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On the edge: demography across latitudinal and elevational gradients for range-expanding whelks

Heidi R. Waite*, Ryan A. Beshai, Cascade J. B. Sorte

Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697-2525, USA

*Corresponding author: hwaite@uci.edu

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ABSTRACT: Marine species worldwide are responding to ocean warming by shifting their ranges to new latitudes and, for intertidal species, elevations. Demographic traits can vary across populations spanning latitudinal and elevational ranges, with impacts on population growth. Understanding how demography varies across gradients from range center to edge could help us predict future shifts, species assemblages, and extinction risks. We investigated demographic traits for 2 range-expanding whelk species: *Acanthinucella spirata* and *Mexacanthina lugubris.* We measured reproductive output across environmental (latitudinal and shore elevation) gradients along the coast of California, USA. We also conducted intensive measurements of offspring condition (survival and thermal tolerance) across shore elevation for *M. lugubris* at one site. We found no difference in reproductive output, body size, or larval survival across shore heights for *M. lugubris,* suggesting that egg-laying behavior buffers developing stages from the relatively high level of thermal variation experienced due to daily tidal emersion. However, across latitudes, reproductive output increased toward the leading range edge for *A. spirata*, and body size increased for both species. Increased vital rates at the leading range edge could increase whelk population growth and expansion, allowing species to persist under climate change even if contractions occur at trailing edges.

KEY WORDS: Range shift · Carryover effects · Climate change · Egg laying · Reproduction · Intertidal

1. INTRODUCTION

As oceans warm at unprecedented rates due to climate change, species worldwide are responding by shifting their ranges to new latitudes and depths (Pecl et al. 2017). Range shifts are leading to cascading changes in population dynamics and ecosystem functioning (Xue et al. 2019), yet processes underlying range shifts are understudied in marine compared to terrestrial systems (Donelson et al. 2019). Sagarin et al. (2016) described demographics, physiology, genetics, and physical factors as key data for teasing out processes determining species ranges. In particular, Angert et al. (2011) showed that reproduction is a key demographic trait which influences colonization and establishment rates in a range-expanding species. Additionally, patterns of abundance and key demographic rates such as reproductive output underlie species range limits and population dynamics (Sagarin et al. 2006), and understanding these patterns can increase our ability to predict future species movement, assemblages, and extinction risks (Urban et al. 2013).

Vital rates, particularly reproductive output, are expected to be lower at leading range edges in expanding species (Buckley et al. 2021). This pattern potentially occurs because novel environmental conditions lead to increased metabolic demand and resource allocation tradeoffs at the range edge, causing abundances to peak at the range center and decline toward range edges (Sagarin et al. 2006). At range edges with theoretically suboptimal environments for expanding species, survival would be prioritized and reproductive output reduced; by contrast, toward the range center, more energy would be invested in growth and reproduction (Sagarin et al. 2006). Lower reproductive output at range margins could also occur because of increased investment towards traits that favor dispersal, and less towards reproduction, growth, or other life history traits (Chuang & Peterson 2016). Finally, range edge populations may experience Allee effects, with lower population size reducing reproductive output due to limited availability of mates and skewed sex ratios (Chuang & Peterson 2016).

Despite theory supporting an expectation of low reproductive output at range edges, evidence for this pattern is mixed (e.g. Sagarin et al. 2006), and some species have increased reproductive output at expanding edges. For non-native invasive species, range-shifting species may experience competitive release and encounter naïve prey at expanding range edges, leading to increased energy for reproduction (Lester et al. 2007). Reproductive output might also be influenced by environmental (e.g. temperature; Helmuth et al. 2006) and biotic factors that vary inconsistently across latitude. Mesoscale variation between sites likely influences reproductive output, such as for the sea urchin *Centrostephanus rodgersii* (Ling et al. 2008) and the purple urchin *Strongylocentrotus purpuratus* (Lester et al. 2007).

Reproductive success is measured in both output (quantity of offspring per female) and offspring condition, which can carry over into later life stages and varies across environmental gradients. For example, in the mussel *Mytilus californianu*s, offspring from range-edge (upper shore elevation) adults hatched from smaller eggs (indicating lower maternal investment per individual) and were less tolerant to thermal stress (Waite & Sorte 2022). Given that younger life stages are particularly vulnerable to environmental stress (Pandori & Sorte 2018), offspring survival is another key response that can give us insight into the expansion potential of range-shifting species. Overall, faster spread is expected when reproductive output and offspring condition are higher at the range edge than in the range center (Chuang & Peterson 2016).

