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CAUSES AND CONSEQUENCES OF RANGE EXPANSION IN MARINE MOLLUSKS

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Dedication

To my wonderful, scientist parents.

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CHAPTER 1: Introduction

1.1 Range expansion in response to climate change

Over the last century, human activities, including the burning of fossil fuels and emission of greenhouse gases have led to accelerating climate changes, including warming in the atmosphere and in the ocean (IPCC 2014). These human-induced climate changes have led to poleward (and elevational) range expansions in numerous terrestrial (Chen et al. 2011, Vesperinas et al. 2001, Parmesan 1999, Thomas and Lennon 1999) and marine organisms (Sorte et al. 2010, Wernberg et al. 2011). Studying the genetic and phenotypic consequences of range expansion in response to past climate changes may help us better predict how species may adapt to range expansions in response to present-day climate changes.

The Pleistocene is a particularly good time to study native expansions because of our understanding of the glacial cycles during this period (Hewitt 1996) and because the faunal similarities with the present allow for a more direct comparison to processes today. Many Northern Hemisphere taxa adjusted their geographic ranges during the Pleistocene in response to glacial advance and retreat (Hewitt 1996, 2000, Bernatchez and Wilson 1998, Valentine and Jablonski 1993, Roy et al. 1996).

Range expansion can be inferred from genetic survey across a species' geographic range. Reduced genetic variation in the recently-expanded portion of the range is typical of most range expansions, and the glacially-induced range shifts of Northern Hemisphere taxa during the late Pleistocene left a signature of reduced genetic variation in many northern as compared to

southern parts of the range (Hewitt 1996, Bernatchez and Wilson 1998, Hellberg et al. 2001, Marko 2004). Alternatively, significant population structure over large spatial scales in some species may suggest long-term regional persistence (Marko et al. 2010). Based on genetic evidence, range expansions following the Last Glacial Maximum were common across plants and other terrestrial organisms (Hewitt 2000, McLachlan et al. 2005, Stewart et al. 2010), as well as marine organisms (Marko et al. 2010, Wares and Cunningham 2001, Hellberg et al. 2001, Bernatchez 2001). In addition to genetic studies, the exceptional fossil preservation of shelly, skeletonized marine species make them record-keepers for geographic distribution over time (Kidwell and Flessa 1995, Valentine et al. 2006) and can further support genetic evidence of range expansion.

Despite the extensive documentation of the climatic fluctuations during the Pleistocene and the accompanying range expansions, the phenotypic consequences of those range expansions have received little attention (Hellberg et al. 2001). Phenotypic changes are expected in the face of new suites of selective pressures, and studying those changes in response to range expansion can add to our understanding of adaptations following exposure to new environments.

1.2 Adaptation to novel environments

Both natural range expansions and anthropogenic invasions bring species into contact with new habitats, with new suites of environmental conditions, new ecological communities, foreign predators, and never-before-seen selective pressures. When habitats become suitable climatically, species have been shown to expand their range individualistically (Valentine and

Jablonski 1993, Stewart et al. 2010, Schweiger et al. 2008), rather than as a whole community. Thus climate changes can give rise to new communities. Adaptations to new biotic and abiotic pressures should follow expansion into novel locales (Reznick and Ghalambor 2001), and indeed many range expansions and human-mediated introductions are met with rapid evolutionary adaptations (Hellberg et al. 2001, Davis and Shaw 2001, Roy et al. 2002, Grosholz and Ruiz 2003, Suarez and Tsutui 2008).

Rapid adaptation in response to novel environments has been studied in marine mollusks in response to native range expansion and human-mediated introductions. Hellberg et al. (2001) investigated the genetic and phenotypic consequences of range expansion in an intertidal gastropod, *Acanthinucella spirata*, which re-colonized the northern part of its geographic range following the Last Glacial Maximum and found novel shell forms in the northern re-colonized part of the range compared to southern and fossil forms. In response to human-mediated introductions, Grosholz and Ruiz (2003) found a pattern of increased body size in non-native compared to native populations of marine species, including marine bivalves and gastropods.

In addition to local adaption, plasticity, or the potential for a single genotype to produce different phenotypes in different environments (Lewontin 1974, West-Eberhard 1989), can also influence local responses to environmental conditions. Phenotypic plasticity should be advantageous over genetic adaptation if populations are distributed among habitats with different fitness requirements. Species may evolve to have higher plasticity if the historical environment was variable or if there is a low cost of maintaining plasticity (Price et al. 2003, Pigliucci 2005).

Understanding the relative contributions of plasticity and local adaptation to phenotypic variation is useful for understanding evolutionary processes across a species' range (Pascoal et al. 2012), but deciphering whether phenotypic variation is the result of local adaptation or phenotypic plasticity often requires experimentation, like reciprocal transplant or common-garden experiments (Kawecki and Ebert 2004). Reciprocal transplant experiments involve transplanting populations between sites and observing the phenotypic response following transplantation (Kawecki and Ebert 2004). Trussell (2000) found phenotypic plasticity in *Littorina obtusata* when northern snails were reciprocally transplanted--southern snails transplanted to northern sites produced lighter, thinner shells, but greater body mass than southern snails in southern sites. Because of ethical and practical issues with reciprocal transplant experiments, common-garden experiments offer an alternative method for detecting plasticity. Common-garden experiments test populations from different habitats in an environment where habitat differences are controlled (Kawecki and Ebert 2004). If the offspring from different parent populations retain their differences under identical environmental conditions, then there is likely little phenotypic plasticity. Due to their direct-developing life mode, which may lead to local adaptation and can facilitate laboratory rearing, *Nucella* gastropods have been the subject of common-garden experiments, such as in Pascoal et al. (2012).

1.3 Similarities between range expansions and human-mediated introductions

Present-day invasions and range expansions (both past and present) share similar processes and dynamics (Roy et al. 2002, Sorte et al. 2010) as they encounter novel environments, and despite their often harmful effects on native populations, invasions offer a real-time window into the

ecological factors that promote successful establishment in new locales and the evolutionary processes that may lead to adaptations (Roy et al. 2002, van Kleunen et al. 2010, Westley 2011, Nawrot et al. 2015).

In order to predict which species might be successful invaders, numerous studies have investigated factors that might promote establishment and invasiveness (Rejmanek and Richardson 1996, Roy et al. 2002, Nawrot et al. 2015). In plants, Rejmanek and Richardson (1996) found mean seed mass, minimum juvenile period, and mean interval between large seed crops to contribute to invasiveness. For marine bivalves, Roy et al. (2002) found body size and geographic range size to contribute to establishment and invasiveness in the Mytilidae. But it is possible that different traits may be beneficial at different times in the course of an invasion. For example, Nawrot et al. (2015) found that large body size was not predictor of establishment, but was a predictor of invasiveness among bivalves entering the Mediterranean from the Red Sea.

In addition to ecological traits that may promote or constrain invasion success, the native environmental niche may also be able to constrain establishment in new environments (Strubbe et al. 2015, Petitpierre et al. 2012, Broennimann et al. 2007). In recent years, niche-based models have increasingly been used to predict species distributions, including for human-mediated introductions. Niche-based models rely on associating occurrence data with environmental data to construct the native niche. Unlike range expansions, human-mediated introductions often involve transplanting populations around the world, and potentially bringing them into contact with environments far different from their native environment. Testing the likelihood that a species will establish outside the native range into unfamiliar environmental

conditions can help us understand how much the native niche constrains invasive establishment and can explore the relationship between the fundamental and realized niche.

1.4 Marine mollusks

Marine mollusks have a deep history of study and have been used as a model for analyzing distribution over time and diversity gradients, past and present (Sepkoski 1981, Jablonski et al. 2006, Tomasovych et al. 2016). Marine mollusks are an ideal group to address questions related to natural range expansions into novel environments and the subsequent phenotypic consequences due to their exceptional fossil preservation (Kidwell and Flessa 1995, Valentine et al. 2006) and documented range expansions in the fossil record and through genetic evidence (Marko 2004, Wares and Cunningham 2001, Hellberg et al. 2001). Marine bivalves also offer the opportunity to address questions related to human-mediated expansions due to numerous introductions around the world (Carlton 1996, Galil 2006, Ruesink et al. 2005), both accidental (in ballast water and through corridors like the Suez Canal) and purposeful (for aquaculture). These different circumstances of invasion offer a powerful comparative framework to address questions about the factors that promote invasion success and the likelihood of niche expansion. Comparing the native and non-native niche relies on accurate native occurrence data, in addition to invasion occurrence data. We have access to exhaustive native occurrence data for marine bivalves owing to a taxonomically-standardized global marine bivalve database (Jablonski et al. 2013).

To address questions of native range expansion in marine mollusks, the rocky intertidal of the Pacific Northwest offers a perfect setting. In addition to documented Pleistocene range expansions along the eastern Pacific coast (Marko et al. 2010, Marko 2004, Hellberg et al. 2001), the availability of Pleistocene terraces allows for phenotypic comparisons between the fossil and present-day populations (Lindberg and Lipps 1996, Wagner 1958, Dyke et al. 1996, Eyles et al. 1991). There has been a long history of interest in the rocky shore communities of the Pacific North West (Kincaid 1957, Paine 1974, Wootton et al. 2008), including the phenotypic responses of intertidal species to abiotic and biotic pressures such as wave action and predation (Kincaid 1957, Etter 1988, Sanford and Swezey 2008). Specifically, *Nucella* gastropods are widespread intertidal predators on the eastern Pacific coast and have been show to exhibit phenotypic variation in the face of differing levels of wave exposure and predation (Kincaid 1957, Appleton and Palmer 1988, Sanford and Swezey 2008), making it an ideal group to investigate the causes of phenotypic variation.

1.5 Overview of chapters

This dissertation explores the causes and consequences of range expansion and human-mediated introduction in marine mollusks. In chapter 1, *Phenotypic consequences of range expansion in two intertidal snails*, I investigate the phenotypic variation across latitude and wave-exposure gradients in *Nucella lamellosa* and *Nucella ostrina*. I also compare present-day forms to ancestral forms (both fossil and midden) in order assess phenotypic differences across time and space in two intertidal gastropods with different expansion histories following the Last Glacial Maximum. In Chapter 2, *Latitudinal and microgeographic clines under plastic control in two*

Nucella rocky shore gastropods, I assess the relative contribution of plasticity to the phenotypic differences I find across wave-exposure and latitudinal gradients in *Nucella lamellosa* and *Nucella ostrina* by raising northern and southern populations from different wave-exposure levels under identical conditions and measuring phenotypic variation in the second generation. Finally, in Chapter 3, *Bivalve invasions are asymmetrical in geography and niche expansion*, we explore the prevalence of niche expansion and the factors that promote invasion success in a set of 120 alien bivalves.

CHAPTER 2: Phenotypic consequences of range expansion in two intertidal snails

2.1 Introduction

Genetic and fossil data, along with direct observation, provide evidence that climate changes drive species to shift their geographic ranges on land and in the ocean (Hellberg et al. 2001, Roy et al. 1996, Davis and Shaw 2001). A wave of range expansions accompanied the warming that followed the Last Glacial Maximum (LGM) (Valentine and Jablonski 1993, Davis and Shaw 2001), and genetic data have been useful in uncovering the expansion history of many Northern Hemisphere taxa (Hewitt 2000, Hellberg et al. 2001, Wares and Cunningham 2001, Marko 2004, Maggs et al. 2008, Marko et al. 2010). However, the phenotypic consequences of post-LGM expansions have received little attention (Hellberg et al. 2001, Mila et al. 2007). By investigating the phenotypic consequences of past range expansion, we may be able to better predict how species will respond to climate change or anthropogenic introduction in the future.

To increase our current understanding of the phenotypic patterns following a rapid range expansion, I surveyed present-day and ancient phenotypes of two intertidal congeneric snails, *Nucella lamellosa* and *N. ostrina*. Genetic data suggest that these two species responded differently to glacial cycles of the recent past (Marko 2004, Marko et al. 2010), with *N. ostrina* expanding to the northern part of its range following the LGM, and *N. lamellosa* likely persisting in at least some sites in the northern part of its range before reconnecting with the southern population following the LGM. These two northeast Pacific coast gastropod species offer the opportunity to compare the phenotypic patterns following a range expansion into recently

vacated regions (*N. ostrina*) with the phenotypic patterns following isolation and re-connection of northern and southern populations (*N. lamellosa*).

As Hellberg et al. (2001) inferred that range-expansion promoted rapid phenotypic diversification, I expected to find larger north to south differences in phenotypic variation in *N. lamellosa* than in *N. ostrina* because populations of *N. lamellosa* were likely isolated during the Pleistocene, giving a protracted time with attenuated or severed gene flow, which might favor greater morphological evolution. Instead, I find that significant morphological evolution has occurred in both species.

2.2 Background & Study System

Climate change has been shown to directly affect species distributions, latitudinally and altitudinally (Roy et al. 1996, Bernatchez and Wilson 1998, Parmesan and Yohe 2003, Lenoir et al. 2008, Assis et al. 2014). During the Pleistocene (~2.5mya - 11 kya), many Northern Hemisphere species adjusted their ranges in response to glacial-interglacial climate cycles (Hewitt 1996, 2000, Bernatchez and Wilson 1998, Roy et al. 1996). While the patterns of range shifting in response to climate change have been reported most widely in terrestrial species, the relatively high resolution of the molluscan fossil record has revealed natural expansions of many marine mollusks (Valentine and Jablonski 1993, Kidwell and Flessa 1995, Kidwell 2015). Although spatially explicit fossil data give the most direct evidence of past distributions, genetic data can also document range expansion. Glacially-induced distribution changes during the late Pleistocene and early Holocene often leave a signature of reduced genetic variation in many high-latitude and high-elevation recently-expanded populations, where habitats had been

previously inhospitable (Hewitt 1996, Bernatchez and Wilson 1998, Hellberg et al. 2001, Marko 2004, Parmesan 2006). Alternatively, relatively high genetic diversity over large spatial scales would suggest long-term regional persistence (Avice 1989, Marko et al. 2010), at least in refuges.

Geographic range adjustments were presumed by Eldredge (1995) to be the first response to environmental changes, followed by adaptations. However, the phenotypic variation that results from geographic range adjustments has been relatively overlooked, especially in the ocean. Hellberg et al. (2001) studied an intertidal muricid gastropod, *Acanthinucella spirata* (subfamily Ocenebrinae) that expanded its range along the California coast since the Pleistocene, as evidenced by both fossil distributions and reduced genetic diversity towards the north. The recently founded northern populations of *A. spirata* harbored novel phenotypes, not seen in present-day southern populations or in Pleistocene fossils, suggesting that significant morphological evolution had been associated with post-glacial range expansion. However, this intriguing result has received little attention. The eastern Pacific gastropods *Nucella lamellosa* and *N. ostrina* (also in subfamily Ocenebrinae) provide an opportunity to test the generality of Hellberg et al.'s (2001) findings. By surveying genetic variation across populations, Marko (2004) found that in *Nucella ostrina*, northern sites are dominated by a single haplotype, suggesting a recent range expansion. However, for *Nucella lamellosa*, northern sites include many unique (likely ancient) haplotypes, suggesting persistence by at least some small refuge populations in the northern part of its range.

I surveyed morphology across time and space in both *Nucella ostrina* and *Nucella lamellosa* to investigate the consequences of post-LGM expansion and to further study the factors that influence shell shape at small and large spatial scales. For present day populations, I

measured phenotypic variation across a range of different local environments (wave-exposed versus wave-protected) within each latitudinal band to test for phenotypic differences associated with habitat, and how they vary along the latitudinal gradient. Wave exposure, predation, and latitude have all been shown to influence gastropod morphology (Table 2.1). Based on previous studies, I expect lower spires to be favored in high-latitude, high-predation locales, larger apertures at high-latitude, high-wave-exposure locales, and thicker shells at low-latitude, high-predation locales.

2.3 Methods

2.3.1 Study system

The genus *Nucella* appears in the fossil record around the Early Miocene, approximately 25 million years before present (Collins et al. 1996). A recent phylogenetic analysis revealed that the genus' radiation likely coincided with the Miocene Climatic Transition (a shift to cooler temperatures) approximately 14 Mya (Marko et al. 2014). Five of the genus' extant species live along the eastern Pacific coast (Figure 2.1). Today, *Nucella ostrina* ranges approximately from Point Conception, California (34°N) to Yakutat, Alaska (60°N) and *N. lamellosa* ranges approximately from Santa Cruz, California (37°N) to the Aleutian Islands (52°N) (Collins et al. 1996). Although the two species are sympatric for much of their geographic range, along with

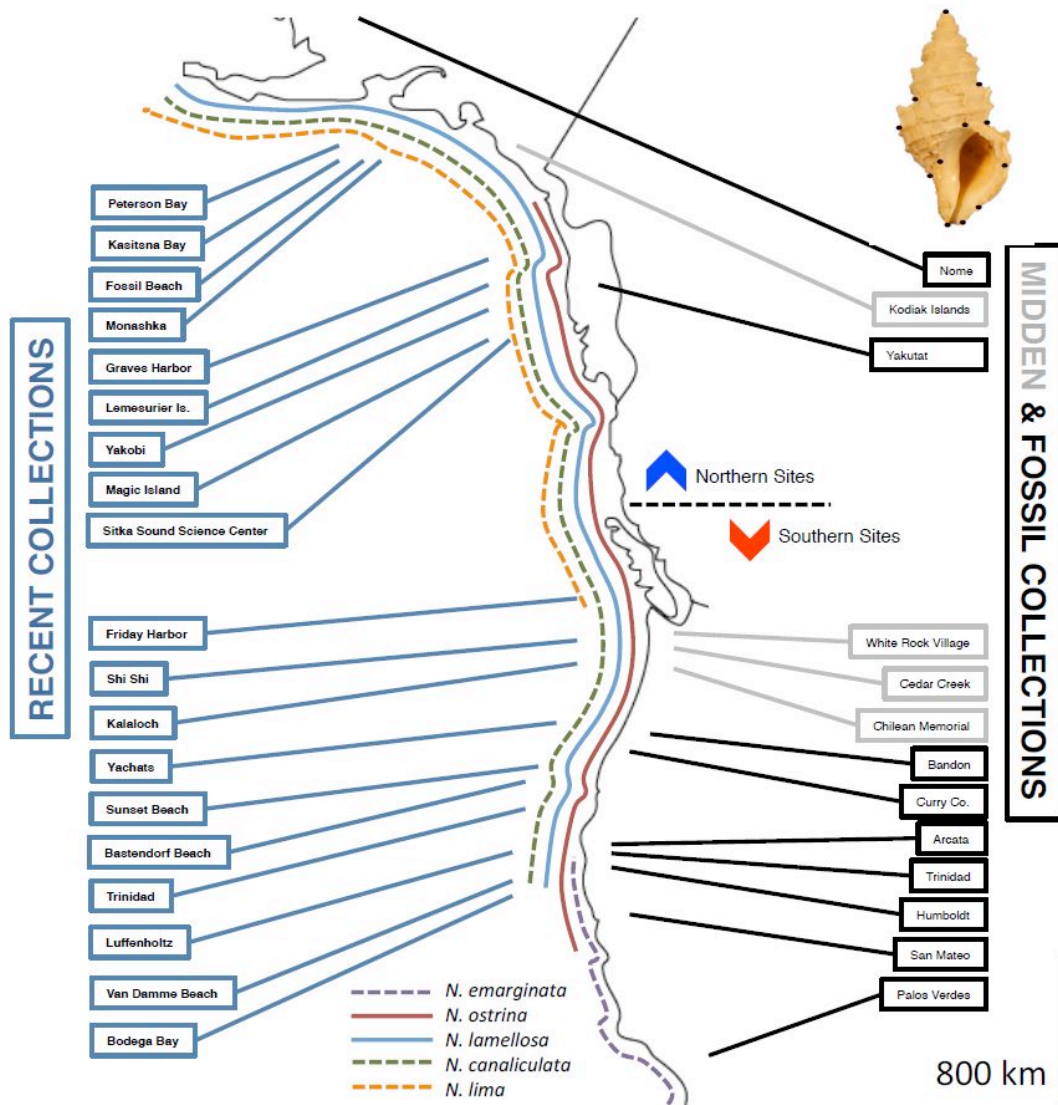


Figure 2.1. Collection sites from the Pacific coast of North America. Present-day collections are shown on the left and ancient collections (fossil in black and midden in gray) are shown on the right. Sites were split into northern and southern groups consistent with genetic breaks in both species in Marko (2004). Present-day geographic ranges are shown in dashed and solid lines for Pacific *Nucella* species according to Collins (1996). *Nucella lamellosa* (blue solid line) and *Nucella ostrina* (red solid line) are included in the present study. *Nucella lima* (orange dashed line), *Nucella canaliculata* (green dashed line), and *Nucella emarginata* (purple dashed line) are congeners that are not included in the present study. Upper right corner shows the twelve positional landmarks used in this study.

