S. balanoides* (Fig. 4). Predictions of reproductive success and failure were similar to field measurements of recruitment and each additional factor improved model accuracy (Table 2). Models of reproductive success were good predictors of the magnitude of reproduction, particularly the full model (Brooding + Fertilization + Dispersal + Adult Density) which explained ~70% of the variance (Table 2). The analysis of the Area Under the Curve (AUC) of the Receiver-Operator-Characteristic (ROC) for the models indicated an improvement from AUC=0.76 for the Brooding + Fertilization model, to AUC=0.94 for the Brooding + Fertilization + Dispersal model, to AUC=0.97 for the

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Brooding + Fertilization + Dispersal + Adult Density model. The incremental improvement of the full model (B+F+D+A) significantly improved AUC when compared to the models without dispersal ($p=0.02$ in both cases). Based on this analysis, the full model generates almost perfect predictions.

Fate of settlers

All settlers were dead by October (Fig. 5). Settlers died earlier in south facing sites when compared to north facing sites (Fig. 5). Temperatures exceeded the temperature for heat coma at 35°C on both north and south facing rocks at all sites, but only exceeded the lethal temperature at 44°C for *S. balanoides* (Foster, 1969) on south facing rocks at Rudee Inlet and Oregon Inlet (Fig. 5). Models of cumulative survival closely matched both the magnitude and timing of observed patterns of survival (Lewes Delaware: North $R^2=0.87$, South $R^2=0.62$; Rudee Inlet Virginia: North $R^2=0.90$, South $R^2=0.62$; Oregon Inlet North Carolina: North $R^2=0.85$, South $R^2=0.91$). Predicted timing of 50% mortality was within two weeks of model predictions (13.5 days \pm 5.3 days) (Fig. 5).

Dispersal modeling

Estimates of connectivity were similar among years (Fig. 6, Fig. S1, S2, S3, Table S1). Connectivity estimates suggest recruits at sites along the outer coast of the Delmarva Peninsula were from that region. Recruits at Cape Charles and Kitopeke also likely originated from the outer coast of the Delmarva Peninsula. The other sites within the Chesapeake Bay had limited connectivity with sites outside of Chesapeake Bay (Fig. S1, S2). Sites near the mouth of the Chesapeake Bay (Kitopeke and Rudee Inlet) were connected to sites both within and outside of the bay (Fig. 6, Fig. S1, S2). The southern coastal sites

between Rudee Inlet and Oregon Inlet had high levels of connectivity with both the northern sites on the outer coast of the Delmarva Peninsula and the other southern coastal sites (Fig. 6., Fig. S1, S2).

When dispersal is considered in the context of the distribution and reproductive potential of adults in source locations, the predicted recruitment patterns are very consistent with the actual distribution of recruits (Table 2). There was low to no observed recruitment in sites with high connectivity to sources outside the permissive zone for reproduction, and recruitment was observed in sites with high connectivity to sources within the permissive zone for reproduction (Table 2, Fig. 6, Fig. S2). We incorrectly predicted recruitment failure in 2016 at Cape Charles (Table 2, Fig. S2). Presumably this is because we did not find the actual source population of adults, which was likely in the upper Chesapeake Bay (Fig. S1). We predicted extremely low probability of recruitment ($p < 10^{-3}$) at the southernmost sites in 2016 (Kitty Hawk, Jennette's Pier, and Oregon Inlet North Carolina) and did not observe any recruitment that year (Table 2, Fig 6, Fig. S2). We correctly predicted recruitment at all sites in 2015 (Table 2, Fig 6, Fig. S2).