The aim of this study was to evaluate key demographic traits across environmental gradients for 2 range-expanding whelks: *Acanthinucella spirata* and *Mexacanthina lugubris*. These whelks inhabit the intertidal zone of eastern Pacific rocky shores and are expanding their ranges northward along the west coast of North America. During the Pleistocene, *A. spirata* underwent a >400 km range expansion north of Point Conception, extending to Tomales Bay, California. Since 2017, this species has expanded further, now occurring from Punta Baja, Mexico, to Cape Mendocino, California (Flagor & Bourdeau 2018). Similarly, over the past ~50 yr, *M. lugubris* has expanded its northern range boundary by ~250 km and now extends from Baja California, Mexico, to Laguna Beach in southern California (Fenberg et al. 2014, Wallingford & Sorte 2022). Understanding the range-shift potential of these species is especially important, as both are top predators in rocky intertidal ecosystems (Fenberg et al. 2014, Zimmer et al. 2016). Novel top predators can have large disruptive impacts on communities (Borer et al. 2006, Pecl et al. 2017).

To evaluate the range shift potential of these 2 whelk species, we combined a survey of demographic rates and population sizes across a broad latitudinal gradient with an intensive local experiment of offspring condition across a shore height gradient. We first asked: how does reproductive output and adult size vary across latitude and shore height? These whelks reproduce locally by depositing eggs in capsules within aggregations (‘masses’) attached to the substratum, and often in rock crevices or among mussel beds (Flagor & Bourdeau 2018). Embryos develop into larvae inside egg capsules, eventually hatching as juveniles. Reproductive output has several components, including the total number of egg capsules and number of offspring per capsule. Our study focuses on the former. We surveyed egg capsules of both species in the intertidal zone across >1000 km of California coastline, spanning the species’ range centers to northern leading edges. Given the theory described above, we hypothesized that whelks lay more egg capsules at their range center than at the range edge.

Second, to better understand how variation in demographic rates across environmental gradients influences offspring condition, we asked: does elevation of whelk egg-laying affect survival and thermal tolerance of offspring? As a case study, we quantified effects of laying location across a shoreline elevation gradient on offspring of *M. lugubris*. We hypothesized that condition (survival and thermal tolerance) is lower for larvae from eggs laid at higher shore heights (more thermally stressful environments) due to tradeoffs between survival and reproduction in parents.

2. MATERIALS AND METHODS

2.1. Study sites

We surveyed the intertidal zone at 19 sites across California to quantify demographic traits of *Acanthinucella spirata* and *Mexacanthina lugubris* (Fig. 1, Table 1). Given latitudinal differences in reproduction timing, sites in southern and northern California were surveyed in April and June 2022, respectively (for details on the timing of egg surveys, see Text S1 in the Supplement at XXXXXXXXXXXXXXXXXXXXXXX). Additionally, we conducted a field study of *M. lugubris* near its range edge at Thousand Steps Beach, Laguna Beach, California, from April to July 2022.

2.2. Latitudinal surveys

At each site, we conducted 2 timed searches (1 h each) in the intertidal zone: 1 for whelks and 1 for egg capsules (see Text S2 for details of our survey approach). For adult whelks, we recorded the species, size (total length in mm, using calipers), and shore height where they were found (m above mean lower-low water, using a laser level and tidal predictions from Willyweather.com). For egg capsules, we took photos and recorded number and species of snails nearby and shore height. Measurements and photos were taken during each timed search.

We used the survey data to calculate total number of egg capsules and adult whelks per site. Each egg mass was assigned to species based on morphology of egg capsules themselves and whelk species congregated nearby. We quantified number of egg capsules per mass from photos using Image J (Version 1.51, National Institute of Health, Bethesda, MD, USA), by counting capsules within a subsample area of the photo and extrapolating across the total area. Total egg capsules per site were calculated by counting the capsules from all masses at each site. For each site, we estimated adult whelk population size as the total number of whelks counted during the 1 h search and body size as the mean size of whelks found.

We conducted GLM analyses in R (R Core Team 2020) to test effects of latitude on (1) reproductive output for each species using total number of capsules per site as our fecundity metric, (2) average shore height of egg capsules per site for each species, and (3) adult whelk sizes (using a Gamma distribution due to non-normality). We used Gaussian distributions for GLM analyses unless otherwise specified. We also conducted a multiple regression analysis with latitude and adult abundance as potential drivers of reproductive output (number of egg capsules per site).