	Predation	Latitude	Wave exposure
Spire	<i>High Predation</i>	<i>High Latitude</i>	<i>High Exposure</i>
	When crab predation is high, a lower spire is advantageous (Boulding & Hay 1993)	At high latitudes, lower spires are expected (Graus 1974), and may result from colder water temperatures leading to slowed growth and a lower spire height to shell length ratio (Boulding & Hay 1993)	High wave-exposure favors low-spired morphs (Palmer 1990)
	<i>Low Predation</i>	<i>Low Latitude</i>	<i>Low Exposure</i>
	When crab predation is low, growth rates are increased leading to a relatively higher spire (Boulding & Hay 1993)	At low latitudes, higher spires may protect against incident radiation by decreasing cross-sectional area (Vermeij 1978, DeWolf 1998); warmer water temperatures at low latitudes may also increase growth rates, leading to a higher spire	Low wave-exposure (often corresponding to high-predation) may favor lower spires (Boulding & Hay 1993), though Crothers (1973) finds higher-spined morphs at wave-protected sites
Aperture	<i>High Predation</i>	<i>High Latitude</i>	<i>High Exposure</i>
	When crab predation is high, narrow, smaller apertures are favored (DeWolf et al. 1998)	High latitudes may favor larger apertures due to latitudinal trend of decreasing wave action and increased heat stress & predation at lower latitudes (DeWolf et al. 1998, Graus 1974)	High wave exposure favors larger apertures corresponding to large foot area, which are better to adhere to rocks (Kitching et al. 1966)
	<i>Low Predation</i>	<i>Low Latitude</i>	<i>Low Exposure</i>
	Where crab predation is lower (often in face of high wave action), larger apertures are expected (DeWolf et al. 1998)	Low latitudes favor smaller apertures due to latitudinal trend of decreasing wave action and increased heat stress & predation at lower latitudes (DeWolf et al. 1998)	Low wave exposure may favor smaller apertures due to increased predation and decreased wave action (Kitching et al. 1966)
Thickness	<i>High Predation</i>	<i>High Latitude</i>	<i>High Exposure</i>
	Where crab predation is high, thicker shells are favored (Boulding & Hay 1993, Edgell & Neufeld 2008)	High latitudes often lead to thinner shells due to low calcification rate (Trussell 2000, Graus 1974)	High wave exposure favors thin shells where “risk of dislodgement is high” (Boulding & Hay 1993)
	<i>Low Predation</i>	<i>Low Latitude</i>	<i>Low Exposure</i>
	Where crab predation is low, thin shells are not disadvantageous (Boulding & Hay 1993).	Low latitudes often lead to thicker shells due to high calcification rate (Trussell 2000, Graus 1974)	Low wave-exposure areas (often with high predation rates, which favors thicker shells

Table 2.1. Morphological consequences of predation, latitude, and wave exposure found in previous studies.

Nucella lima and *Nucella canaliculata* (Figure 2.1), *N. lamellosa* typically inhabits the lower intertidal zone, and subtidal populations are common, whereas *N. ostrina* typically inhabits the high intertidal zone (maximum height of 20-30 cm above the high-shore barnacle zone), with no subtidal populations (Collins 1996).

2.3.2 Survey of present-day and ancient phenotypes

To assess phenotypic changes in time and space I surveyed both present-day and ancient samples from both species. For present-day phenotypes, I collected across twenty intertidal sites from Bodega Bay, California (38.3°N, 123.06°W) to Kodiak Island, Alaska (57.8°N, 152.4°W), spanning nearly 20 degrees of latitude (Figure 2.1, Supplementary Table S2.1). Twenty to 60 individuals of each species were collected at each site, and photographed in three views. To survey ancient phenotypes, I photographed Pliocene/Pleistocene collections of *Nucella* at the California Academy of Sciences, at the University of California Museum of Paleontology, and the personal collection of Anne Pasch from the Gulf of Alaska (Pasch et al. 2010). The fossil specimens from Pliocene and Pleistocene (~5- 0.012 Ma) collections are treated as a single time bin in order to simplify the comparison between past morphologies and present-day morphologies. These collections provided fossil specimens across *Nucella lamellosa*'s geographic range (California through Alaska), but only the southern part of *Nucella ostrina*'s range (California and Oregon). In addition, I photographed midden (~500-2000 years old) collections of *Nucella* at Olympic National Park, Washington and at the Burke Museum at the University of Washington. Collections were grouped into northern (Alaska) and southern (California, Oregon, and Washington) populations consistent with glacial cover during the LGM

and with genetic breaks in both *Nucella ostrina* and *Nucella lamellosa* (Marko 2004, Marko et al. 2010), and collections were also analyzed with latitude as a continuous covariate. Due to the influence of wave exposure on phenotype in these snails (Kitching et al. 1966, Boulding & Hay 1983, Palmer 1990, Webster & Palmer 2016), sites were categorized as exposed, protected or intermediate. For Alaska, wave exposure categories were based on the NOAA ShoreZone website (<https://alaskafisheries.noaa.gov/habitat/shorezone>), which categorizes stretches of the coastline from very wave-protected to very wave-exposed. Unfortunately, the same resource is not available for California, Oregon and Washington, so literature sources and personal observations were used to classify sites as wave-exposed, wave-protected, or intermediate (Supplementary Table S2.1).

2.3.3 Geometric morphometrics for shape analysis

I used ImageJ software to digitize the photographs of present-day and ancient populations for landmark-based geometric morphometrics. To quantify shell shape, I digitized 12 positional landmarks (Figure 2.1) that could be reliably recognized in both species, like in Pascoal et al. (2012). Procrustes superimposition was performed using the CoordGen program (version 8) within the IMP software package. Procrustes superimposition rescales all landmark configurations (for each specimen) to remove differences in size, rotates configurations to remove differences in orientation, and centers configurations on the centroid to align landmarks (Webster and Sheets 2010). Data visualizations and statistics used the Geomorph package in R and the IMP software suite (including CoordGen, PCAGen, TwoGroup) (<http://www3.canisius.edu/~sheets/morphsoft.html>). In total, I digitized 1123 specimens of *Nucella* in three views for this study. Caliper measurements of shell traits--shell length, aperture

length, aperture width, and lip thickness (like Palmer 1990)-- were used to supplement the landmark-based morphometrics. Notably, shell thickness is more difficult to reliably quantify using images alone.

Modern and fossil specimens were combined into a principal components analysis using both the Geomorph package in R and the IMP software suite. The first five principal components explained 78.85% of the total variance for *N. ostrina* (PC1=52.79%, PC2=10.32%, PC3=6.4%, PC4=5.49%, PC5=3.85%) and 78.11% of the total variance for *N. lamellosa* (PC1=45.07%, PC2=11.2%, PC3=10.11%, PC4=6.5%, PC5=5.23%). To compare northern versus southern populations, and fossil versus present-day, I performed Hotelling's T^2 tests using IMP TwoGroup software on the Bookstein coordinates from the Procrustes superimposition (non-size-standardized, see below). All Hotelling's T^2 tests use the first and seventh landmarks as baseline endpoints. A two-way MANOVA on the partial warp scores (not size-standardized) was performed for *Nucella lamellosa* to compare the effects of age (modern vs. fossil) and geography (north vs. south). To account for the unbalanced MANOVA, I used the 'car' package in R for Type II and Type III tests. Unfortunately, due to a lack of northern fossil collections, I could not perform the same two-way MANOVA for *Nucella ostrina*. In addition to comparing northern and southern populations in multivariate shape, I also compared univariate traits (shell length, aperture length, aperture width, and lip thickness) as a function of latitude in a linear mixed effects model, with site as a random effect, using the lme4 package in R. Aperture length, aperture width, and lip thickness were also regressed against shell length (as in Palmer 1990) to compare how shell traits varied with shell size for northern and southern groups, and across wave-exposed and wave-protected populations. Aperture length, aperture width and lip thickness as a function of shell length (a proxy for size) were compared in an ANCOVA in R using the aov

function [with geography (north, south) or wave exposure (protected, intermediate, exposed) as a fixed effect, and site as a random effect].

2.3.4 Controlling for ontogenetic changes in shell shape

Because of growth allometry in *Nucella*, I attempted to collect only larger snails to minimize the effects of shape changes with ontogeny. According to Spight (1975), *N. ostrina* are mature at >21.5 mm and *N. lamellosa* are mature at >29 mm. However Palmer (1983), considers *N. ostrina* individuals approximately >13 mm to be small adults and *N. lamellosa* individuals approximately >23mm to be small adults by (Bean [2012] even considers shells >10mm to be adults). Of the present-day material in my study, 89% of *N. ostrina* specimens were >13mm (21% >21.5mm), and 87.5% of *N. lamellosa* specimens were >23mm (62% >29mm).

Despite attempts to minimize the influence of ontogeny, I find significant allometry in both species (*N. ostrina*: $F=41.315$, $df=1$, $p=0.002$; *N. lamellosa*: $F=44.133$, $df=1$, $p=0.002$) using the `procDallometry` function in `geomorph` (Supplementary Figure S2.1). However, the regression of multivariate shape on log centroid size only accounted for 6.5% of shape variation in *N. lamellosa* and 12.5% of shape variation in *N. ostrina*. Both species show a trend towards more slender, higher-spined shells with increasing size. While size-standardization by using the residuals from the regression and standardizing to a common size could control for ontogenetic shape changes, it relies on a linear relationship between shape and size. Unfortunately, *Nucella* shows some non-linearity in ontogeny when each partial warp score is plotted against centroid size (Supplementary Figure S2.4, Supplementary Figure S2.5). Applying a size-standardization procedure to non-linear allometry could result in incorrect phenotypic variation at the standardized size, potentially biasing interpretation.

2. 4 Results

2.4.1 Phenotypic variation across latitude and time

Nucella lamellosa

Grouping populations into northern and southern subsets (as in Hellberg et al. 2001), *N. lamellosa*'s present-day northern populations differ significantly from present-day southern populations in multivariate shape (Hotelling's T^2 test in IMP; F-score: 50.85, p-value <0.01), and in aperture shape and shell thickness (for a given shell length) (Figure 2.2, Figure 2.4). In *N. lamellosa* apertures are significantly longer and wider, and shells are significantly thicker, for a given size at southern compared to northern sites (Figure 2.2). Although the differences in north vs. south groupings are quite striking in both the morphospace (Figure 2.4) and the shell trait slopes (Figure 2.2), when latitude is treated as a continuous variable, with site as a random effect, multivariate shape of *Nucella lamellosa* (Procrustes distance) does not vary significantly with latitude (df=19, p=0.19). Similarly when univariate traits are compared across latitude, we find that none of the shell traits (shell length, aperture length, aperture width, and lip thickness) show a significant latitudinal cline (Figure 2.6). In addition to phenotypic differences over space, *Nucella lamellosa* also exhibits significant differences in shell shape over time (two-way MANOVA (F(age & geography)=26.016, F(age)=25.6, F(geography)=39.98 (DF=554, p(age, geography, age & geography) = <0.01). When northern present-day morphs were compared to northern fossil morphs, and southern present-day morphs were compared to southern fossil morphs, both comparisons show significant differences in multivariate shape between present-day and fossil morphs (Hotelling's T^2 test ; North fossils vs. North present-day: F-score=43.84, df=24, 227, p< 0.01; South fossil vs. South present-day: F-score=17.99, df=24,

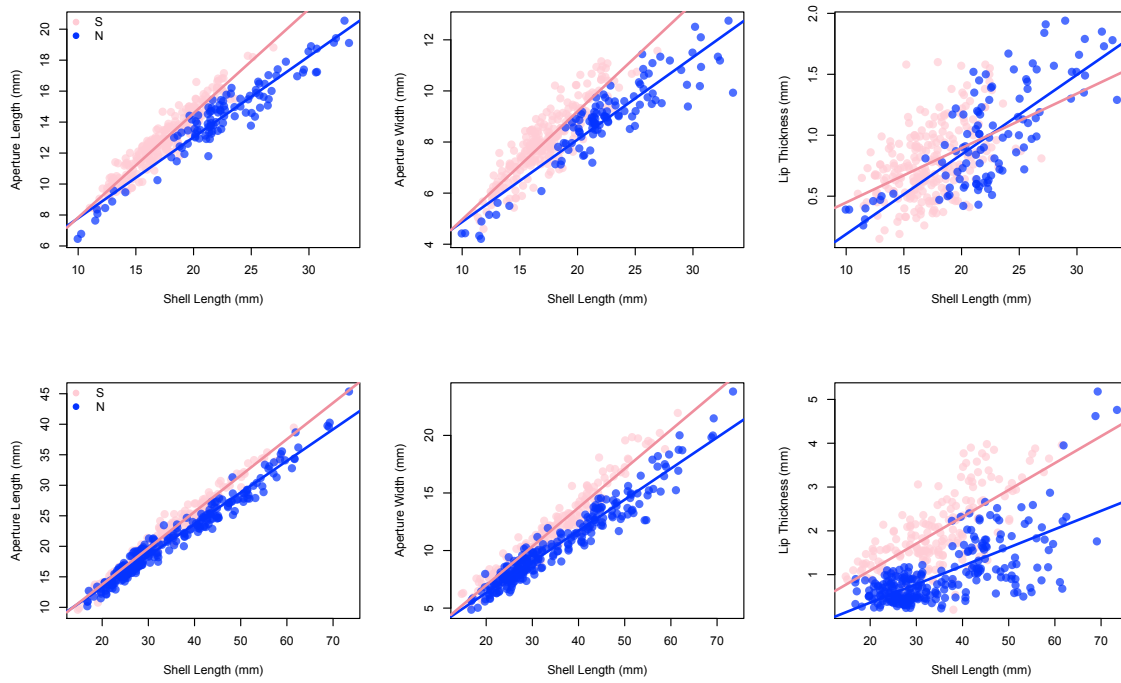


Figure 2.2. Shell traits (aperture length, aperture width, and lip thickness) plotted against shell length for *Nucella ostrina* (top three panels) and *Nucella lamellosa* (bottom three panels) showing the difference between north (blue) and south (pink) populations. Based on an ANCOVA, all of the traits as a function of size are significantly different by geography for *N. lamellosa*, and aperture length and width are significantly different by geography for *N. ostrina*.

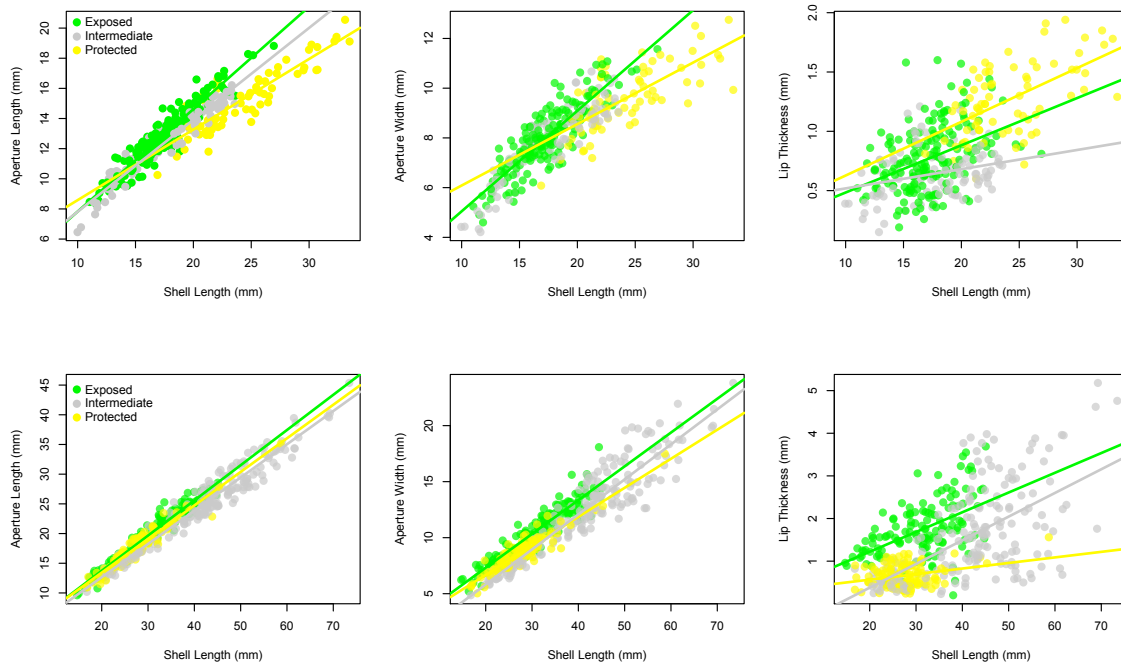


Figure 2.3. Shell traits (aperture length, aperture width, and lip thickness) plotted against shell length for *Nucella ostrina* (top three panels) and *Nucella lamellosa* (bottom three panels) showing the difference between exposed (green), intermediate (gray), and protected (yellow) populations. Based on an ANCOVA, none of the traits as a function of size are significantly different by wave exposure level for *N. lamellosa*, and only lip thickness is significantly different by exposure level for *N. ostrina*.