Discussion

Climate change is altering the distribution and abundance of species over decadal to centennial time scales making identification of the mechanisms driving these changes challenging (Parmesan *et al.*, 2003; Chen *et al.*, 2011). Biological responses to climate variation over shorter time scales can provide both a window into the past as well as the future to understand the drivers of changes on the distribution and abundance of species (Wetthey *et al.*, 2011). The southern range limit of *S. balanoides* has retracted poleward 350 km on the east coast of the USA in the past 50 years (Jones *et al.*, 2012). Following the

colder than average winter of 2014/2015 we found recruits as far south as the historical southern range limit of *S. balanoides* near Cape Hatteras North Carolina. We used the presence of *S. balanoides* throughout the historical range of *S. balanoides* as an opportunity to test which mechanisms are responsible for driving the long-term range retraction.

No single mechanism limited the distribution of *S. balanoides*. Predictions of the southern limits of reproductive success between 1870 and 2014 remained relatively unchanged (Fig. 4). Historically, reproductive failure likely limited the colonization of sites south of Cape Hatteras, but does not explain the range retraction documented in 2007. However, the predicted poleward movement of the limit to reproductive success in the winter of 2015/2016 suggests that reproductive failure may play an increasingly important role in limiting the distribution of *S. balanoides* in the future (Fig. 4).

Recruitment can be the main determinate of adult density in *S. balanoides* (Svensson *et al.*, 2004; 2005; Poloczanska *et al.*, 2008). Within the interior of the range reproductive failure was predicted in 1948, 1986, 1999, 2001, and 2015. The abundant center hypothesis predicts species should be most abundant at the center of their distributions and decrease in abundance towards the periphery (Andrewartha & Birch, 1954). Empirical evidence to support this idea is limited at best, and runs counter to the idea of troughs or gaps in abundance within the interior of species' distributions (Sagarin & Gaines, 2002; Sagarin *et al.*, 2006), which were predicted by our reproductive success model (Fig. 4). In terrestrial ecosystems predictions of interior, climate-mediated range fragmentation are not uncommon (Calkins *et al.*, 2011; Jeffress *et al.*, 2013; Stewart *et al.*, 2015). In marine ecosystems evidence for these types of patterns is limited (but see Lima *et al.*, 2006; 2007). For example, models from Wethey *et al.* (2011; 2016) predicted climate-mediated interior range fragmentation for the polychaetes *Diopatra* spp. and *Arenicola marina*, and to a lesser extent for the barnacles *S. balanoides* and *Chthamalus* spp. along the coastline of continental

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Europe. Interior range fragmentation in marine organisms with high dispersal capacity may be challenging to detect when compared to terrestrial organisms with more limited dispersal. In marine organisms, regions of interior range fragmentation are likely ephemeral and filled in by adjacent source regions in subsequent years (e.g. Lima *et al.*, 2006; Sousa *et al.*, 2012). In our predictions we did not find more than a single year with reproductive failure (Fig. 4), making a scenario of ephemeral failure and range filling plausible.

Other factors during the larval period could also generate within range gaps of distribution or dips in abundance. Mismatched timing of larval release and the phytoplankton bloom can result in near recruitment failure (Barnes 1956, 1957, 1962; Crisp & Spencer, 1958; Hawkins & Hartnoll, 1982; Kendall *et al.*, 1985), and the probability of phytoplankton mismatch is high within the interior of some portions of the range of *S. balanoides* in Europe matching dips in abundance of *S. balanoides* (Crickenberger & Wethey, 2017). Larval transport both near shore, and at larger spatial scales, can also influence site specific recruitment rates of *S. balanoides* and other barnacles along complex coastlines (Bennell, 1981; Hawkins & Hartnoll, 1982; Kendall *et al.*, 1982; Burrows *et al.*, 2010; Keith *et al.*, 2011). Near the range edge along the east coast of the USA phytoplankton mismatch is extremely unlikely (Crickenberger & Wethey, 2017), and we found limited evidence of oceanographic currents generating a dispersal barrier for *S. balanoides*. Further north in the Gulf of Maine the probability of phytoplankton mismatch is higher (Crickenberger & Wethey, 2017), and complex oceanographic processes may create barriers to larval dispersal (Yund *et al.* 2015), potentially leading to dips in abundance of *S. balanoides* within some sites in this region similar to those documented in Europe.