2.3. Field experiment across a shoreline elevation gradient

To quantify effects of shore height of eggs on offspring survival, we conducted an intensive field study of *M. lugubris* near its range edge at Thousand Steps Beach, California (Text S3). Briefly, we determined thermal stress experienced by egg capsules across shore heights using temperature dataloggers and calculated mean daily maximum temperatures. Egg capsules spanning the shoreline were allowed to develop in the field to the pre-competent larval stage, when 1 capsule per egg mass was collected for thermal survival trials (as in Waite & Sorte 2022; details in Methods S3). Capsules were collected from centers of egg masses to avoid differences in temperature exposure. We placed 3 larvae from each capsule in 1.5 ml plastic centrifuge tubes filled with seawater and exposed each tube to of 5 temperatures (control, 32, 35, 38, and 40°C) for 1 h (see Methods S3 for details). After the thermal exposure, survival was evaluated by visually inspecting larvae for movement under a dissecting microscope. We calculated LT_{50} values (temperature at which 50% of individuals die) using binomial regressions between assay temperatures and larval survival. A GLM analysis (Gaussian distribution) in R was used to test the effect of shore height on field thermal exposure and LT_{50} values (with larval length as a covariate).

3. RESULTS

Reproductive output (total egg capsules per site) increased with latitude towards the range edge for *Acanthinucella spirata* ($t = 4.01$, df = 6, $p = 0.0103$) but not for *Mexacanthina lugubris* ($t = 0.78$, df = 3, $p = 0.515$; Fig. 2). Egg masses were primarily found sheltered in rock crevices or among mussel beds, attached to hard rock substrates, with rare cases of eggs in direct sunlight. Adult whelks were larger at higher latitudes for both species (*A. spirata*: $t = –14.30$, df = 326, $p < 0.0001$; *M. lugubris*: $t = 4.12$, df = 116, $p < 0.0001$; Fig. S2). Between the southern- and northern-most sites, adult whelks increased in size by 32.4 and 37.4% for *A. spirata* and *M. lugubris*, respectively. Additionally, adult whelk abundances increased with latitude for *A. spirata* (GLM; $t = 3.716$, df = 10, $p = 0.005$) but not for *M. lugubris* ($t = 0.550$, df = 4, $p = 0.621$; Fig. S6). Latitude ($R^2 = 0.93$, $F = 12.49$, df = 3, $p = 0.04$), but not adult abundance ($R^2 = 0.93$, $F = 12.49$, df = 3, $p = 0.09$), predicted reproductive output. Across elevations, maximum temperature increased with shore height at our field experiment site (Fig. S1), yet *M. lugubris* larval survival was not influenced by thermal exposure ($t = –0.232$, df = 13, $p = 0.821$; Fig. S3).

4. DISCUSSION

Our investigation of key demographic traits across environmental gradients unexpectedly revealed that reproductive output increased with latitude toward the leading range edge for *Acanthinucella spirata*, although there was no latitudinal pattern across the relatively small range of *Mexacanthina lugubris* in California. Though surprising, higher reproductive output toward range edges in expanding species is not unfounded (e.g. Lester et al. 2007, Ling et al. 2008). Resource availability and competition, a congruence of reproductive and dispersal traits, or founder effects might contribute to the pattern of increased reproductive output of *A. spirata* at its range edge. It is also worth noting that we measured only 1 component of reproductive output (total number of egg capsules). The number of offspring per capsule could also vary by latitude and shore height (although we did not find a relationship between shore height and offspring per capsule for *M. lugubris,* Fig. S5).

Higher food availability can increase reproductive output (e.g. Donelson et al. 2010) and lead to larger body sizes (e.g. Spight & Emlen 1976). There is some evidence that for barnacles (a major food source for whelks), abundance (Blanchette et al. 2008) and recruitment (Broitman et al. 2008) are higher in northern California than locations in the southern part of the range of *A. spirata*. Lower competition may also lead to surplus energy to invest in reproduction and growth. Competitors of *A. spirata* decreased with increasing latitude (R. A. Beshai et al. unpubl. data). Together, lower interspecific competition and increased food availability at the range edge might have contributed to the higher reproductive output we measured for *A. spirata*. Future studies should investigate the role of resource availability in driving demography across species ranges.

Other site-specific factors, such as wave exposure, could influence reproductive output. Wave splash can buffer both adults and developing larvae in capsules from temperature stress and is typically higher in coastal systems north of Point Conception (Helmuth et al. 2006), especially in range-shifted sites for *A. spirata*. Expansions of both species should be monitored in the future to determine if the latitudinal patterns in reproductive output hold and to identify potential environmental or biotic drivers. Given that these are relatively recent expansions, we are somewhat limited in our number of range-shift sites.