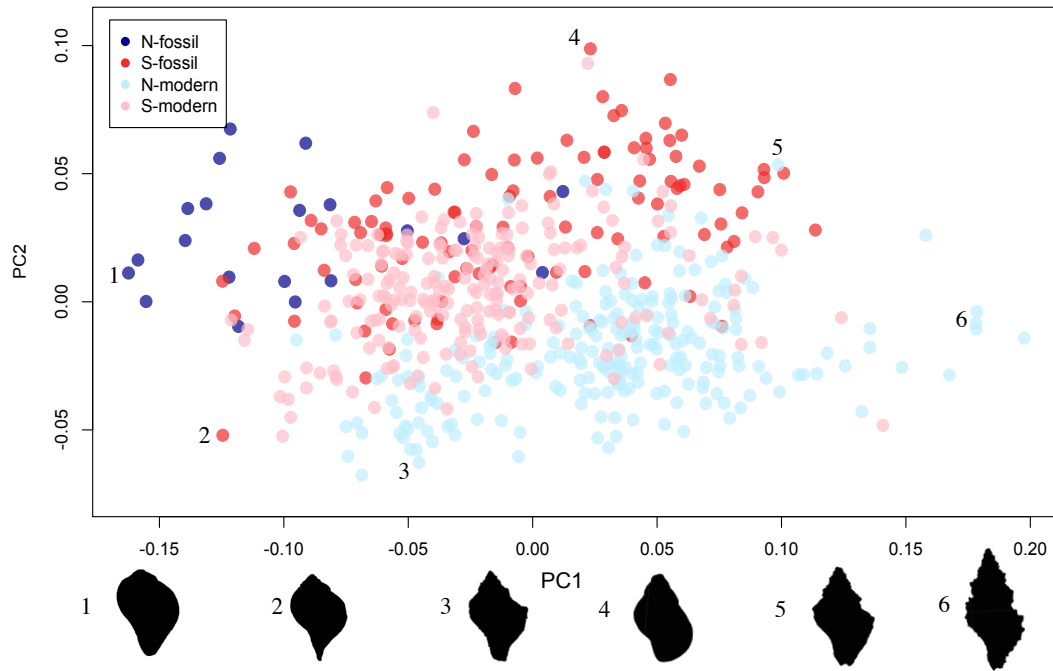


Figure 2.4. Morphospace plot for *Nucella lamellosa*. PC1 represents 45.07% of the variance in shell shape and PC2 represents 11.2% of the variance in shell shape. Shell shapes across the morphospace are shown by the silhouettes corresponding to the numbered point. PC1 seems to reflect differences in spire height, and PC2 seems to reflect differences in aperture shape. Northern vs. southern specimens seem to differ along both PC1 and PC2, but especially along PC2. The first five principal components explained 78.11% of the total variance for *N. lamellosa* (PC1=45.07%, PC2=11.2%, PC3=10.11%, PC4=6.5%, PC5=5.23%).

300, $p < 0.01$). Specifically, both northern and southern present-day populations differ from fossils in aperture shape (PC2 in Figure 2.4), with present-day populations tending to exhibit larger apertures than their corresponding fossil specimens.

Nucella ostrina

Present-day northern populations of *N. ostrina* differ significantly from present-day southern populations in multivariate shape (Hotelling's T^2 test in IMP; F-score: 33.71, p -value < 0.01) (Figure 2.5) and in aperture shape (for a given shell length) (Figure 2.2). In *N. ostrina*, apertures are significantly longer and wider for a given size at southern compared to northern sites (Figure 2.2). When latitude is treated as a continuous variable, with site as a fixed effect, shape of *N. ostrina* (Procrustes distance) varies nearly significantly with latitude ($df=12$, $p=0.058$), but none of the univariate traits show a significant latitudinal cline in *Nucella ostrina* (Figure 2.6). As in *N. lamellosa*, *N. ostrina* southern present-day morphs differ significantly from southern fossil morphs, but do not show the same pattern of differences as the *N. lamellosa* present-day to fossil comparisons. *Nucella ostrina* fossils are slightly higher-spired than present-day populations, resembling present-day northern forms (F-score=11.09, $p < 0.01$). Unfortunately, the lack of northern fossil *N. ostrina* prevented the complete array of comparisons.

Box plots show differences in means of PC1 and PC2 between groups for both *Nucella lamellosa* and *Nucella ostrina* and serve as a comparison to Hellberg et al.'s *Acanthinucella spirata* study (Supplementary Figure S2.2, Supplementary Table S2.2). In addition to fossil vs. present-day comparisons, midden collections offer a unique opportunity to compare present-day populations with collections in the recent past (approximately 500 to 2000 years ago).

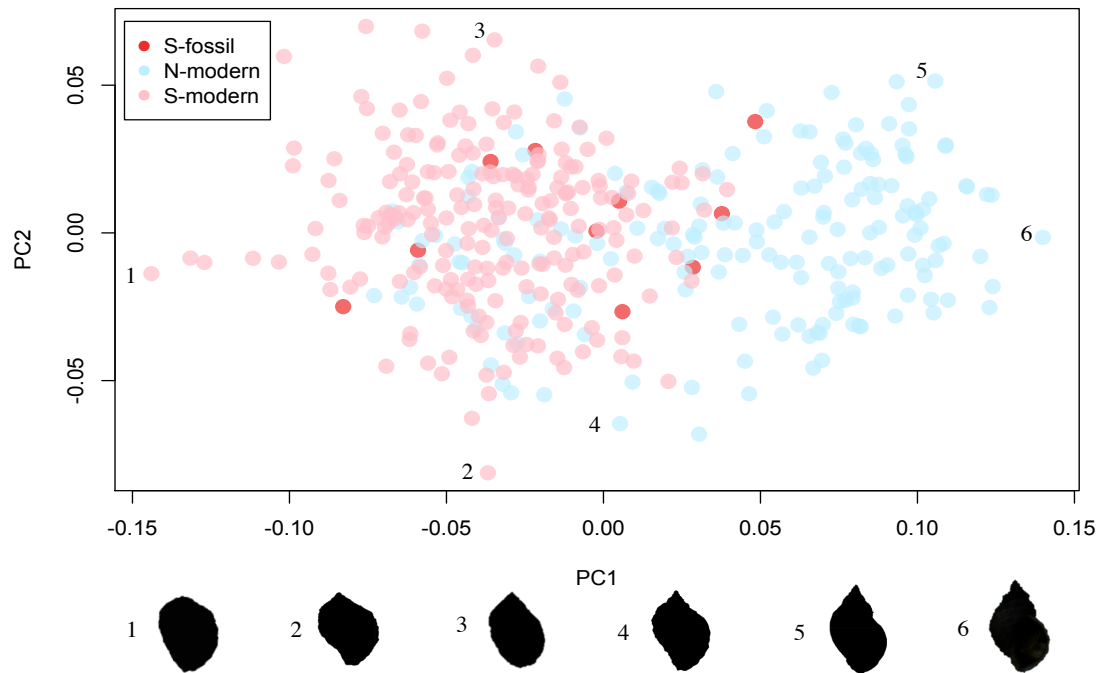


Figure 2.5. Morphospace plot for *Nucella ostrina*. PC1 represents 52.79% of the variance in shell shape and PC2 represents 10.32 % of the variance in shell shape. Shell shapes across the morphospace are shown by the silhouettes below corresponding to the numbered points in the plot. PC1 seems to reflect differences in spire height, and PC2 seems to reflect differences in aperture shape. Northern vs. southern specimens differ significantly along PC1. The first five principal components explained 78.85% of the total variance for *N. ostrina* (PC1=52.79%, PC2=10.32%, PC3=6.4%, PC4=5.49%, PC5=3.85%)

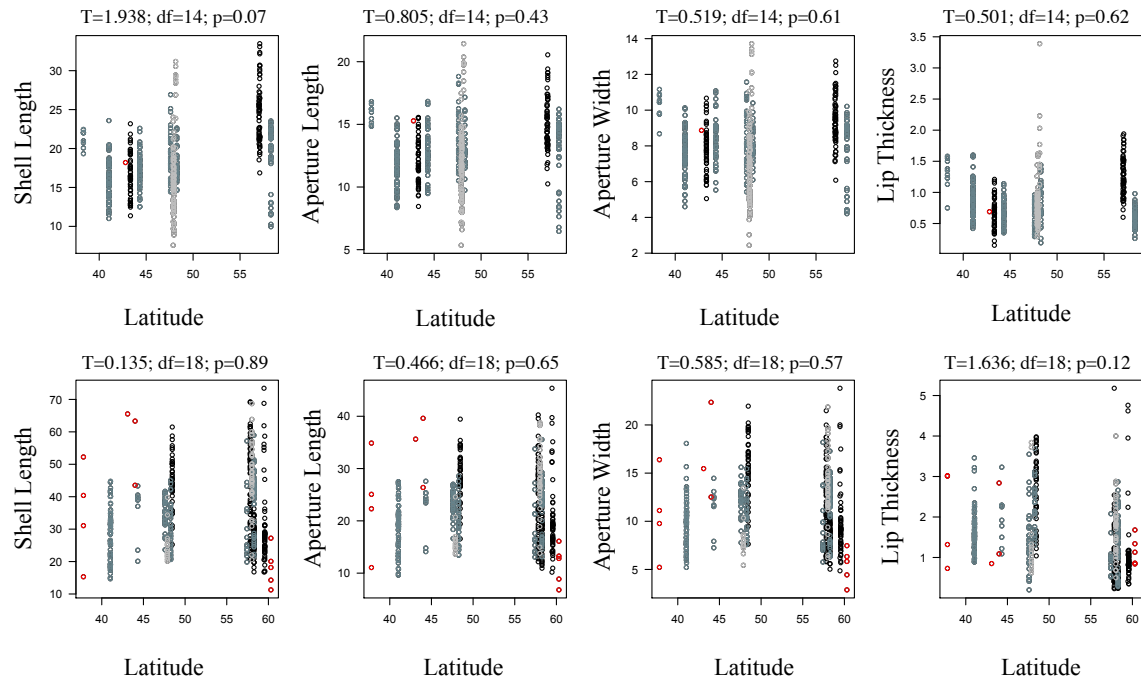


Figure 2.6. *Nucella* shell measurements by latitude. Top four panels show *Nucella ostrina* shell caliper measurements by latitude; bottom four panels show *Nucella lamellosa* shell caliper measurements by latitude (shell length by latitude on the left, and shell thickness by latitude on the right). Black points are present-day specimens from protected sites, blue are present-day specimens exposed sites, red points are fossil species, and gray points are midden specimens. T-values and p-scores above plots are from a linear mixed effects model (where site is a random effect) are shown in each panel.

For *N. lamellosa*, present-day northern morphs are significantly different from northern midden morphs in a Hotellings T^2 test (F-score=17.61, df=24, 235, $p<0.01$), and present-day southern morphs are significantly different from southern midden morphs (F-score=2.64, df=24, 203, $p<0.01$). Rather than midden snails resembling present-day snails from the corresponding region (i.e. northern midden and northern present-day populations), the northern and southern middens tend to have an intermediate morphology between present-day northern and present-day southern *N. lamellosa*, especially along PC1 (spire height). Similarly, for *N. ostrina*, present-day southern morphs are significantly different from southern midden morphs (F-score=15.93, df=24, 294, $p<0.01$). As in *N. lamellosa*, midden (southern) *N. ostrina* exhibit an intermediate morphology compared to present-day northern and present-day southern populations, especially in spire height. No midden collections of *N. ostrina* were found in the northern part of its range.

Overall, these results imply that both geographic distance and time affect phenotypic differences. Northern populations have been shown to exhibit different morphologies from southern populations in both multivariate shape and univariate traits. However, while morphologies of both *N. lamellosa* and *N. ostrina* vary with latitude when grouped into northern vs. southern populations (both multivariate and univariate), univariate traits do not vary with latitude when latitude is treated as driving a linear trend. For *N. ostrina*, the differences are primarily in spire height, with northern populations showing higher-spired forms than southern ones. For *N. lamellosa*, the differences are primarily in aperture shape, though there is also a trend towards higher-spired forms in northern populations.

2.4.2 Influence of wave exposure on morphology

Wave exposure has been shown to influence shell morphology in *Nucella* (Kitching et al. 1966, Boulding & Hay 1983, Palmer 1990, Webster & Palmer 2016). To test for the influence of wave exposure on shell shape across the geographic ranges of both species in this dataset, I compared northern exposed to protected and southern exposed to protected morphologies in both species. All pairwise comparisons between protected and exposed populations are significantly different (Hotelling's T^2 tests, Supplementary Figure S2.3, Supplementary Table S2.3). A morphospace that incorporates specimens from both *Nucella lamellosa* and *Nucella ostrina* (Figure 2.7) shows that northern protected morphologies are especially high-spired, which may indicate a combinatory effect of northern latitudes and protected shores to produce higher-spired morphologies. A striking difference between the two species, however, can be seen in the position of northern exposed populations in morphospace (Figure 2.7). For *N. ostrina*, northern exposed populations group with all southern forms (exposed, protected, and intermediate), whereas for *N. lamellosa*, northern exposed populations tend to be more similar to other northern populations. When univariate shell traits (aperture length, aperture width, and lip thickness) are plotted against shell length wave-exposed populations tend to exhibit larger apertures and thinner shells than wave-protected populations in *Nucella ostrina* (Figure 2.3). *Nucella lamellosa* exhibit wider (but not longer) apertures, but do not show the expected pattern in shell thickness.

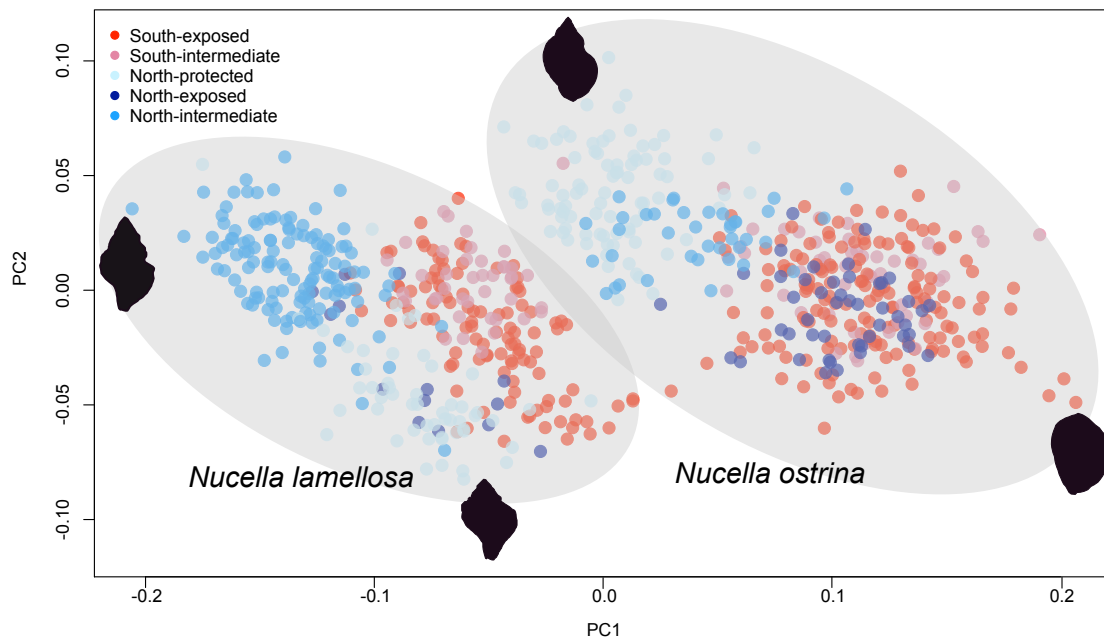


Figure 2.7. Morphospace with *Nucella lamellosa* and *Nucella ostrina* plotted together to show similar differences between northern and southern morphs. PC1 represents 69% of the variance and PC2 represents 8% of the variance. Gray clouds show which points are *N. lamellosa* versus *N. ostrina*. Blue points represent specimens from northern sites (dark blue = exposed, blue = intermediate exposure, light blue=protected) and red points represent specimens from southern sites (red= exposed, pink = intermediate exposure).

2.5 Discussion

Nucella lamellosa and *N. ostrina* exhibit morphological variation across large and small spatial scales and across time. Here I compare phenotypic patterns evidently shaped by localized wave-exposure and inferred predation gradients with patterns evidently controlled by latitudinal distance (either via isolation of populations in the case of *N. lamellosa* or recent expansion following the LGM in the case of *N. ostrina*). Based on Marko's (2004, 2010) genetic study of *N. lamellosa* and *N. ostrina*, relatively high haplotypic diversity in the northern sites of *N. lamellosa* indicate that the species likely persisted to some extent in glacial refugia during the LGM, whereas little haplotypic diversity in northern sites of *N. ostrina* indicate a recent post-LGM northern expansion. For both *N. lamellosa* and *N. ostrina*, northern present-day populations represent a change in shell shape from southern present-day populations and fossils. However, while both species show changes between northern, southern, and ancestral forms, the changes in shape are different for *N. lamellosa* and *N. ostrina*. For *N. lamellosa*, northern present-day populations have smaller apertures than southern present-day populations and fossil specimens, whereas for *N. ostrina*, northern present-day populations are higher-spined than southern present-day populations and fossil specimens.

Phenotypic changes across a wave-exposure and predation gradient have received considerable attention (Kitching et al. 1966, Boulding & Hay 1983, Palmer 1990, Webster & Palmer 2016, Edgell and Neufeld 2008). Based on predictions from previous studies, wave-exposed *Nucella* were expected to have relatively larger apertures and thinner shells for a given size than wave-protected *Nucella*, which should have smaller apertures and thicker shells as a result of increased predation associated with wave-protected shores (Table 2.1). Thinner shells

with larger apertures (and therefore larger foot area) are less likely to dislodge from intertidal rocks in areas of high wave exposure (Kitching et al. 1966). Predation has been found to induce thickening of the shell and narrowing of the aperture (as well as developing apertural teeth) presumably as a response to detecting crab effluent or the scent of damaged conspecifics (Appleton and Palmer 1988). Smaller apertures have been found to have a selective advantage where crab predation is common (Palmer 1990, Gibbs 1993). Predation on gastropods, especially by crabs, tends to be more intense on wave-protected shores, and predation intensity also tends to increase with decreasing latitude from temperate to tropical marine shores (Vermeij 1978). While there is no direct evidence that predation on *Nucella* decreases from southern California to the Aleutians, previous studies suggest that general pattern (Fawcett 1984). Taking all the sites together, I find the expected differences in lip thickness and a trend towards larger apertures (though not significant) in *N. ostrina* at wave-exposed sites, but not in *N. lamellosa* (none of the traits were significantly different by wave exposure) (Figure 2.3). *Nucella lamellosa*'s position lower in the intertidal may buffer it from the stark differences in wave action at exposed sites, resulting in less pressure to enlarge the aperture at exposed sites. However, the differences between wave-exposed and wave-protected morphs are not nearly as pronounced as the difference between northern and southern morphs (Figure 2.2).

While some of the shell differences across latitude in *N. lamellosa* and *N. ostrina* are consistent with expectations, others are not. Consistent with expectations from latitudinal trends in calcification (Graus 1974, Trussell 2000, Table 2.1) and with increased predation at lower latitudes, both species have thicker shells at lower latitudes (Figure 2.2). However, contrary to expectations (Graus 1974, Vermeij 1978, DeWolf 1998), spire height increases (Figures 2.4, 2.5) and aperture length and width decrease for a given shell length at higher latitudes in both species

(Figure 2.2). Higher-spined, small aperture morphologies at higher latitudes are contrary to expectations from Graus 1984, Vermeij 1978, Crothers 1973 and DeWolf et al. 1998, who predict higher-spined morphs at lower latitudes due to greater likelihood of heat stress and higher predation. Similarly, Hellberg et al. (2001) found northern *Acanthinucella spirata* to be shorter-spined than southern morphs. However, numerous others have claimed that increased predation selects for lower-spined morphologies (see especially Kitching et al. 1966 and Boulding and Hay 1983). These findings of reduced aperture size and increased spire height at northern sites are contrary to the expectation that predation (which we might expect to be higher at low latitudes) would drive aperture size reductions and spire height increases. Therefore, we might predict that either predation is not decreasing with increasing latitude, or, more likely, that predation is not driving the differences in shell shape between northern and southern sites. Because spire height may be affected by different conditions (temperature, wave action, predation), *Nucella* may be responding to pressures other than predation, for example, *N. lamellosa*'s smaller apertures at northern sites may be an adaptation to lower wave exposure at northern sites, or could have been an adaptation to historical environments during the LGM when it persisted in northern refuges.