Settlers did not survive in any of the monitored quadrats, and all were predicted to die from exposure to several warm days in a row (Fig. 5). However, in both 2015 and 2016 adult barnacles were present at southern, shaded microhabitats on the outer coast following years when reproductive success was predicted to be high (Fig. 3). These shaded coastal microhabitats (Jennette's Pier and Duck Pier) are not dependent on stepping-stone dispersal and may receive recruits annually from further north in addition to local sources of recruits when temperatures are permissive to reproduction (Fig. 6, Fig. S1, S2). In contrast, colonization of sites near and within the Chesapeake Bay appear to be dependent on stepping-stone dispersal through either successful recruitment and survival at sites near the mouth of the bay followed by temperatures permissive to reproduction in the subsequent winter or cooler winters permissive of reproduction at more southern sites (Fig. 3, Fig. 6, Fig. S1, S2). Microhabitats are known to play an important role in altering patterns of survival in intertidal invertebrates (Wetthey, 1983; Jones *et al.*, 2012; Jurgens & Gaylord, 2018), particularly near retracting range edges (Lima *et al.*, 2016). The persistence of *S. balanoides* in cooler microhabitat sites will be dependent on the density and reproductive success of other populations further upstream. If adult density and reproductive success continue to decrease along the Delmarva peninsula these microhabitat populations will go extinct, through either the direct lethal effects of temperature, or possibly through indirect effects on recruitment.

Larval competency period is often cited as limiting connectivity in benthic marine organisms (Jackson & Strathmann, 1981; Marsh *et al.*, 2001), and connectivity is predicted to decrease in warmer oceans due to faster larval growth and a reduction in competency period (O'Connor *et al.*, 2007). Cooler temperatures during the winter of 2014/2015 led to successful reproduction and recruitment throughout the historical range of *S. balanoides*, while warmer temperatures during the winter of 2015/2016 reduced reproductive success and recruitment throughout the historical range (Fig. 3). Interestingly, predicted patterns of

connectivity among southern coastal sites and more northern sites were similar in 2015 and 2016, despite their differences in temperature (Fig. 6, Fig. S1, S2, S3, Table S1). Therefore, we did not find any evidence that temperature dependent competency period limited connectivity from our models. Instead, limited patterns of colonization documented in 2016 may have been driven by both a more restricted distribution of adults and a reduced larval pool due to warmer temperatures during the processes of fertilization and brooding as suggested by our reproductive success models and recruitment surveys in 2016 (Fig. 6, Fig. S2).

Population dynamics near the range edges of species with long distance dispersive life history stages are complex making the mechanisms responsible for limiting distributions difficult to isolate (Broennimann *et al.*, 2006; Jiguet *et al.*, 2007). Climate variation coupled with mechanistic modeling is a useful way to understand the relative contribution of various life-history stages to determining range limits. In *S. balanoides* reproductive failure did not explain historical patterns of range retraction. However, the magnitude of reproductive success did influence connectivity, which likely determines whether or not *S. balanoides* populations at southern, shaded microhabitats are able to persist (Fig. 6, Figure S2). This complexity leads to an uncoupling from large scale oceanographic patterns like the Atlantic Multidecadal Oscillation; for example mean annual AMO (NOAA, 2018) was only weakly correlated to predicted recruitment success at some latitudes (linear regressions, $p=0.004$ to 0.06 , $R^2=0.002$ to 0.06). Mechanistic understanding of range limitation is essential for predicting how species will respond to future environmental conditions (Kearney & Porter, 2009; Seabra *et al.*, 2015). In most cases mechanistic models are validated by comparing predictions of historical and current distributions prior to making future predictions. If the winter of 2015/2016 is an indicator of future environmental conditions, reproductive failure will become increasingly important in mediating the persistence of *S. balanoides* at its southern

range limit in the western Atlantic meaning mechanisms of range limitation can change through time. Mechanistic models which consider the entire life-histories of organisms are the only way to capture these types of changes in range limiting mechanism through time and accurately predict the consequences of climate change on future distributions.