While trailing edges are typically dominated by survival constraints, population persistence and expansion at leading edges require a balance of reproductive output and dispersal constraints (Buckley et al. 2021). These whelks lay benthic egg cases and thus, long-distance dispersal of these whelks most likely occurs via drifting on wood or algae (Flagor & Bourdeau 2018). A trade-off between reproduction and dispersal is unlikely, as greater reproductive output increases the probability of chance dispersal events. On the other hand, the higher body size and reproductive output we observed at the range edge could be due to genetically determined founder effects (Chuang et al. 2015). Although the relationship between body size and latitude for *M. lugubris* paralleled that of *A. spirata,* reproductive output did not differ by latitude for *M. lugubris*. However, because *M. lugubris* occurs farther south than *A. spirata*, we sampled a more limited portion of its range. Future studies should incorporate data from the historic range of this species in Mexico.

Interestingly, we did not find significant demographic variation across a shore height gradient for *M. lugubris*, possibly indicating that egg-laying behaviors buffer offspring from environmental variation. Rawlings (1999) suggested that intertidal snail egg cases are poorly protected from stresses of aerial exposure, leaving developing embryos vulnerable to increased mortality under climate change at range edges. Yet, although field temperatures increased with shore height, we did not observe differences in survival under experimental thermal exposure. In our study, nearly all eggs were laid in rock crevices or mussel beds. Cooler microhabitats within the elevational gradient may have buffered larvae from negative effects of stress on demographic rates. Additionally, average temperatures were consistent across shore height, which could also help buffer the eggs from shorter periods of thermal stress (maximum temperatures).

As oceans warm, predicting species range expansions is essential for anticipating future biodiversity patterns. Increased reproductive output at edges might facilitate further spread of *A. spirata*, and higher body sizes at the range edge (and lack of local stress effects on offspring) suggest robust range-edge populations of *M. lugubris.* Our findings highlight the need to evaluate impacts of these species on communities they move into, as further expansions are possible under climate change.

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Table 1. Sites surveyed for adult whelks and egg cases in northern and southern California, USA. Dashes = no adult whelks or eggs found; italics = only adult whelks found (no eggs). At Thousand Steps, *Acanthinucella spirata* adults and eggs were observed at a location adjacent to our main field site but were not served (ND = no data)

					M. lugubris	*A. spirata*
Site	Code	Lat	Long	Region	range	range
Cape Mendocino	CM	40.396	–124.379	Northern	▨	Extended
Cape Mendocino South	CS	40.394	–124.379	Northern	▨	Extended
Mussel Rock	MR	40.347	–124.364	Northern	▨	▨
Moat Creek	MC	38.880	–123.679	Northern	▨	▨

Sea Ranch Shell Beach	SS	38.731	–123.490	Northern	▨	▨
Dillon Beach	DB	38.254	–122.970	Northern	▨	Historic
Kenneth Norris Rancho Marino	RM	35.540	–121.092	Northern	▨	▨
Coal Oil	CO	34.406	–119.878	Northern	▨	Historic
Little Corona del Mar	LC	33.588	–117.869	Southern	▨	Historic
Crystal Cove	CC	33.565	–117.834	Southern	▨	Historic
Shaw's Cove	SC	33.544	–117.799	Southern	▨	Historic
Heisler Park	HP	33.542	–117.789	Southern	Extended	▨
Thousand Steps	TS	33.493	–117.739	Southern	Extended	Historic (ND)
Victoria Beach	VB	33.419	–117.761	Southern	Extended	▨
Goff Island	GI	33.513	–117.761	Southern	Extended	▨
Dana Point	DP	33.460	–117.715	Southern	▨	Historic
Swami's Beach	SB	33.034	–117.715	Southern	Extended	Historic
Cardiff State Beach	CB	33.009	–117.280	Southern	Extended	Historic
Scripps Reserve	SR	32.874	–117.252	Southern	Extended	Historic

Fig. 1. Locations (site codes in Table 1) of egg masses of the whelks *Acanthinucella spirata* (orange) and *Mexacanthina lugubris* (purple). White circles = no eggs found

Fig. 2. Reproductive output (egg capsules per site during 1 h timed counts) across historic (closed circles) and extended (open circles) ranges of *Acanthinucella spirata* (orange) and *Mexacanthina lugubris* (purple). Reproductive output increased from the range center to leading edge (south to north) for *A. spirata* only (p = 0.0103). See Table 1 for site codes