Visualizing the combined effect of latitude and wave exposure on morphology in both species, northern wave-exposed and wave-protected populations of *N. lamellosa* show separation from southern populations in morphospace, but wave-exposed northern populations of *N. ostrina* seem to be more similar to southern populations than to northern protected populations. Perhaps for *N. ostrina*, northern wave-protected and intermediate-exposure sites provide novel pressures, e.g. owing to a different suite of predators compared to northern wave-exposed sites.

Alternatively, the relatively recent rapid expansion in *N. ostrina* without persistence in northern refuges might be responsible for the consistent morphology in exposed sites across latitudes in *N.*

ostrina. Surveys of *Nucella* predators across their geographic range, especially comparing northern wave-protected and northern wave-exposed sites could help test whether the novel shell forms in northern wave-protected sites are the result of novel predation pressures.

In addition to genetic evolution leading to local adaptation, plasticity--the potential for a single genotype to produce different phenotypes in different environments (West-Eberhard 1989)--can also influence local responses to environmental conditions. Studies on the genus *Nucella* have shown that local factors such as wave exposure and predation intensity can dramatically influence shell shape and shell thickness (Etter 1989, Palmer 1990), and both local genetic adaptation and plasticity have been implicated (Pascoal et al. 2012). *Nucella lamellosa* exhibits high morphological plasticity in response to biotic and abiotic conditions (Spight 1973, Appleton and Palmer 1988, Pascoal et al. 2012), and has been used as a model for determining the genetic and plastic components of phenotypic variation through common-garden experiments (Pascoal et al. 2012). A common-garden or reciprocal transplant test could test whether the phenotypic differences observed across time and space in *Nucella lamellosa* and *Nucella ostrina* are the result of plastic responses to different environmental conditions or evolved genetic differences between northern and southern groups. Teasing apart the influence of plasticity could give additional insight into the influence of the different histories of expansion and rapid phenotypic change in these two gastropods.

The morphospace plots in this study show differences in shell shape across latitudes when northern and southern groups are compared, but univariate shell traits do not vary significantly with latitude (Figure 2.6). For *Nucella ostrina*, this seeming contradiction in the results might be due to one outlier population, the most northern site, where it was difficult to find any large individuals. When northernmost site is excluded, snails significantly increase in

size with increasing latitude. However, the discrepancy between morphospace results (Figure 2.4) and shell traits as a function of latitude (Figure 2.6) persists in *Nucella lamellosa*. In both the Hotelling's T^2 tests and two-way MANOVA (*Nucella lamellosa* only), the smaller sample size of the fossil collections is likely responsible for the lower variance in shell shape. I collected ancient phenotypes across the geographic range of *Nucella lamellosa*, but was unable to collect ancient phenotypes for *Nucella ostrina* in the northern part of the range (fossil material only from California and midden material only from Washington). The lack of ancient *Nucella ostrina* shells from northern sites makes it difficult to determine whether the present-day northern forms differ (and therefore are recently evolved) from ancient forms.

Adaptations to past and present range expansions have been studied across numerous systems, such as terrestrial plants, where species adapted locally to the climatic conditions into which they expanded (Davis and Shaw 2001), and North American birds, where new morphotypes were found in a newly-colonized region (Mila et al. 2007). Even present-day plant and marine invasions, which offer a real-time look at adaptation to novel habitats, have been shown to exhibit different phenotypes than those seen in their native ranges (Maron et al. 2004, Roy et al. 2002, Grosholz and Ruiz 2003, Suarez and Tsutsui 2008). In addition to expansion and invasion leading to adaptation, refugial populations have also been found to produce distinct phenotypes and potentially lead to speciation, such as in numerous examples in birds and amphibians (Zink and Dittman 1993, Garcia-Moreno & Fjeldsa 2000, Weir 2006, Hoskin et al. 2011), though some studies have questioned whether isolation in refugia commonly promotes dramatic phenotypic differentiation among populations (Schneider and Moritz 1999, Schneider et al. 1999). Despite the initial prediction that *N. lamellosa* would have had a greater time to accumulate morphological differences between northern and southern forms due to persistence in

northern refuges and attenuated gene flow with southern populations during the LGM, I find shape differences across latitudes in both species, supporting the notion that both rapid adaptation following range expansion and adaptations in isolation can produce population-level differences over time and space.

2.6 Conclusion

The present work adds to the limited number of studies on morphological evolution in the course of range expansion for marine invertebrates. For *Nucella ostrina*, the differences in present-day northern populations from southern and ancestral ones likely reflect a rapid evolution in response to novel conditions in the northern part of the range following the LGM. However, for *Nucella lamellosa*, the differences in present-day northern populations from southern and ancestral ones could either reflect differences accumulated in isolation or rapid evolution to novel conditions in the previously unoccupied areas of the northern range. In either case, these results demonstrate that morphological evolution can occur in a variety of contexts. This study also adds to previous work on the drivers of shell shape at a more localized scale, where wave action and predation can vary over short distances.

CHAPTER 3: Latitudinal and microgeographic clines under plastic control in two *Nucella* rocky shore gastropods

3.1 Introduction

Rapid phenotypic changes associated with range expansions and human-mediated introductions have been found across terrestrial and marine taxa (Hellberg et al. 2001, Davis and Shaw 2001, Grosholz and Ruiz 2003, Sax et al. 2007, Colautti and Barrett 2013). Morphological variation may be the result of a plastic response to environmental conditions--a single genotype giving rise to different phenotypes under different conditions (West-Eberhard 1989)--or may be the result of local adaptation. However, apart from short-lived species (Hoffmann et al. 2005, Chown and Gaston 2010), teasing apart heritable local adaptation from a plastic phenotypic response has been difficult and rare (Gienapp et al. 2008, Pascoal et al. 2012). Phenotypic plasticity should be advantageous over local adaptation if populations are distributed among habitats with different fitness requirements, which may result from a high dispersal life mode bringing populations into contact with a range of environmental conditions, and if the cost of maintaining plasticity is low (Price et al. 2003, Pigliucci 2005). Alternatively, a low-dispersal life mode, where populations stay relatively sedentary, little historical variation in environmental conditions, and high costs of maintaining phenotypic plasticity should favor local adaptation (Kawecki and Ebert 2004, Hollander 2008). Understanding the relative contributions of plasticity and genetic evolution to phenotypic variation is important for understanding evolutionary processes across a species' range (Pascoal et al. 2012).

Snails in the genus *Nucella* exhibit remarkable morphological variation across habitats and latitudinal distance. Numerous studies have found plasticity in *Nucella* in response to varying levels of wave action (Etter 1989, 1996, Gibbs 1993) and predation (Hughes and Elner 1979, Appleton and Palmer 1988, Bourdeau 2009, Webster and Palmer 2016). *Nucella* snails at wave-protected sites, which tend to experience higher rates of predation by crabs have thicker shells (Appleton and Palmer 1988, Pascoal et al. 2012) and smaller apertures (Hughes and Elner 1979) than wave-exposed snails, which exhibit larger apertures corresponding to larger foot area to better adhere to intertidal rocks. However, due to *Nucella*'s direct-developing life habit, which inhibits high levels of dispersal among populations, there is also an opportunity for local adaptation.

While both plasticity and local adaptation have been found to control phenotypic variation across a wave-exposure and predation gradient in *Nucella* (Pascoal et al. 2012), relatively little attention has been paid to the contribution of plasticity across the latitudinal gradient in morphology in *Nucella*. The historical isolation and range expansion experienced by *Nucella* species during the Last Glacial Maximum (LGM) likely structures the phenotypic variation latitudinally. In this paper I compare *N. lamellosa* and *N. ostrina*, two common molluscan predators on eastern Pacific rocky shores in the light of their inferred Pleistocene history. *Nucella ostrina*'s northern sites are dominated by a single haplotype, suggesting a recent range expansion (Marko 2004). In contrast, *N. lamellosa*'s northern sites include many unique (likely ancient) haplotypes, suggesting persistence by at least some small refuge populations in the northern part of its range (Marko 2004).

Kincaid (1957), in extensive observational studies of *N. lamellosa* across its geographic range, questioned the heritable and plastic aspects of morphology across microgeographic and latitudinal clines:

“The great diversity and localized character of the immense number of populations of *Thais* [now *Nucella*] *lamellosa* inhabiting the Pacific Coast of North America, is due primarily to genetic segregation in an extremely unstable hereditary constitution and the effects of geographic and microgeographic isolation... The populations of *Thais*, although they are extremely varied and heterogeneous in character, nevertheless show indications of groupings that are presumably related to the early distributional pattern of the species, when presumably it was segmented for vast periods of time as the glaciers advanced and retreated during the Pleistocene.”

While Kincaid (1957) observed a great variety of forms and seemed to infer a role for both plasticity and local adaptation, attributing phenotypic variation to plasticity or local adaptation often requires reciprocal transplants or common-garden experiments. Reciprocal transplant experiments involve transplanting populations between sites and observing the phenotypic response following transplantation (Kawecki and Ebert 2004, Trussell 2000), but can be practically difficult and can bring up ethical concerns if populations are transplanted far from their native sites. An alternative, a common-garden experiment, explores phenotypic variation under identical environmental conditions. If the offspring from different parent populations retain their differences under identical conditions, it is likely that local adaptation controls phenotypic variation (Bossdorf et al. 2005). Persistence of parental forms in the second generation would suggest local adaptation, rather than plasticity or maternal effects. Previous common-garden studies have found plasticity in gastropod morphology across wave-exposure and predation gradients (Appleton and Palmer 1988, Trussell 2000, Pascoal et al 2012), but plasticity across a latitudinal gradient remains underexplored. To investigate whether morphological differences across latitude in *N. lamellosa* and *N. ostrina* can be attributed to

plasticity or local adaptation, I raised populations of both species in a common-garden experiment. I assess multivariate shape in addition to univariate shell traits (shell length, aperture length, aperture width, and lip thickness) to test whether the offspring populations show phenotypic plasticity and converge on a similar shape under common-garden conditions, or if the offspring populations show little phenotypic plasticity and exhibit shapes similar to those in the parent populations.

3.2 Methods

3.2.1 Collection sites

I collected *N. lamellosa* and *N. ostrina* from multiple sites near their northern and southern geographic range limits (Table 3.1). For *N. ostrina*, populations were collected at Bodega Bay, California (egg capsules and adults) (wave-protected), Van Damme, California (egg capsules only) (wave-exposed), Sitka, Alaska (wave-protected), Graves Harbor, Alaska (wave-intermediate), and Yakobi, Alaska (wave-intermediate). For *N. lamellosa*, populations were collected at Friday Harbor Labs (egg capsules and adults) (wave-intermediate), Monashka, Alaska (wave-intermediate), Fossil Beach, Alaska (wave-intermediate), Lemesurier Island, Alaska (wave-intermediate), and Murphy Cove, Alaska (wave-protected). Collection and transportation permits were obtained from the California Department of Fish and Wildlife, Friday Harbor Laboratory, and Alaska Department of Fish and Game (CF-14-044, FTP 14J-1012).

Site	Lat/Long	Exposure	Exposure Reference	Notes
<i>Nucella ostrina</i>				
Bodega Bay, California	38°19' 59, -123°02' 53	Protected	Hahn 1998	~40 adults introduced into common-garden tanks; eggs were laid and hatched in May/June 2014; 4 offspring snails grew to sufficient size to be photographed
Van Damme, California	39°16' 24, -123°47' 29	Exposed	Sanford & Swezey 2008	Egg capsules laid at the site were introduced into the common-garden tanks, which hatched, but did not grow to sufficient size to be photographed
Sitka Sound Science Center, Alaska	57°02' 57.4, -135°19' 22.61	Protected	NOAA Shorezone	~50 adults were introduced into the tanks; eggs were laid and hatched in July/August 2015; 3 offspring snails grew to sufficient size to be photographed
Hoktaheen (Yakobi), Alaska	58°03' 36.6, -136°33' 48.3	Exposed	NOAA Shorezone	~40 adults were introduced into the tanks; eggs were laid and hatched in October 2014; 6 offspring snails grew to sufficient size to be photographed
Murk Bay (Graves Harbor), Alaska	58°17' 24, -136°44' 03	Intermediate (Semi-exposed)	NOAA Shorezone	~30 adults were introduced into the tanks; eggs were laid and hatched in October 2014, but did not grow to sufficient size to be photographed
<i>Nucella lamellosa</i>				
Kalaloch, Washington	47°36' 18.38, -124°22' 30.75	Exposed	Dethier et al. 2003	2 adults from Kalaloch were introduced in the tanks; no eggs were laid in the tanks
Cattle Point, Friday Harbor, Washington	48°27' 00, -122°57' 46	Intermediate	Menge 1974, Spight 1973, Schoch 1999, Carrington et al. 2008 & Hohenlohe 2003	~40 adults introduced into the tanks; none of the adults laid eggs in the tanks, but egg capsules were collected at the site and three egg capsules were laid in transport from Washington to Chicago; those three egg capsules hatched in May 2014; 5 offspring snails grew to sufficient size to be photographed
Fossil Beach, Kodiak, AK	57°25' 39.34, -152°21' 22.27	Intermediate (Semi-exposed)	NOAA Shorezone	14 adults were introduced in the tanks; no eggs were laid in the tanks
Monashka Beach, Alaska	57°49' 42.19, -152°22' 40.97	Intermediate (Semi-protected)	NOAA Shorezone	~40 adults were introduced in the tanks; no eggs were laid in the tanks
Murphy Cove (exposed), Alaska	58°15' 52.4, -136°43' 30.2	Intermediate (Semi-exposed)	NOAA Shorezone	7 adults were introduced in the tanks; no eggs were laid in the tanks
Murphy Cove (protected), Alaska	58°16' 08.3, -136°43' 06.8	Protected	NOAA Shorezone	7 adults were introduced in the tanks; no eggs were laid in the tanks
Lemesurier Island, Alaska	58°16' 26.1, -136°03' 44.3	Intermediate (Semi-protected)	NOAA Shorezone	11 adults were introduced in the tanks; no eggs were laid in the tanks

Table 3.1. Collection sites with latitudinal and longitudinal coordinates, and wave-exposure classification (with the reference for wave exposure assignment), and notes on fate of each population

3.2.2 Common-garden

All populations were maintained at the University of Chicago in two ~60 gallon tanks (one for each species) set up in an 11°C cold room. Salinity was kept between 32-35 ppt InstantOceanTM. Adults were labeled shortly after they were introduced into the tanks in Chicago using nail polish at the growing edge of the aperture (both to number individuals and to track post-arrival growth). Snails were sorted by source population into plastic containers with mesh screens to allow water to flow into the containers and keep populations separated while controlling for tank effects by holding them within the same larger tank. Lighting in the cold room was on a twelve-hour cycle, but no attempts were made to simulate natural tide cycles. Barnacles (*Balanus spp.*) from the Marine Biological Laboratory in Woods Hole were placed in the tanks approximately every two weeks as prey (each bi-weekly shipment usually contained enough barnacle-covered rocks to place one (with ~20-100 barnacles) into each population's smaller plastic container).

All populations of *N. ostrina* laid eggs in the tanks, but none of the *N. lamellosa* populations did. Thus the only offspring *N. lamellosa* population was from Friday Harbor, where egg capsules had been collected at the site and shipped to Chicago. These egg capsules hatched in May 2014, approximately 4 months after the start of the experiment. *Nucella ostrina* egg capsules from Bodega Bay hatched in May/June 2014, from Van Damme hatched in April 2014 (but none survived long enough to be photographed (>10mm growth), from Graves Harbor and Yakobi hatched in October 2014 (but only Graves Harbor survived long enough to be photographed), and from Sitka hatched during the Summer of 2015. Post-hatching, offspring snails were split into two groups per population and transferred into small replicate containers to

control for any possible tank effects. These replicate containers had mesh screens and were still within the same larger tank and so they shared water.

3.2.3 Geometric morphometrics

Photographs and caliper measurements (shell length, aperture length, aperture width, and lip thickness) of all populations were taken approximately every 3-6 months post-introduction into the tanks. Offspring snails were photographed approximately 6 months post-hatching and/or when they had grown approximately 10mm. I used FIJI software (<http://imagej.net/Fiji>) to digitize the photographs of populations for landmark-based geometric morphometrics. To quantify shell shape, I digitized 12 landmarks (Figure 3.1) that could be reliably recognized in both species, following Pascoal et al. (2012). Procrustes superimposition was performed using the CoordGen program (version 8) within the IMP software package. Procrustes superimposition rescales all landmark configurations (for each specimen) to remove differences in size, rotates configurations to remove differences in orientation, and centers configurations on the centroid to align landmarks (Webster and Sheets 2010). I performed a principal components analysis (PCA) on each of the species to visualize differences in shape between parent and offspring populations. To assess differences between parent and offspring populations, I compared multivariate shape in a Hotelling's T^2 test using TwoGroup8 in IMP software. In addition, I compared shape and size between parental populations and offspring using the Reg.proj score from the 'geomorph' package in R. Data visualizations, including PCA, and statistics used the Geomorph package in R and the IMP (Integrated Morphometrics Package) software suite (including CoordGen8, PCAGen8, TwoGroup8) (<http://www3.canisius.edu/~sheets/IMP%208.htm>).

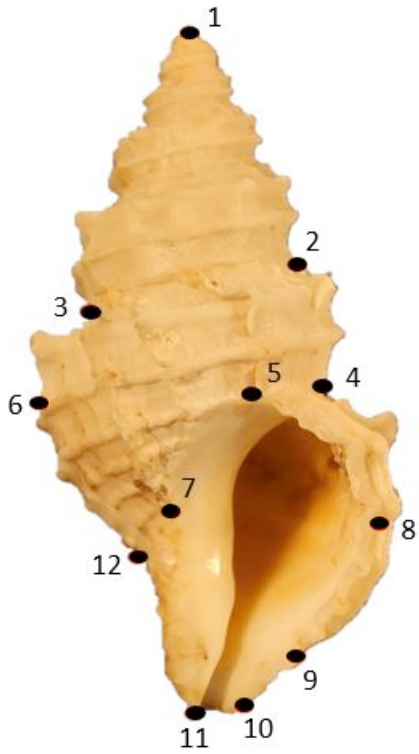


Figure 3.1. Twelve landmarks used in this study for geometric morphometrics for both *N. lamellosa* and *N. ostrina*. Landmarks are shown on a specimen of *N. lamellosa*.

Shape scores (Reg.proj in the geomorph package) were regressed against log centroid size to compare allometry in the offspring snails with allometry in the parent populations. I tested convergence of the offspring populations under common-garden conditions by comparing distance of mean shape of each parental population to the grand mean of parental populations and distance of mean shape of each offspring population to the grand mean of offspring populations using the DisparityBox8 program in IMP. I also tested convergence using pairwise parent comparisons of each population and pairwise offspring comparisons of each population to test if the Procrustes distances between offspring from different populations was less than the Procrustes distances between parents from different populations.

Caliper measurements of shell traits--shell length, aperture length, aperture width, and lip thickness (as in Palmer 1990)-- were used to supplement the landmark-based morphometric data. Notably, shell thickness is more difficult to reliably quantify using images alone. Shell thickness in offspring and parent populations was compared using a t-test. Because shell thickness can covary with shell size in some snails, shell thickness (and other univariate traits) were also regressed against size.