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Tables

Table 1. Sites surveyed for the presence of *Semibalanus balanoides* adults and recruits.

Site Name	Abbreviation	Latitude	Longitude	Dates Surveyed
Manomet, MA	MA	41.9272	-70.5413	23-03-2015
Guilford, CT	GU	41.2592	-72.7309	22-03-2015
Lewes, DE	LE	38.7911	-75.1584	24-03-2015, 11-04-2015, 31-03-2016
Indian River Inlet, DE	IR	38.6076	-75.0608	24-03-2015, 10-04-2015, 31-03-2016
Ocean City, MD	OC	38.3243	-75.0851	24-03-2015, 10-04-2015, 31-03-2016
Chincoteague Island, VA	CI	37.9010	-75.4075	10-05-2015, 01-04-2016
Cape Charles, VA	CC	37.2668	-76.0263	09-04-2015, 01-04-2016
Kitopeke State Park, VA	KP	37.1673	-75.9887	09-04-2015, 01-04-2016
Fort Monroe, VA	FM	37.0022	-76.3029	09-04-2015, 02-04-2016
East Ocean Ave, VA	EO	36.9503	-76.242	09-04-2015, 02-04-2016
East Beach, VA	EB	36.9306	-76.1828	09-04-2015, 02-04-2016
Lynnhaven Pier, VA	LP	36.9135	-76.0778	10-04-2015, 02-04-2016
Rudee Inlet, VA	RI	36.8304	-75.9671	25-03-2015, 08-04-2015, 02-04-2016
Duck Pier, NC	DP	36.1823	-75.7503	07-04-2015, 09-05-2016
Kitty Hawk Pier, NC	KH	36.1014	-75.7109	07-04-2015, 04-04-2016
Jennette's Pier, NC	JP	35.9101	-75.5954	07-04-2015, 04-04-2016
Oregon Inlet, NC	OI	35.7715	-75.5284	25-03-2015, 06-04-2016

Table 2. Verification statistics, AUC groupings based on one-tailed DeLong tests, coefficients of determination, and *p*-values for log-log regressions of observed vs. predicted recruitment for predictions of models of reproductive success. Accuracy and bias estimates assume predictions less than 1 individual per 100 cm² are predictions of zero recruitment for Hadley SST source and predictions less than 10 are predictions of zero recruitment for OSTIA SST source. Accuracy ranges from 0 to 1 with 1 being a perfect score. A perfect score for model bias is 1 with values above 1 indicating overprediction and values less than 1 indicating underprediction. AUC values of 0.5 indicate the model predictions are no better than random and 1 is a perfect score. Letters for AUC groups indicate significant differences between models for each SST source (*p* < 0.05). B=Brooding, F=Fertilization, D=Dispersal, A=Adult.

Model	SST source	Accuracy	Bias	AUC	AUC Groups	R ²	<i>P</i> (regression)
B	Hadley	0.8	1.10	0.76	A	0.203	0.007
B+F	Hadley	0.80	1.10	0.76	A	0.177	0.01
B+F+D	Hadley	0.90	0.95	0.94	AB	0.606	<0.0001
B+F+D+A	Hadley	0.93	0.90	0.97	B	0.695	<0.0001
B	OSTIA	0.87	1.19	1.0	A	0.622	<0.0001
B+F	OSTIA	0.87	1.19	1.0	A	0.626	<0.0001
B+F+D	OSTIA	0.93	0.90	1.0	A	0.75	<0.0001
B+F+D+A	OSTIA	0.93	0.90	0.97	A	0.787	<0.0001

Figure captions

Fig. 1. Sampling sites for *Semibalanus balanoides* (a) along the entire east coast of the USA and (b) in the region of range retraction and recolonization. Black box in (a) outlines the enlarged region in (b). See Table 1 for site abbreviations.

Fig. 2. Density (mean \pm SE, n=4-6) of *Semibalanus balanoides* cyprids, pink uncalcified recruits, and white calcified recruits between 22 and 25 March 2015. Sites listed north to south. See Table 1 for site abbreviations.