3.4 Results

3.4.1 Allometry

Plotting shape against log centroid size, I find significant differences in both size and shape between parent and offspring populations of *N. lamellosa* and *N. ostrina* (Figure 3.2, Table 3.2). In order to control for those differences in size (and age), I performed a size-standardization using the Standard8 IMP program, in which I used the average offspring size as the size to standardize the parent population (Supplementary Materials—Figures S3.1-4).

Nucella ostrina

Three of the *N. ostrina* populations that had been transplanted into the common-garden aquaria tanks laid eggs (Table 3.1), which hatched and grew to sufficient size for comparison to the parent populations (from Bodega Bay, CA, Graves Harbor, AK, and Sitka, AK). Two populations (from Van Damme, CA and from Yakobi, AK) laid eggs that hatched, but did not grow to a sufficient size for comparison to the parent populations. Although photographs of the offspring snails were taken regularly after they had gained sufficient size, I compare the most recent photographs and measurements of offspring snails (at their ontogenetically oldest stage reached during the duration of the experiment) to parent populations to allow for as much growth as possible and thereby minimize effects of allometry. At the time of the final photographs and measurements, Bodega Bay offspring snails were ~26 months post-hatching, Graves Harbor offspring snails were ~22 months post-hatching, and Sitka offspring snails were ~12 months post-hatching. *Nucella ostrina* snails have been found to reach maturation at approximately 1 year post-hatching (Gosselin and Qian 1997), and so most, if not all, of the offspring *N. ostrina* snails had reached maturation. In fact, the offspring snails from Bodega Bay and from Graves Harbor laid eggs in the tank (producing second-generation snails). However none of the second-generation snails had grown to sufficient size by the end of this study.

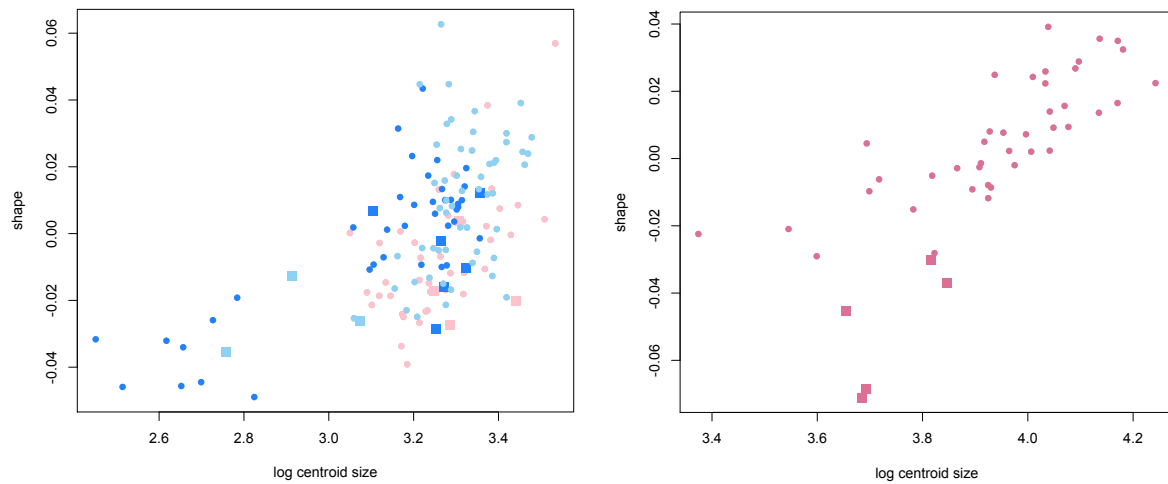


Figure 3.2. Allometry plotted using the geomorph package in R. Points represent individual snails and are colored by offspring and parent populations with log centroid size on the x-axis and shape (Reg.proj from geomorph) on the y-axis (squares represent offspring populations and circles represent parental populations); *Nucella ostrina* on the left with three offspring/parent population comparisons (Blue=Sitka, Light blue=Graves Harbor, Red=Bodega Bay); *Nucella lamellosa* on the right with one F1/parent population comparison (Red=Friday Harbor).

Species	Site & Sample Size	Shape Scores (Reg.Proj)			Log Centroid Size		
		F1 (mean & SE)	Adult (mean & SE)	T-Test	F1 (mean & SE)	Adult (mean & SE)	T-Test
<i>N. ostrina</i>	Bodega Bay F1=4 Adult=39	0.039180076 +/- 0.004155556	-0.00401847 +/- 0.004114386	T = 10.44699*	3.321176 +/- 0.04212689	3.262281 +/- 0.01865183	T= 1.807852
<i>N. ostrina</i>	Graves Harbor F1=6 Adult=39	0.042570665 +/- 0.006249730	-0.0065493 +/- 0.004966718	T = 8.701816*	3.262294 +/- 0.03569071	3.101547 +/- 0.04174536	T= 4.139101*
<i>N. ostrina</i>	Sitka F1=3 Adult=54	-0.0922824 +/- 0.003920295	0.005126802 +/- 0.002695106	T= -28.9568*	2.914410 +/- 0.09082345	3.313158 +/- 0.01194937	T= -6.155862*
<i>N. lamellosa</i>	Friday Habor F1= 5 Adult= 41	-0.0504252 +/- 0.008279161	0.006149415 +/- 0.002772690	T= -9.163619*	3.738811 +/- 0.03863127	3.944039 +/- 0.02830001	T= -6.060723*

Table 3.2. Results from comparisons of parent versus offspring shape and size using shape and size metrics from allometry plots in ‘geomorph’ package in R. Each pair (parent & offspring) are analyzed separately (i.e. allometry was just calculated based on the specimens in that site). All populations are significantly different in shape, and all except Bodega Bay are significantly different in size

In a principal components analysis including both the offspring populations and size-standardized parent populations, all offspring populations appear to diverge from their parental populations and converge on a more similar morphology similar (Figure 3.3, Supplementary Figure 3.5). All offspring populations show striking movement away from the parent populations in morphospace (Figure 3.3), and all offspring populations are significantly different from their parent populations in shape using comparisons of Reg.proj (a shape score from the ‘geomorph’ package in R) between parent and offspring populations (Table 3.2) and in Hotelling’s T^2 test performed using TwoGroup8 in the IMP program (Table 3.3) with landmarks 1 and 7 as baseline endpoints. To test convergence in morphospace, I performed an F-test on distance between each population’s mean form to the grand mean form for parental populations and distance between each population’s mean form to the grand mean form for offspring populations, with the expectation that offspring mean forms would be less distant to the grand mean than parental mean forms to their grand mean if there is convergence under common-garden conditions. Consistent with expectations, I find that offspring pairwise comparisons are closer in Procrustes distance than the corresponding parental pairwise comparisons (except for the Graves to Sitka comparison), indicative of convergence on a similar morphology under common-garden conditions (Table 3.4). I used the IMP DisparityBox8 software for another test of convergence and I find that offspring populations are less distant to the offspring grand mean than parental populations to the parental grand mean, but not significantly ($F=3.43$, $df=2, 2$, $p=0.226$). Despite the convergence towards a more similar form among the offspring populations, the significant differences between the offspring populations (Table 3.4) are also indicative of effects of local adaptation or maternal effects from the parental population.

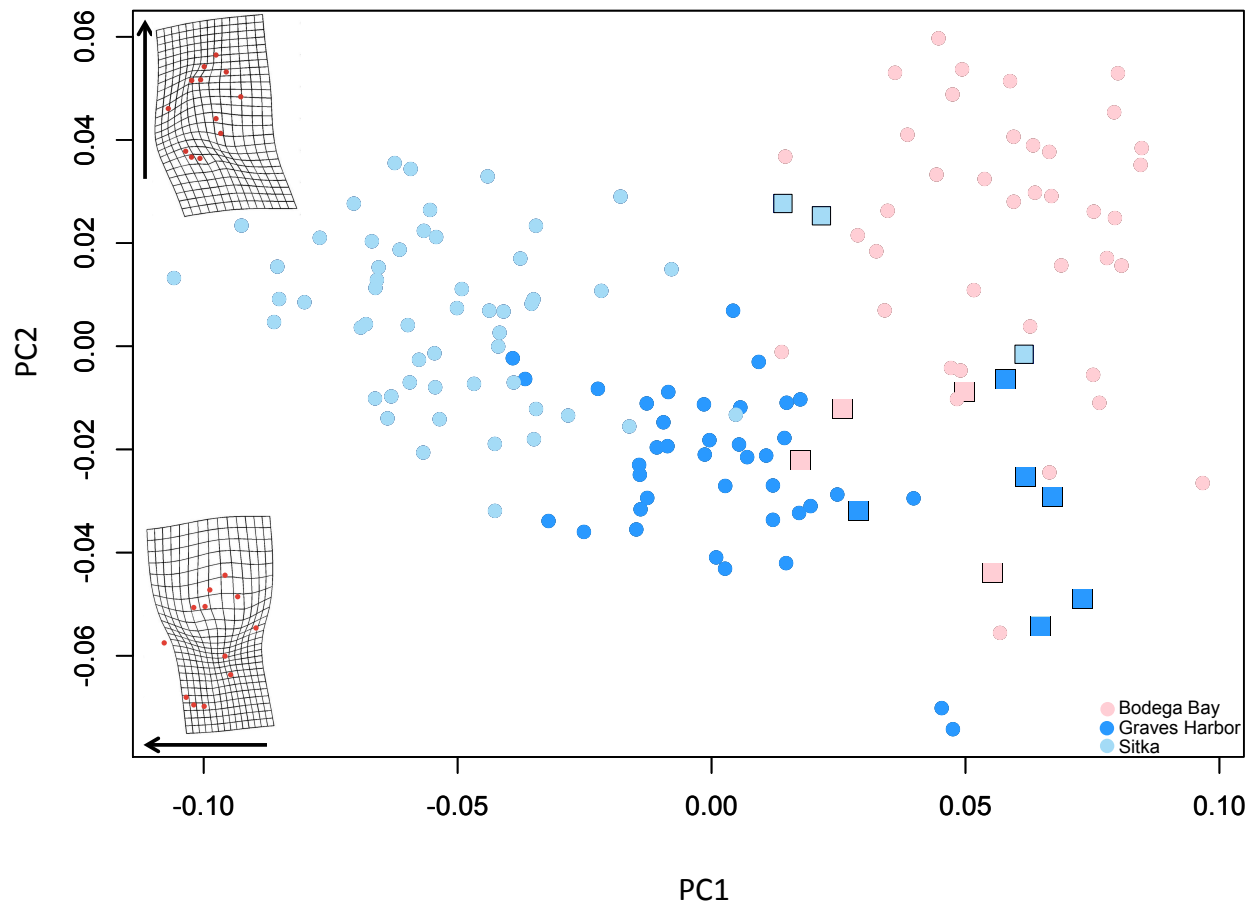


Figure 3.3. *Nucella ostrina* morphospace plot with *N. ostrina* populations from Bodega Bay, CA, Sitka, AK and Graves Harbor, AK. Points are colored according site. Offspring populations are shown in square points. Size-standardized parent populations are the circle points. PC1 is strongly influenced by shell spire height, and PC2 by aperture shape. Deformation grids show the shape variation along PC1 (lower left corner) and PC2 (upper left corner). PC1 represents 47.91% of the shape variance, PC2=13.26%, PC3=9.57%, PC4=5.7%, PC5=4.8%.

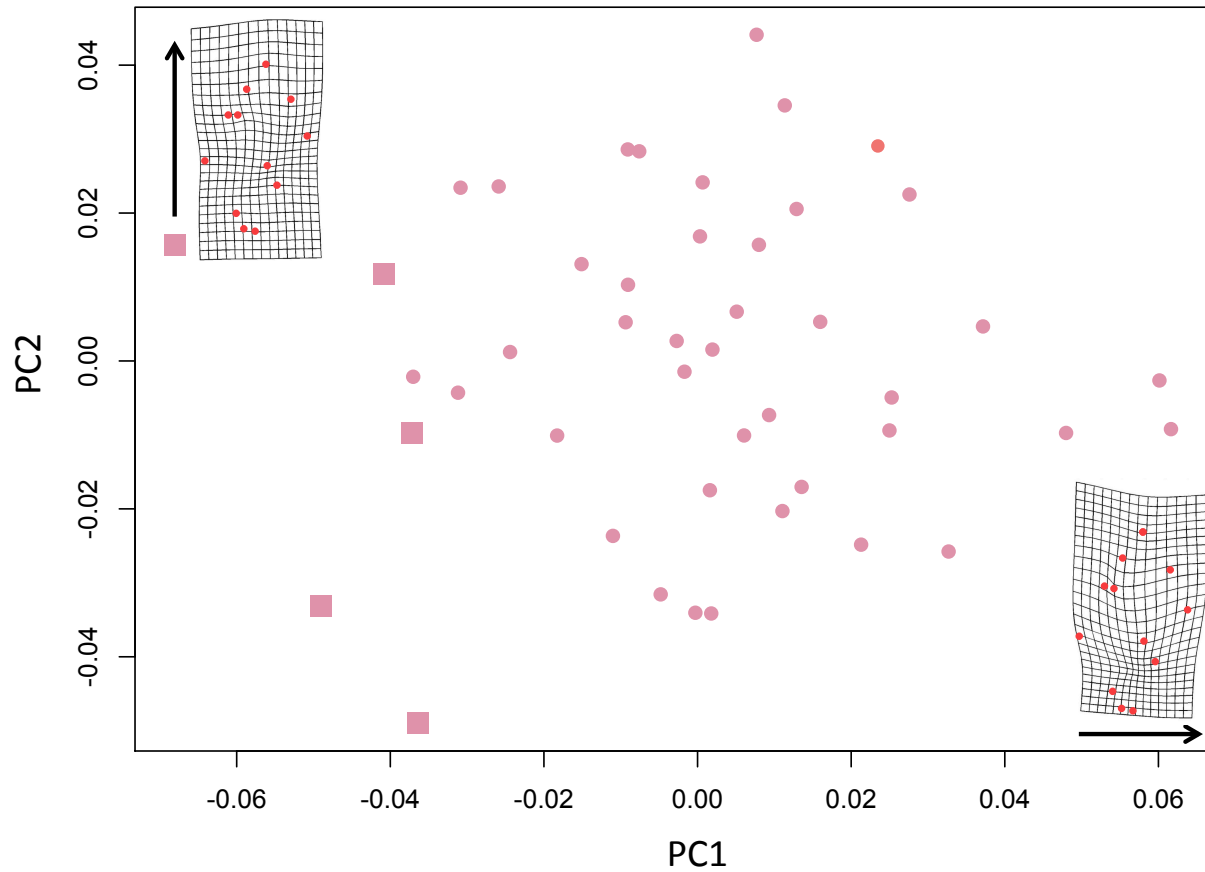


Figure 3.4. *Nucella lamellosa* morphospace plot with parent population from Friday Harbor, WA. The offspring population is shown in square points. Size-standardized parental populations is shown in the circle points. PC1 is strongly influenced by shell spire height, and PC2 by aperture shape. Deformation grids show the shape variation along PC1 (lower left corner) and PC2 (upper left corner). PC1 represents 26.35% of the shape variance, PC2=15.73%, PC3=13.48%, PC4=10.86%, PC5=7.83%.

Comparison of parent to offspring	Df	F	p	Distance between means
Friday Harbor (<i>N. lamellosa</i>)	24, 21	5.34	0.000128	0.3062
Bodega Bay (<i>N. ostrina</i>)	24, 18	6.53	<0.01	0.2622
Graves Harbor (<i>N. ostrina</i>)	24, 20	21.94	<0.01	0.6749
Sitka (<i>N. ostrina</i>)	24, 32	15.81	<0.01	0.5048

Table 3.3. Results from Hotelling's T^2 tests between parent and offspring populations.

Comparison	Sample Size	F	p	Distance between means
Parent population comparisons				
Sitka: Graves	54, 39	42.24	0.01	0.0674
Sitka: Bodega	54, 39	103.81	0.01	0.1132
Bodega: Graves	39, 39	44.73	0.01	0.0744
Offspring population comparisons				
Sitka: Graves	3, 6	4.4	0.01	0.0688
Sitka: Bodega	3, 4	2.61	0.03	0.062
Bodega: Graves	4, 6	3.3	0.01	0.0583

Table 3.4. Results from pairwise disparity tests to assess convergence in the offspring populations compared to the parent populations. Pairwise tests were performed in a Resampling F-test using the TwoGroup8 package (IMP) with 100 bootstraps.

In addition to changes in multivariate shape in offspring snails detected using landmark-based morphometrics, offspring snails with parents from wave-protected sites (Bodega Bay and Sitka) also exhibit significantly thinner shells than parent populations, when absolute shell thickness is plotted (Figure 3.5). When regressed against shell length (Figure 3.6), Bodega Bay (wave protected) and Sitka (wave protected) offspring exhibit thinner shells than parental populations for a given size, but Graves Harbor (intermediate wave action) offspring show the opposite pattern (Figure 3.5, 3.6).

Nucella lamellosa

None of the transplanted *N. lamellosa* laid eggs in the common-garden aquaria tanks, despite efforts to induce spawning by providing an abundance of prey as has worked in other *Nucella* experiments (Sanford, pers. comm.). Egg capsules were collected at Friday Harbor and transported to the University of Chicago, but only three egg capsules (which may have been laid in transport since they were on the shell of one of the adult snails) yielded offspring of sufficient size for comparison to the parent population. These egg capsules hatched in May of 2014, and were ~27 months post-hatching when the last photographs and caliper measurements were taken. While *N. lamellosa* may not reach maturation until ~4 years post-hatching (Gosselin and Qian 1997), the offspring snails had grown to > 2cm, placing them in the middle of the size distribution of the adult snails in the tanks, and minimizing the effects of shape changes with ontogeny (shell lengths of offspring and parent populations are plotted in Figure 3.7).

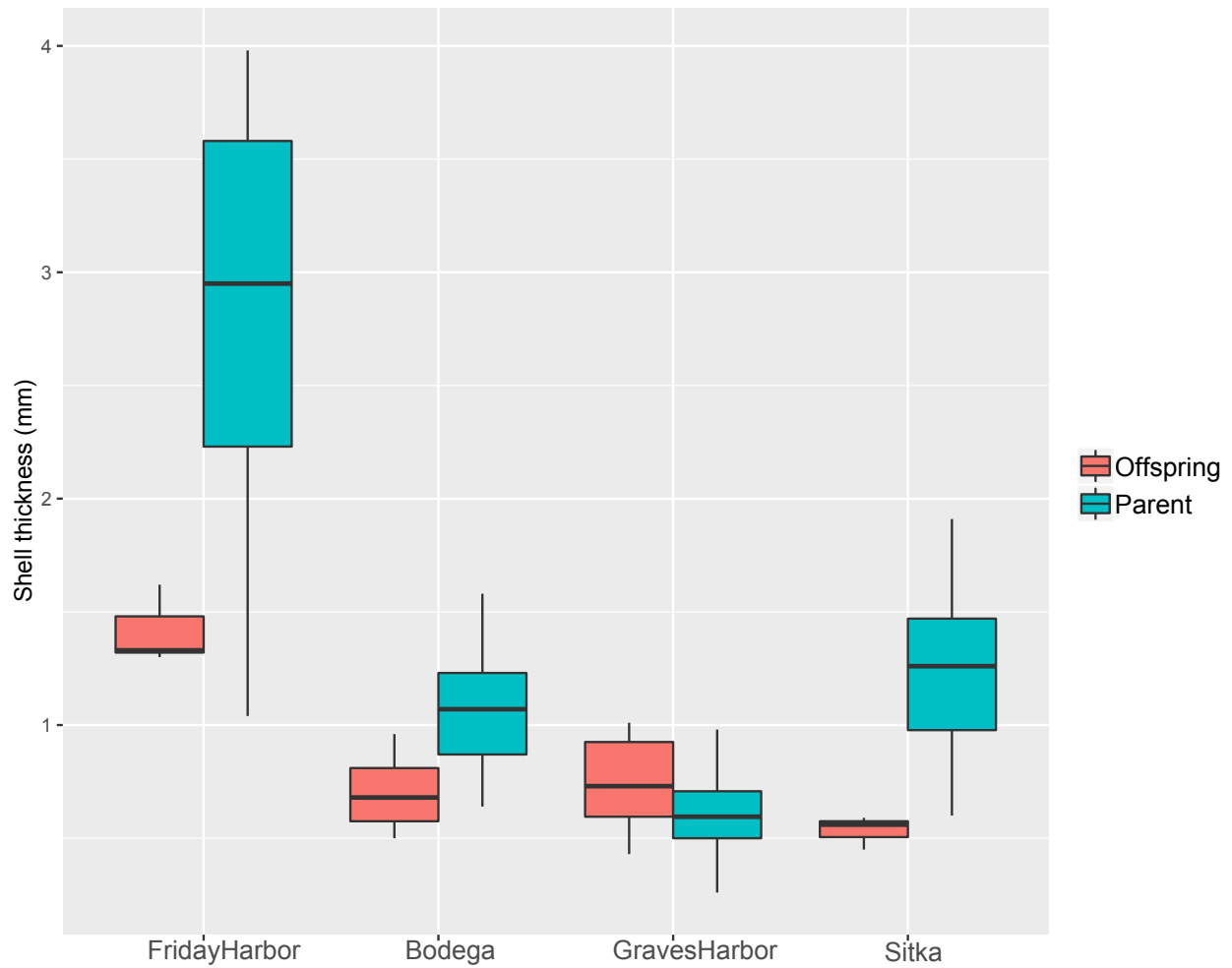


Figure 3.5. Shell thickness by site comparing offspring to parent populations. Shells are significantly thinner for all offspring populations compared to parent populations, except for Graves Harbor shells. Friday Harbor snails are *Nucella lamellosa* and the other three sites are *Nucella ostrina*.

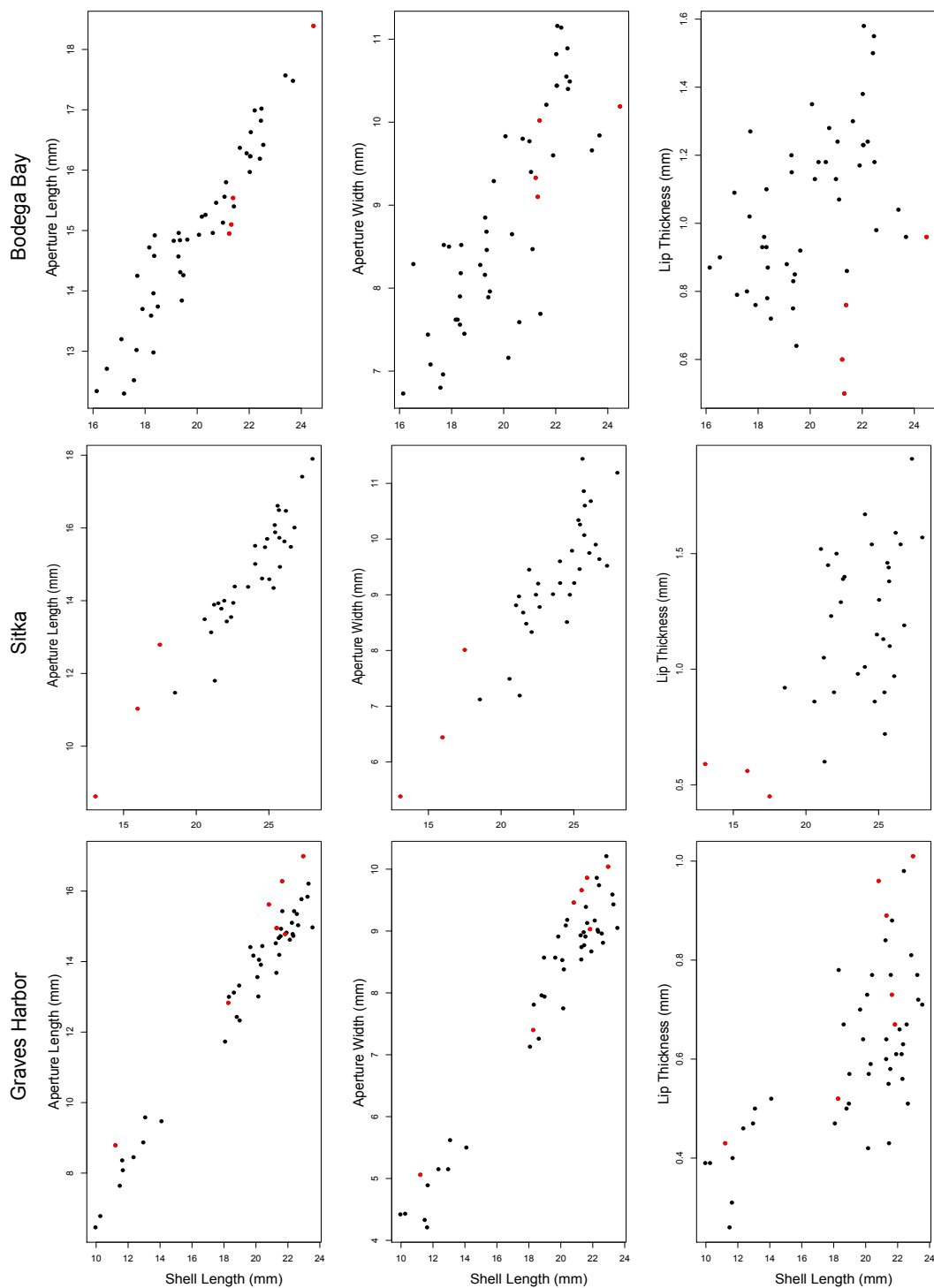


Figure 3.6. Shell traits (aperture length, aperture width, and lip thickness) plotted against shell length for *Nucella ostrina* showing the difference between parent (black) and offspring (red) populations.

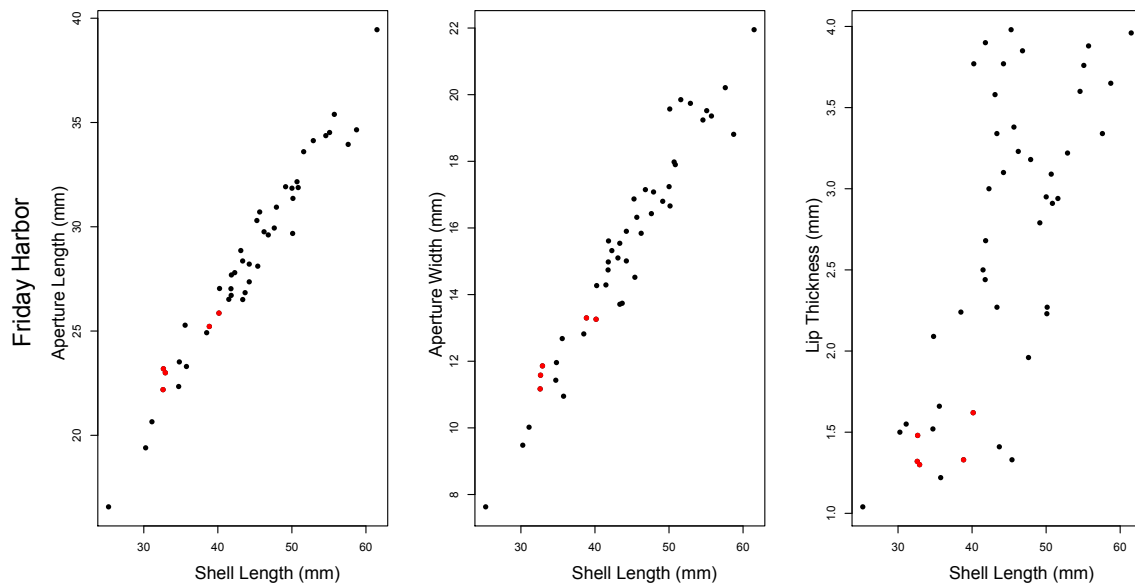


Figure 3.7. Shell traits (aperture length, aperture width, and lip thickness) plotted against shell length for *Nucella lamellosa* showing the difference between parent (black) and offspring (red) populations.

As with *N. ostrina*, shape is significantly different in the Friday Harbor offspring *N. lamellosa* compared to the parent population (Figure 3.4, Supplementary Figure S3.6) using both a comparison of shape using Reg.proj shape scores from the ‘geomorph’ R package (Figure 3.2, Table 3.2) and in a Hotelling’s T^2 test using size-standardized Bookstein coordinates for the parent population (Table 3.3). In addition to multivariate shape differences (from landmark-based analysis), the offspring Friday Harbor snails are thinner-shelled than the parent population when absolute shell thickness is plotted (Figure 3.5) and when regressed against shell length (Figure 3.7).

3.5 Discussion

Nucella ostrina

Intertidal snails at sites with heavy wave action tend to exhibit larger apertures, thinner shells, and shorter spires than snails at sites with low wave action (Hughes and Elnor 1979, Etter 1989, 1996, Gibbs 1993). Wave-exposed snails likely exhibit larger apertures (corresponding to larger foot area) to better adhere to intertidal rocks. Shortened spire and thinner shells of wave exposed snails compared to wave-protected snails are likely due to the relative absence of predators on wave-exposed rocks—predation (which tends to be more severe at wave protected sites) has been found to induce thickening and spire height increases in laboratory and natural settings (Appleton and Palmer 1988, Pascoal et al. 2012). With an absence of wave action in the common-garden aquaria, we might expect offspring snails to show a version of the wave-protected morphology. Instead, *N. ostrina* offspring snails under common-garden conditions diverge from their parents’ wave-protected form and appear to converge on a morphology more

similar to wave-exposed forms in morphospace. In addition to landmark-based morphometric data showing convergence on a wave-exposed morphology, *N. ostrina* offspring snails whose parents were collected from wave-protected sites exhibit thinner shells under common-garden conditions than parent populations. The thinner shells seen in common-garden offspring are consistent with the expectation that *Nucella*, in the absence of predators, will not induce shell thickening (as a defensive mechanism against predation). In the presence of predators, *Nucella* and other gastropods have been found to induce shell-thickening both in laboratory experiments (Appleton and Palmer 1988, Pascoal 2012), and in observations before and after the invasion of a crab predator, *Carcinus maenas*, on the western Atlantic coast (Trussell 2000). The thinner offspring shells resemble shells from wave-exposed sites, where predators are less common and shell thickening is, therefore, less advantageous. Thinner shells are also “less expensive to produce energetically” (Palmer 1990), however it is unlikely that the thin shells are attributable to low food availability (despite the relatively lower number of barnacles available to the snails in the tanks than in a natural setting) because shell thickening comes at the expense of linear shell growth (Palmer 1981, Trussell 2003) due to a maximum rate of calcification. Furthermore, in the presence of predation, snails tend to respond phenotypically by thickening their shell but behaviorally spending less time feeding, and so there does not seem to be a direct relationship between food consumption and shell thickness. While it is advantageous for juveniles to grow quickly until maturation, resulting in a thinner shell at a young age (Palmer 1981), it is unlikely that the thin shells in this experiment are due solely to size or age because all populations of *N. ostrina* snails were mature at the time of the measurements (and had even produced second generation hatchlings). Also, snails from the field of equivalent size to offspring snails reared in the common-garden experiment show much thicker shells, especially from Bodega Bay (*N.*

ostrina) and Friday Harbor (Figure 3.6). It is possible, however, that shell calcification in the tanks is lower than in natural settings if calcium concentration or pH is low, though effects of aquarium conditions (and Instant Ocean™) on calcification are mixed (Carlson 1999, Langdon 2000). However, offspring *N. ostrina* from Graves Harbor (a more exposed site) are thicker in the tanks than their parental forms, which lessens concerns about lower calcification in the common-garden experiment than natural settings, and gives further support for snails from wave-protected (likely high-predation) sites thinning their shells in the absence of predators in the common-garden tanks.

While the thin offspring shells observed here resemble wave-exposed morphs, *N. ostrina* offspring populations do not generally show an enlargement of the aperture, which is advantageous at wave-exposed sites because it increases adhesion strength (Kitching 1966, Crothers 1973, Gibbs 1993, De Wolf 1998, Rolan et al. 2004). Therefore, while the thinner shells in the offspring populations are similar to the thinner shells at exposed compared to protected sites possibly because the aquaria is lacking predators, the offspring snails lack other morphological characteristics of wave-exposed snails, perhaps because the aquaria are also lacking any wave action. The dissociation between larger apertures and thinner shells (characteristic of wave-exposed forms) in offspring populations reinforces how nuanced *Nucella* shell morphology can be in the presence of different selective pressures.

Parental populations show greater morphological disparity in multivariate shape across latitudes than offspring populations (Figure 3.3, Table 3.4). The striking difference of the two northern offspring populations from their parent populations in morphospace suggests that at least some of the phenotypic differences observed across a latitudinal gradient in *N. ostrina* are attributable to plasticity. While plasticity is likely responsible for some of the convergence in *N.*

ostrina shell morphology under common-garden conditions, the significant differences between offspring populations under common-garden conditions could also suggest some influence of local adaptation on morphology.

Nucella lamellosa

As in *N. ostrina*, the offspring population of *N. lamellosa* (from Friday Harbor egg capsules) differs from its parent population in morphospace. While there is one offspring population of *N. lamellosa* to compare to its parent population, the lack of additional offspring to parent comparisons does not allow a test of whether offspring populations in *N. lamellosa* converge on a similar morphology under common-garden conditions, as seen in *N. ostrina*. However, the difference that in morphospace and in the allometric growth trajectory does suggest that *N. lamellosa* morphology also has high plasticity. Given the high likelihood that all the *N. lamellosa* offspring snails are siblings, the 5 snails that grew to sufficient size for this study show remarkable phenotypic variation in the morphospace, and imply a high degree of developmental variation in *N. lamellosa* even under common-garden conditions.

In a comparison of univariate traits between the offspring and parent population from Friday Harbor, offspring populations are thinner than the parental population both absolutely and when regressed against shell size. The consistent trend towards thinner shells under common-garden conditions in both *N. lamellosa* and *N. ostrina* further supports the expectation that the absence of predators (and predation cues) in the aquaria does not induce shell thickening. For *N. lamellosa*, shell thickness is strikingly different across latitudes in addition to across wave-exposure, with southern snails exhibiting much thicker shells than northern ones, which supports

the prediction that presumably higher predation rates at southern latitudes would lead to more anti-predatory. The offspring *N. lamellosa* population exhibits thinner shells than the southern populations (parental), but thicker shells than the northern populations (Supplementary Figure S3.7), corroborating previous studies showing that shell thickness is under plastic control (Appleton and Palmer 1988, Pascoal et al. 2012).

Phenotypic plasticity across a latitudinal gradient remains little studied, especially in the ocean. However, *Nucella* gastropods have become a useful genus for studies on plasticity across wave-exposure and predation gradients due to their remarkable phenotypic variation and also due to their direct-developing life mode, facilitating laboratory rearing. *Nucella* has been found to exhibit plasticity in response to predation (Appleton and Palmer 1988, Pascoal et al. 2012, Trussell et al. 2003) and my findings agree with previous results. The convergence of *N. ostrina* populations across latitudes on a similar morphology under common-garden conditions suggests that plasticity likely has a large role in phenotypic variation. The plasticity found in *Nucella* from different latitudes under common-garden conditions suggests that populations are coming into contact with different environmental conditions either because conditions are not consistent through time or because the snails are sufficiently mobile between sites despite their direct-developing life mode (Pascoal et al. 2012). However, despite the plasticity in *Nucella* morphology, significant differences in multivariate shape of *N. ostrina* in pairwise offspring comparisons is at least suggestive of local adaptation, and indicates that both plasticity and local adaptation are likely responsible for morphological variation across a wave-exposure and latitudinal gradient.

This study attempted to investigate plasticity in shell variation in *N. lamellosa* and *N. ostrina* that is found both across a latitudinal and a wave-exposure gradient. The convergence of

laboratory populations toward a similar, thin-shelled morphology, suggests that phenotypic variation across latitudes and wave exposures is under plastic control, at least to some extent, and the significant shape difference between *N. ostrina* offspring suggests that local adaptation likely also has a role.

4.1 Introduction

Invasive species can have devastating effects on native communities, but represent an unprecedented biological experiment with the potential to yield insights into the consequences of a species encountering a novel habitat with little or no gene flow with the source population. Owing to the documented adverse effects of many invasive species on native biota and ecosystem services (Mooney and Hobbs 2000, Pejchar and Mooney 2009), there has been interest in developing models to predict species invasions (Rejmanek and Richardson 1996, Miller et al. 2007, Roy et al. 2002). Niche models rely on associating observed occurrence locations (the realized niche) with geographically referenced environmental variables to estimate the range of environments that the species can tolerate (Broennimann et al. 2012).

Studies that have applied environmental niche models to invasive species have seen mixed results. Investigating niche expansion in invasive species of Europe and North America, Petitpierre et al. (2012) found little expansion out of the native environmental niche in plants and Strubbe et al. (2015) found that niche expansion was also rare in terrestrial vertebrates. However, in one of the few marine studies on niche conservatism in non-native species, Parravicini et al. (2015) found that Mediterranean fish invaders often spread beyond the native niche. Additional marine examples would test whether marine species tend to escape their native niche more often than terrestrial species, and allow us to make predictions about marine invasion risk. This study attempts to combine environmental niche modeling with a trait-based analysis to investigate how the native niche and ecological traits may constrain or promote invasion in marine bivalves that

¹ This chapter was written in collaboration with Samantha Chiang, Stewart Edie, and Dr. David Jablonski at The University of Chicago.

are introduced via three primary pathways: shipping, corridor migration, or aquaculture.

Marine bivalves are a particularly good study system because there have been over 150 documented introductions (not all of which became established), the introductions have occurred across the world, and the introductions represent a mix of invasion vectors. Our dataset includes 120 established alien marine bivalves with >900 non-native occurrence records. We partition our analysis of niche expansion according to three primary vectors of marine introduction above (Ruiz et al. 1997, 2000) because they represent fundamentally different pathways of introduction, each with its own likelihood of invasion success and potential trait selectivity.

4.1.1 Three Vectors of Invasion

Shipping

Of the three most common marine invasion pathways, shipping has been considered the most dominant. One of the first instances of human-mediated bivalve invasions may have been in the 13th century, when Vikings are proposed to have carried *Mya arenaria*, the softshell clam, from North America to Europe (Petersen et al. 1992). The number of marine organisms introduced solely by shipping has increased exponentially over the last 50 years, and shipping is responsible for 62% of the North American marine invasions since the 1970s (Ruiz et al. 2000). Because ship size is correlated with both ballast-water volume and hull surface area (Ruiz et al. 2000), ports saw a tremendous increase in propagules from foreign seas as ship size and traffic increased over in the second half of the 20th century, likely one of the main factors contributing to the exponential rise in shipping-related invasions. Carlton (1996) estimates that more than 3000 marine species may be in transport via ballast water globally on any given day. The spatial variation in marine introductions has been attributed to trade corridors (Ruiz et al. 2000), where

dominant trade corridors between the Western Pacific and Eastern Pacific have led to numerous marine introductions of West Pacific species into Eastern Pacific ports, particularly San Francisco Bay.