Fig. 3. Distribution and abundance of *Semibalanus balanoides* along the east coast of the USA between (a) between 1854 and 1916 (Darwin, 1854; Pilsbry, 1916), (b) between 1942 and 1963 (McDougall, 1943; Wells *et al.*, 1960; Jones *et al.*, 2012), and (c) in 2007 (Jones *et al.*, 2012). The distribution and abundance of the total number of *Semibalanus balanoides* cyprids, pink uncalcified recruits, and white calcified recruits between (d) 22 and 25 March 2015. Distribution and abundance of *Semibalanus balanoides* (e) adults and (f) recruits in April to May 2015 and (g) adults and (h) recruits in March to May 2016. Total reproductive success contour at 25 recruits per 100 cm² (grey line), in (f) Recruits 2015 and (h) Recruits 2016, corresponds to a nearest neighbour distances of 1 cm, which is the limiting distance for successful mating of neighbouring barnacles assuming individuals are evenly distributed. ACFORN density scales after Crisp & Southward 1958: A= abundant, C= common, F= frequent, O= occasional, R= rare, N= none. Recruit densities are based on a similar scale where A = 10 to 100 individuals cm⁻², C = 1 to 10 individuals cm⁻², F = 0.1 to 1 individuals cm⁻², O = .01 to 0.1 individuals cm⁻², R = 0 to .01 individuals cm⁻², and N = 0 individuals cm.

Fig. 4. Predicted recruits per 100 cm² of *Semibalanus balanoides* between (a) 1870 and 2016 and (b) 1980 and 2016 to illustrate the occasional range fragmentation in the southern portion of the range. Interior range fragmentation due to reproductive failure was predicted in 1948, 1986, 1999, 2001, and 2015. White regions had predictions of fewer than 25 recruits per 100 cm² corresponding to a nearest neighbour distances of 1 cm, which is the limiting distance for successful mating of neighbouring barnacles assuming individuals are evenly distributed. Historical southern range limits (black squares), record of a single *Semibalanus balanoides* (black circle), and southern limit of recruits found in the spring of 2015 and 2016 (black triangles).

Fig. 5. Predicted (lines) and mean observed (circles) cumulative percent survival of *Semibalanus balanoides* in quadrats (n=6) on north (black circles, solid lines) and south (white circles, dashed lines) facing rocks at (a) Lewes Delaware, (d) Rudee Inlet Virginia, and (g) Oregon Inlet North Carolina. Temperatures from iButtons at Lewes Delaware on (b) north and (c) south facing rocks, at Rudee Inlet Virginia on (e) north and (f) south facing rocks, and at Oregon Inlet North Carolina on (h) north and (i) south facing rocks. Horizontal lines indicate the acute temperature limits to heat coma (35°C, Southward 1964) and the acute lethal limit (44°C, Foster 1969). Models of cumulative survival closely matched observed patterns of survival (Lewes, DE: North R²=0.87, South R²=0.62; Rudee Inlet, VA: North R²=0.90, South R²=0.62; Oregon Inlet, NC: North R²=0.85, South R²=0.91).

Fig. 6. Predicted patterns of realized connectivity (connectivity adjusted for observed adult density in the source population) in 2015 and 2016 in representative sites in the northern (IR: Indian River Inlet Delaware), central (KP: Kitopeke State Park Virginia and RI: Rudee Inlet

Virginia), and southern portion (JP: Jennette's Pier North Carolina) of the region studied.

Circles represent source locations for larvae (\log_{10} of fraction of particles in competency dependent dispersal models) and plus symbols (+) and arrows indicate the location of each site of recruitment. Open squares represent locations of observed recruitment in each year.

Populations north of the contour (gray line) were predicted to be reproductively successful (> 25 recruits per 100 cm^2) and populations south of the contour were predicted to experience reproductive failure (< 25 recruits per 100 cm^2).