Lessepsian Migration

The Mediterranean Sea and the Red Sea have a storied history of connectedness due to past sea level rises during interglacial times, and anthropogenic alterations of the landscape. Trade routes between the Indo-West Pacific and the Mediterranean date as far back as the reign of Egyptian ruler, Ramses II (1279-1213BC). However, the “pharaonic channels” that existed nearly 3000 years ago used branches of the Nile delta, which would have imposed freshwater barriers difficult for marine organisms to cross (Por 1971). Only with the massive engineering feat led by Ferdinand de Lesseps (hence the term ‘Lessepsian migrants’) with the 1869 opening of the Suez Canal did movement of organisms between the two seas become relatively easy (Por 1971). While the first migrants into the Mediterranean from the Red Sea were fishes and swimming crabs, benthic organisms, such as marine mollusks, entered the Mediterranean within a decade of the canal opening (Por 1971), and 8 bivalve species had entered by 1905 (based on our date assignments from literature searches). Today, approximately 17,000 transits go through the Suez Canal annually (shipmap.org), and more than 300 Indo-Pacific species are recorded in the Mediterranean (Galil 2000). Por (1971) suggests that the majority of the Lessepsian migrants into the Mediterranean are the result of natural dispersal rather than transport via shipping, using evidence that few ships coming through the Suez Canal called at Israeli Mediterranean ports, and yet the vast majority of Lessepsian migrants are initially found in Israel. However, we find that many Lessepsian migrants occur at ports far from the entry of the Suez Canal (Italy, Turkey),

including migrations of the last few decades, implying not only natural dispersal but also shipping are likely responsible for the extent of the Lessepsian migration.

Migration through the Suez Canal is strikingly asymmetrical (Por 1971). For marine bivalves, 38 species have migrated into the Mediterranean from the Red Sea through the Suez Canal (though nearly as many have entered the Mediterranean via other vectors), while only 3 species have migrated into the Red Sea from the Mediterranean, and those three (*Venerupis decussata*, *Cerastoderma glaucum*, and *Chama gryphoides*) have not penetrated very far into the Red Sea. Although the journey for the Mediterranean species is likely more difficult than for the Red Sea species (judging by the longer distance from Port Said to Lake Timsah compared to that from Suez to the Bitter Lakes and current flow), the most convincing explanation for this asymmetry seems to be the relatively depauperate fauna of the Eastern Mediterranean compared to the Red Sea, which had been separated for 16Myr until the opening of the Suez Canal (Vermeij 2012).

Aquaculture

Although introductions via aquaculture are much less common than via shipping or Lessepsian migration for marine bivalves, aquaculture activities have produced a disproportionate number of highly invasive marine bivalves (having spread quickly or extensively from their point of introduction, or that have invaded many localities around the world). While contributing to less than a quarter of global bivalve introductions, aquaculture accounts for nearly half of the bivalves considered highly invasive (Supplementary Table S4.1). The increased rate of invasiveness among species introduced for aquaculture may be due to attempts by importers to match native and non-native habitats and increase propagule pressure

(Grosholz et al. 2015). Both purposeful introductions for aquaculture and the accidental introductions brought along with aquaculture trade (“hitchhikers”) are included in the “Aquaculture” category, even though these two pathways (purposeful vs. hitchhiker) likely represent different levels of effort to establish the populations.

In addition to the three vectors described above, which account for 105 of the 120 alien bivalves in this dataset, 15 bivalves (13% of global bivalve introductions) have been introduced via multiple vectors. While natural range expansion (in response to climate change) can also be considered a vector of introduction, we do not include marine bivalves that have invaded new habitats via this pathway due to the difficulty in identifying truly non-native localities and the additional difficulty of deciding when to begin considering such climate-driven range expansions as anthropogenic invasions.

Here, we test the prediction that non-native species will tend to inhabit areas that are similar to the environmental conditions in their native range, and expect that different vectors may be more likely to lead to niche expansion than others. The opening of the Suez Canal brought together two seas, making new environments accessible to species on both sides of the corridor. We might expect that species whose native ranges encompassed conditions present through the canal and on the non-native side would be the first invaders (see Nawrot et al. 2015). However, high propagule pressure from the source region in the case of a corridor vector, like the Lessepsian migration, might allow for niche expansion, by providing a continual source of propagules. Aquaculture introductions, too, often see high levels of propagule pressure as aquaculturists import thousands of bivalve spat to encourage the target species to establish (e.g. 5 bushels of Pacific oyster seed from Seattle to Maine, Shatkin et al. 1997; thirty-six thousand *Crassostrea rhizophorae* seed were transplanted in Wales, Mann 1983). In addition to high

propagule pressure, aquaculture introductions, unlike the other introduction vectors, often benefit from attempts to match native to introduced environmental conditions to maximize the likelihood of establishment (Grosholz et al. 2015).

Unlike corridor (Lessepsian) and aquaculture introductions, we expect introductions via shipping to have relatively low propagule pressure due to distance from the source region (except for very heavily trafficked shipping routes), which may decrease the likelihood of establishment or niche expansion. However, for heavily trafficked shipping ports, disturbance is likely high, which should promote establishment and perhaps even niche expansion.

In addition to the niche matching between the native and non-native locales, the establishment and spread of organisms outside their native range may also depend on ecological traits of the introduced species (Knop and Reusser 2012). Determining the correlates of introduced species success for the purposes of prediction has received increased attention over the last decade (Jeschke and Strayer 2006, Duyck et al. 2007, Rejmanek and Richardson 1996, Roy et al. 2002, Miller et al. 2007), though the generality of those correlates, particularly in marine systems, is uncertain. With respect to the traits that may influence invasion success, we ask two questions. First, among all bivalves, which traits (if any) promote establishment into a non-native region? And second, among alien bivalves, which traits (if any) promote expansion out of the native niche or make species more likely to be highly invasive (classified in Supplementary Table S4.1).

4.2 Materials & Methods

4.2.1 Data collection

Based on an extensive search of the literature, we compiled a taxonomically standardized database of over 900 non-native occurrences for 120 alien marine bivalves (Figure 4.1, Supplementary Table S4.1) using non-native locality information from over 250 academic articles, governmental sources, and regional invasion inventories. Teredinid bivalves were excluded due to taxonomic issues, as in Nawrot et al. 2015. If not published along with non-native occurrence, latitudinal and longitudinal coordinates were assigned to each locality from Google Earth. Latitudinal and longitudinal coordinates were used to create shapefiles for non-native range distributions in QGIS software. We attempted to restrict non-native records to established populations, but it is possible that some single records are not actually be established, or that an introduction was transient (Colautti and MacIsaac 2004), which would artificially increase the non-native range extent. This may be especially likely for older records. However, we believe that in most cases, the non-native localities are actually a conservative estimate of an introduced species' non-native extent because we are not capturing localities that have not been sampled.

Using an extensive global marine bivalve database (Jablonski et al. 2013), we compiled native locality information for each of the alien marine bivalves and create complementary native range shapefiles in QGIS. We use a “range-through” method for the native range shapefile (assuming continuous occupation across grid cells between the most northern and southern occurrence, and most eastern and western). However, due to the nature of bivalve introductions (often restricted to a port area or unlikely to have spread to the next nearest recorded locality), non-native ranges consist of point localities or small geographic boxes, again providing a conservative estimate of non-native ranges.

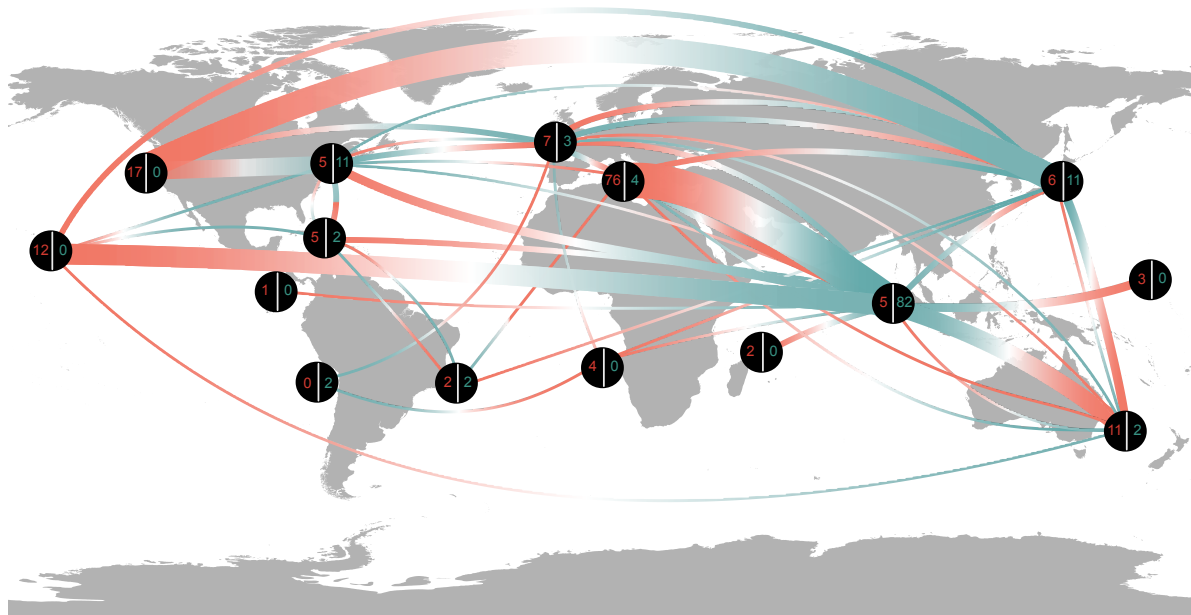


Figure 4.1. Invasion routes for the bivalves used in this study. Routes show native region (blue) to invasive region (red). Line thickness corresponds to the number of invasives that are introduced via that route. The Indo-West Pacific, North West Pacific and North West Atlantic donate many more species than they receive, while regions like the North East Pacific, Hawaii, and South East Atlantic receive numerous invasions and yet donate none. Number of species donated (green) and number of species received (red) for each region are shown in the black circles.

Using the QGIS shapefiles, we assigned native and non-native occupancy to equal-area grid cells across the world by intersecting the range shapefiles with global equal-area cells in QGIS. Each grid cell was associated with temperature, salinity, and net primary productivity values [temperature and salinity from MARSPEC (http://www.marspec.org/Modern_Data.html); productivity from Oregon State MODIS (<http://omel.coas.oregonstate.edu/MODIS/>)]. We include temperature, salinity and productivity in our niche model because they have been found to affect marine community composition and therefore may be most likely to limit the spread of invasives (Sunday et al. 2011, Belanger et al. 2012), and they are the environmental variables for which we have high-resolution data. Annual mean and standard deviations were assigned to each grid cell based on monthly temperature, salinity, and productivity values, as well as minimum and maximum values for temperature and salinity by grid cell. These values were then used to create native and non-native climate envelopes for each species.

In addition to non-native locality information, date and place of first non-native record were extracted from literature searches (Supplementary Table S4.1). Where available, date of first record was used as date of introduction, although understudied localities and cryptic species may have significant mismatches between date of introduction and date of first record. Dates are particularly uncertain pre-1900, and so we used a best estimate from literature sources. For 10 of our 120 bivalves, literature sources gave a range of dates for their introductions. In those cases, we took the mid-point (e.g. if the source said “1800s,” we recorded the introduction as 1850, or “1980s” would be 1985).

Introduction vector (shipping, aquaculture, Lessepsian migration, multiple vector) was extracted from literature searches (Supplementary Table S4.1). For Lessepsian migrants, there is

some uncertainty about whether bivalves passively moved through the canal or invaded the Mediterranean in ballast water via shipping. For those species that expanded far from the entry point of the Suez Canal in the Mediterranean, and with a discontinuous range (based on localities that had been heavily sampled), we classified as shipping introductions (rather than Lessepsian), but it is possible that both shipping and passive dispersal may have contributed to success of some Mediterranean aliens (some classified as multiple vector introductions). For aquaculture introductions, we attempted to identify localities where introductions failed to establish, but numerous aquaculture introductions have not been assessed recently, making it difficult to determine the extent of the established populations. In addition, it is possible that some aquaculture facilities have been modified to support aquaculture establishment (like in the case of *Saccostrea glomerata* where reproduction in southwestern Australia is only possible because of artificially heated water, Lam and Morton 2006). If we find evidence for environmental modifications in aquaculture facilities, we omitted those localities.

Family assignments and ecological traits (substrate, feeding, fixation, mobility, native geographic range size) were obtained from the Jablonski bivalve database.

4.2.2 Data analyses

1) Niche expansion

To assess niche expansion among our set of 120 alien marine bivalves, we compared the native and non-native niches. Many studies focusing on niche changes between the native and non-native range have calculated both niche expansion (non-native populations established in areas with novel environmental conditions) and niche under-filling (non-native populations established in areas that only represent a subset of the native environmental conditions) (Strubbe

et al. 2015, Petitpierre et al. 2012). However, niche under-filling often represents either the lack of native conditions in the non-native range or insufficient time since introduction to expand in the non-native range, and so we focus only on niche expansion, which may represent rapid adaptations to novel environments.

For each species, we identified the maximum and minimum values for temperature, salinity, and primary productivity in the native and non-native ranges. We calculated the excursion (or difference) in minimum values between native and non-native niches, and maximum values between native and non-native niches (for temperature, salinity, and productivity). We compared this observed excursion to a null distribution of environmental values, created by filling in the number of native grid cells and non-native grid cells with native grid cell values (with replacement), with the expectation that a bivalve would establish in non-native localities with environmental values within the native range of environmental values. A species was deemed a niche expander if the observed excursion in maximum or minimum exceeded the 5% confidence interval cutoff.

In addition to the comparison to null ranges, we evaluated the excursion of niche-expanding species outside the native range by taking the observed difference between the invasive and native maximum (or minimum) value and dividing by the native range of values to calculate the proportion of the excursion outside the native range.

2) Traits associated with niche expansion

Ecological traits such as size, feeding guild, and bathymetry have also been shown to influence invasion success (Rejmanek and Richardson 1996, Lake and Leishman 2004, Roy et al. 2002, Nawrot et al. 2015). First we test whether ecological traits, including body size,

geographic range size, relation to substratum, mobility, feeding, and fixation, affect whether a bivalve becomes established in a non-native locale by comparing the ecological traits among our set of 120 established alien bivalves to the database of taxonomically standardized bivalve species worldwide (5455 for which we have range and ecological data). We perform a logistic regression to assess the significance of the relationships between traits and non-native establishment. Second, among our set of alien bivalves, we ask if those same ecological traits or the circumstances of introduction (date and vector) affect a bivalve's ability to expand its native niche or become highly invasive (categorized in Supplementary Table S4.1). We compare the subset of alien bivalves that are niche-expanders to the full set of alien bivalves (120). Again, we used a logistic regression to investigate the significance of the following traits on the likelihood of an alien bivalve species being a niche-expander (or highly invasive): date of introduction, introduction vector, body size, geographic range size, substrate, mobility, feeding, and fixation.

4.3 Results

4.3.1 Niche expansion & geographical asymmetry of invasion

Of the 120 alien species, 44 (36%) show niche expansion along at least one environmental axis. Of those 44 species, 15 show excursions in temperature, 24 show excursions in productivity, and 30 show excursions in salinity (Table 4.1, Figure 4.2). Non-native populations tend to be more often in saline, cooler, and more productive locales than their native locales. Of the 44 niche-expanding species, 24 (20%) of them expanded more than 10% outside the native range of values. Niche expanders with narrow native geographic ranges have higher proportional expansion than niche expanders with large native geographic ranges (Figure 4.2).

	Lessepsian (IWP to Mediterranean)	Anti- Lessepsian (Mediterranean to IWP)	Aquaculture	Shipping	Multiple
Total	38	3	17	47	15
Highly Invasive Niche expander	1	0	7	8	9
Temperature	Higher: 0 Lower: 3	Higher: 0 Lower: 0	Higher: 1 Lower: 2	Higher: 2 Lower: 3	Higher: 1 Lower: 1
Productivity	Higher: 1 Lower: 6	Higher: 0 Lower: 0	Higher: 6 Lower: 1	Higher: 5 Lower: 2	Higher: 0 Lower: 2
Salinity	Higher: 1 Lower: 1	Higher: 3 Lower: 0	Higher: 4 Lower: 6	Higher: 6 Lower: 4	Higher: 3 Lower: 1

Table 4.1. Counts of species that are highly invasive and niche expanders by invasion vector.

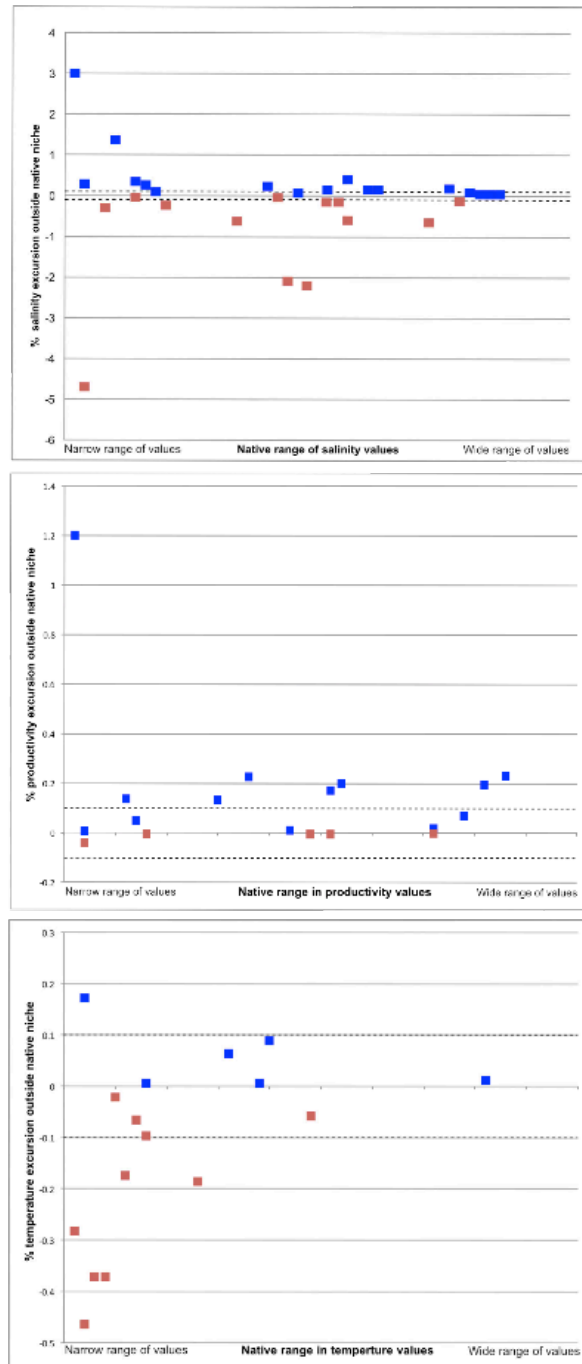


Figure 4.2. Environmental niche expansion plot. Each panel represents the proportional excursion values between minimum (or maximum) non-native value and the minimum (or maximum) native value for each of the three environmental variable. Blue points correspond to alien bivalves with environmental maximums higher than the native maximum and red points correspond to alien bivalves with environmental minimums lower than the native minimum.

Introductions are geographically asymmetrical in marine bivalves, with many alien bivalves originating from the Indo-West Pacific and Northwest Pacific and few originating from the Eastern Pacific or Eastern Atlantic (Figure 4.1). Fewer than a dozen non-native bivalves have been recorded in the tropics, and the majority of those found in the tropics have either a tropical origin or was purposefully introduced for aquaculture (or both), whereas >80 species have been introduced into temperate latitudes from the tropics (though 71 are from the Indo-West Pacific to Mediterranean). While the tropics are generally undersampled compared to the temperate regions (Jablonski et al. 2006) which might bias the results towards more temperate compared to tropical invasions, there are invasion corridors that have been well-studied in both directions, such as the temperate eastern Pacific compared to the temperate western Pacific (a heavily trafficked shipping route) that still show a striking asymmetry. Nine species have been introduced from the temperate western Pacific to temperate eastern Pacific, but there have been no documented invasions in the opposite direction, despite heavy shipping traffic in both directions.

4.3.2 Traits associated with invasion and niche expansion

Among all bivalves (5455), body size, geographic range size, and substrate had a significant effect on whether or not a bivalve became established in a non-native locale, with larger-bodied, wider-ranging, and infaunal bivalves more likely to be aliens (Figure 4.3, Table S4.2). When all bivalves are subset by family, seven families contribute more than 5 alien bivalves [Arcidae (6), Chamidae (6), Mytilidae (18), Ostreidae (10), Pectinidae (6), Pteriidae (7), and Veneridae (18)]. Within each of these seven most-common families, geographic range size predicts which of the species are aliens in four of them (Chamidae, Mytilidae, Pteriidae, and Veneridae).

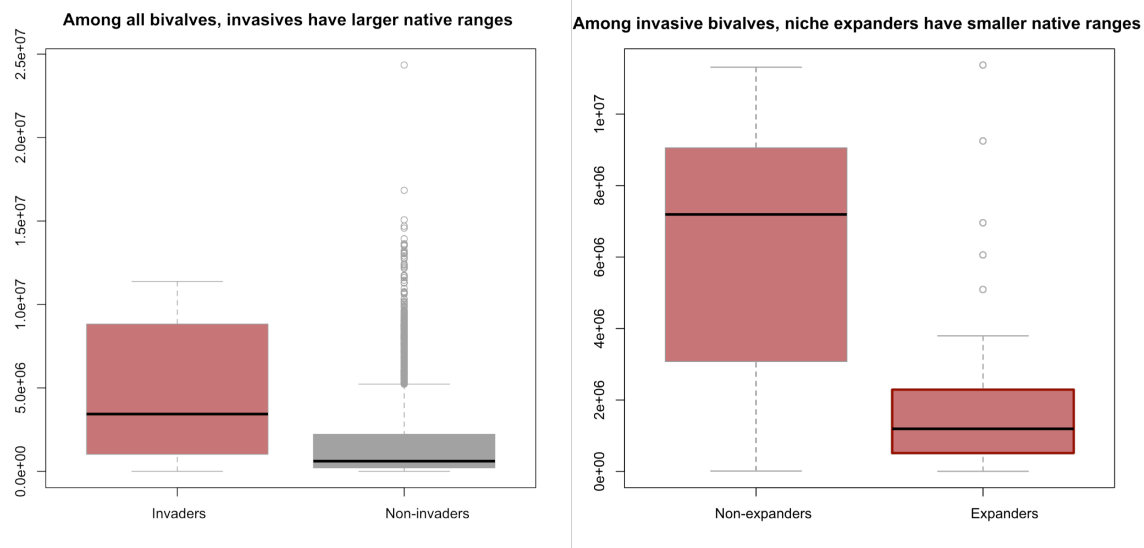


Figure 4.3. Geographic range size for all bivalves, split between invaders and non-invaders (right panel), and geographic range size for all bivalve invaders, split between niche expanders and non-expanders. Among all bivalves, invaders have significantly larger ranges than non-invaders. When split by family, of the seven families that donate 5+ invasive species, invaders have significantly larger geographic ranges in four of the families. Among the 120 invasive bivalves, niche expanders have significantly smaller geographic ranges than non-expanders.

Among the 120 alien bivalves, geographic range size and date of introduction w significantly influenced niche expansion and invasiveness (Figure 4.3, Table S4.2). Alien bivalves with smaller native ranges were significantly more likely to be niche expanders than alien bivalves with larger native ranges. Taken together, these results suggest that bivalves with a large native range may be more likely to become established in non-native locales, but less likely to be niche expanders.

4.4 Discussion

4.4.1 Niche expansion & geographical asymmetry in bivalve invasions

More than one-third of alien marine bivalves expand outside their native niche (44 out of 120 species). However of those, only 20% expand outside the native range by more than 10%, compared to 35% of non-native marine fishes (Parravicini et al. 2015), 17% of non-native vertebrates (Strubbe et al. 2015), and fewer than 15% of non-native plants (Petitpierre et al. 2012). The lower rates of niche expansion in non-native marine bivalves compared to non-native marine fishes may suggest that there is not a common trend towards higher levels of niche expansion in marine species. Alternatively, plants may be less likely to expand than animals, land or sea.

The majority of the niche-expanders show excursions in salinity, especially moving towards more saline locales. The relative commonness of escaping the native niche in salinity raises questions about its role as a limiting environmental variable, but also about the coarseness of the data. Considering the relatively fine spatial scale over which salinities may differ, a grid cell could potentially include salinity values outside the range that the organism experiences in either its native or non-native range. On the other hand, there are relatively few niche expansions

in temperature (7) and productivity (9) that are more than 10% outside the native niche, possibly suggesting that temperature and productivity are more constraining than salinity. For those species that do expand more than 10% outside the native niche in temperature, only one is moving to warmer locales, whereas 6 move to cooler locales. Niche expanders with narrower native ranges tend to see greater proportional expansion outside the native niche, possibly suggesting that the absolute expansion is more important than the proportional expansion outside the native range. This may suggest that either larger-ranging bivalves are experiencing most global environments or that narrower-ranging bivalves are not at their environmental limits and may be geographically limited by other factors, like competition or predation.

In addition to the niche expanders, among all the alien bivalves in our dataset, marine bivalves tend to move into cooler rather than warmer non-native localities. Moving from warmer to cooler waters is consistent with the general expectation that it is easier to move to temperate regions from tropical ones due to the relatively unsaturated temperate fauna compared to tropical and greater likelihood that a tropical species would invade the temperate zone simply because there are more tropical than temperate species (Carlton 1987, Jablonski et al. 2006). The biotic resistance hypothesis, articulated by Elton (1958), predicts that diverse communities better resist invasion by introduced species (Vermeij 1996, Levine and D'Antonio 1999, Freestone et al. 2011, Sax and Brown 2000). In addition to affecting an introduced species' ability to establish, the diversity of the community in the introduced locality may also affect the success of introduced species in expanding from the entry point. In both experimental (Freestone et al. 2011) and model simulations (Case 1990), highly diverse communities have shown some degree of buffering against invasion. Since highly diverse communities tend to be in the tropics, tropical coasts better resist invasion than temperate coasts, and we find this pattern in the non-native

localities in our database. Less than 10% of the marine bivalves in this dataset are introduced into the tropics, and the majority of those that do have either a tropical origin or were purposefully introduced for aquaculture (or both), pointing to the difficulty of tropical invasion. Specific examples of alien bivalves also underscore the difficulty of invading the tropics. *Mytilus galloprovincialis* has become established in 28 non-native locations around the globe (Eastern Pacific, Australia, South America, South Africa, Western Pacific), but has no tropical non-native localities. Perhaps the most convincing evidence in support of the biotic resistance hypothesis is the striking asymmetry in the direction of migration via the Suez Canal. Seventy-one bivalves have expanded into the Mediterranean from the Indo-West Pacific, while only 3 species have expanded into the Red Sea from the Mediterranean. The Mediterranean is particularly receptive to Indo-West Pacific alien species because of its historical depletion of taxa caused by isolation from the Indo-West Pacific in the Middle Miocene, approximately 16 Ma, and periodic cooling from the Oligocene to the Pleistocene (Vermeij 2012), and present and future warming that makes the Mediterranean environment more similar to that of the Indo-West Pacific (Vermeij 2012). All three of the Red Sea aliens from the Mediterranean expanded outside their native niche, while only 10 (of the 71) Mediterranean aliens from the Red Sea expanded outside their native niche, which suggests that Mediterranean species may be especially unlikely to establish in the Red Sea because of an environmental mis-match between native and non-native locales, in addition to the highly diverse community on the other side of the Suez Canal. None of the three Red Sea aliens from the Mediterranean spread very far beyond the Suez Canal, and so these species may represent sink populations, perhaps maintained by propagules from the Mediterranean.

Our findings support previous work on geographical asymmetry in introductions, where

introductions have been found to be concentrated between regions that are connected by newly established corridors, like the Suez Canal, or anthropogenic corridors created by trade routes, such as between the Northwest Pacific and the Northeast Pacific; and along those predominant corridor routes, we find a stark asymmetry in introductions (Indo-West Pacific donates many more species than the Mediterranean, and the Northwest Pacific donates many more species than the Northeast Pacific) (Ruiz et al. 2000, Vermeij 2005, Galil 2006, Fridley and Sax 2014).

4.4.2 Traits associated with niche expansion

We find geographic range size to significantly influence both the likelihood that a bivalve will be established in a non-native locale, and that an alien bivalve will be a niche expander. Bivalves with larger geographic ranges are more likely to become established in a non-native locale than bivalves with small geographic ranges, perhaps due to both greater tolerance to a wide range of environmental conditions and an increased likelihood that a wide-ranging bivalve will be picked up via shipping traffic (or would be present in the Red Sea, accessing the anthropogenic corridor into the Mediterranean). Similarly, Nawrot et al. (2015) found that Red Sea natives with broad native ranges (corresponding to broad environmental tolerances) are better invaders into the Mediterranean. However, among our set of alien bivalves, species with smaller native ranges are significantly more likely to expand outside their native niche than species with large native ranges, perhaps because bivalves with large native ranges already experience a large range of environments in their native range, so that few non-native localities are outside the range of native values. Alternatively, those bivalves with narrower native ranges might have a smaller realized niche relative to their fundamental niche (Hutchinson 1957), and unable to access environments that they could tolerate due to competition, predation or

geographical barriers. In addition to large geographic range, larger-bodied bivalves were more likely to become established in a non-native locality when all bivalves are included, but body size did not promote highly invasiveness or niche expansion among the alien bivalves. In a study on invasive bivalves in the Mytilidae family, Roy et al. (2002) found that invaders were larger-bodied than non-invaders, consistent with our finding both for alien bivalves overall and when we specifically subset by Mytilidae.

While vector of introduction does not seem to influence niche expansion or invasiveness among alien bivalves, we do see some patterns in the frequency of expansion given different vectors. Anti-Lessepsian (into the Red Sea) migrants and aquaculture introductions were much more likely than other vectors to results in niche expansion (all 3 of the anti-Lessepsian migrants expanded outside the native niche, as did 65% of the aquaculture introductions expanded outside the native niche). However, Lessepsian introductions (into the Mediterranean) were less likely to promote niche expansion (less than 25% of Lessepsian migrants expanded outside the native niche). This is consistent with expectations from Vermeij (2012) that Lessepsian migrants find similar environments in the Mediterranean, especially as the Mediterranean gets warmer and more oligotrophic. Among the highly-invasive bivalves, the majority (13 of 25) have been introduced via aquaculture (either solely via aquaculture or multiple vectors), despite aquaculture contributing less than a quarter of alien bivalves overall. Species introduced via aquaculture may have been more suited to the environmental conditions in the non-native region because aquaculturist generally attempt to introduce species where they would be most successful, and would have likely benefitted from high propagule pressure, potentially making it easier to become established in non-native regions.

4.5 Conclusion

We find that approximately 20% of alien marine bivalves expand more than 10% outside their native niche. Our findings suggest that while marine bivalves tend to expand more often than terrestrial plants and vertebrates (14% and 17% of species expand more than 10%, respectively), bivalves do not expand out of the native niche nearly to the same extent as marine fishes (33% expand more than 10%) (Petitpierre et al. 2012, Parravicini et al. 2015, Strubbe et al. 2015). Niche expansion in salinity was common among niche expanders, but relatively rare in temperature and primary productivity, suggesting that temperature and productivity may be particularly limiting for marine bivalves. Caution is needed regarding salinity, however, because it can vary over a finer scale than our sampling scheme. Our results suggest the biotic resistance hypothesis, as we find that fewer than 10% of alien marine bivalve species become established in the tropics relative to the less-diverse temperate zones, and only 3 of the 44 Lessepsian migrants move from the less-diverse Mediterranean to the more-diverse Red Sea. Additional studies that use genetic information to determine specific source regions will enhance our ability to identify niche expansion and rapid evolutionary change in invasive species and may lead to better predictive tools in the future.

CHAPTER 5: Conclusion

In this dissertation I have attempted to combine studies of natural range expansion with human-mediated expansion via transplantation and the opening of corridors, like the Suez Canal. In both natural range expansions and human-mediated introductions, species come into contact with new habitats and new ecological communities, which has the potential to bring about novel phenotypes. Exploring the consequences of past range expansions may help us better predict the causes and consequences of present-day range expansion and invasion.

In Chapter 2, I investigated the phenotypic consequences of range expansion in two intertidal gastropods, *Nucella lamellosa* and *Nucella ostrina*, which expanded their range northward in response to warming following the Last Glacial Maximum (Marko 2004). I find significantly different morphologies across time (present-day to Pliocene/Pleistocene fossils) and across latitude. Present-day northern snails are higher-spined than southern and ancestral forms, especially in *N. ostrina*. For *N. ostrina*, the differences in present-day northern populations from southern and ancestral ones likely reflect rapid evolution in response to novel conditions in the northern part of the range following the LGM. However, for *Nucella lamellosa*, the differences in present-day northern populations from southern and ancestral ones could either reflect differences accumulated in isolation or rapid evolution to novel conditions in the previously unoccupied areas of the northern range. This study assessed phenotypic variation over a latitudinal gradient and over time, and adds to previous work on the drivers of shell shape at a more localized scale, where wave action and predation can vary over short distances.

In Chapter 3, I follow up on the work in Chapter 2 by assessing the contribution of plasticity to the phenotypic variation observed across the geographic range of *N. lamellosa* and *N. ostrina* in a common-garden experiment. Despite a lack of wave action in the common-garden aquaria, I find that offspring populations of *N. ostrina* converge on a similar, thin-shelled morphology, typical of a wave-exposed site. The lack of predatory cues in the aquaria are likely responsible, as predation has been found to induce shell thickening and aperture narrowing in experimental manipulations (Appleton and Palmer 1988, Pascoal et al. 2012). The convergence among offspring populations suggests that phenotypic variation across latitudes and wave exposures is under plastic control, at least to some extent. Despite the convergence (smaller distance between mean forms of populations and grand mean in offspring than parental populations), I still find that offspring populations from different sites are significantly different from one other, which may suggest that local adaptation likely also has a role in structuring phenotypic variation across the geographic range.

In Chapter 4, we explored niche expansion in alien marine bivalves, and the traits that might lead to invasion success. We found that approximately 20% of alien bivalves expand more than 10% outside their native niche (temperature, salinity, productivity), which is relatively comparable to terrestrial plants (14% expand more than 10%) and terrestrial vertebrates (17% expand more than 10%) (Petitpierre et al. 2014, Strubbe et al. 2015), but not to marine fishes (33% of species expand more than 10% outside the native niche, Parravicini et al. 2015). For those bivalves that did expand into conditions outside their native range, the most common expansion was in salinity, suggesting that native temperature and productivity may be more constraining. We found geographic range size to be both a predictor of a bivalve establishing in a non-native locale

and a predictor of niche expansion among alien bivalves. Wide-ranging bivalves are likely to become established in a non-native locale (compared to bivalves that haven't established in a non-native locale), but among our set of alien bivalves, narrow-ranging species are more likely to expand out of the native niche. In addition to niche expansion and the traits associated with invasion success, this study further underscores the striking asymmetry in the geographical direction of invasion, with the majority of invasions coming from the Indo-West Pacific region, a region of extremely high molluscan biodiversity compared to other regions. Our results promote the biotic resistance hypothesis since we find that fewer than 10% of marine bivalves become established in the highly-diverse tropics, and only 3 of the 44 Lessepsian migrants move from the less-diverse Mediterranean to the more-diverse Red Sea. While this study did not address the phenotypic changes that often accompany human-mediated invasions, there are numerous examples (Roy et al. 2002, Grosholz and Ruiz 2003). As in range expansions, the phenotypic changes associated with invasions could be due to rapid local adaptation or plasticity. Future studies could investigate the role of plasticity in supporting invasion success using common-garden techniques like the ones presented in Chapter 3 in the context of native range expansion.

Appendix A: Supplementary Materials for Chapter 2

Site	Lat/Long	Exposure	Reference
Bodega Bay, California	38°19' 59, -123°02' 53	Protected	Hahn 1998
Van Damme, California	39°16' 24, -123°47' 29	Exposed	Sanford & Swezey 2008
Luffenholtz Beach, California	41°02' 25.57, -124°07' 14.51	Exposed	Hochberg 1999; Martin 2007
Trinidad Sate Beach, California	41°03' 36.55, -124°08' 55.93	Exposed	Hochberg 1999; Martin 2007
Sunset Bay, Oregon	43°20' 04.01, -124°22' 34.35	Intermediate	“Moderately exposed” in D’Antonio 1986 but tidal heights are 0-0.7, which is lower than the 1.0 m min. used to define ‘high-energy coasts’ (McKay & Terich 1992)
Bastendorff Beach, Oregon	43°20' 59.68, -124°20' 18.54	Intermediate	“Semi-exposed” according to Jarrin 2007; D’Antonio 1986; Shanks et al. 2010 says it’s a “dissipative beach”
Yachats, Oregon	44°19' 25.46, -124°06' 20.51	Exposed	Dahlhoff et al. 2002
Kalaloch, Washington	47°36' 18.38, -124°22' 30.75	Exposed	Dethier et al. 2003
Shi Shi Beach, Washington	48°16' 49.44, -124°41' 00.85	Exposed	Sebens 1981; Menge 1974
Cattle Point, Friday Harbor, Washington	48°27' 00, -122°57' 46	Intermediate	Menge 1974 says CP is “exposed to severe wave shock during winter storms”; Spight 1973, Schoch 1999; “Moderate exposure” according to Carrington et al. 2008 & Hohenlohe 2003 (lower than outer coast, but higher than other sites in Friday Harbor)
Sitka Sound Science Center, Alaska	57°02' 57.4, -135°19' 22.61	Protected	NOAA Shorezone
Magic Island, Sitka Alaska	57°06' 15.14, -135°24' 04.25	Protected	NOAA Shorezone
Fossil Beach, Kodiak, AK	57°25' 39.34, -152°21' 22.27	Intermediate (Semi-exposed)	NOAA Shorezone
Monashka Beach, Kodiak, Alaska	57°49' 42.19, -152°22' 40.97	Intermediate (Semi-protected)	NOAA Shorezone
Hoktaheen, Alaska	58°03' 36.6, -136°33' 48.3	Exposed	NOAA Shorezone
Murphy Cove (exposed), Alaska	58°15' 52.4, -136°43' 30.2	Intermediate (Semi-exposed)	NOAA Shorezone
Murphy Cove (protected), Alaska	58°16' 08.3, -136°43' 06.8	Protected	NOAA Shorezone
Lemesurier Island, Alaska	58°16' 26.1, -136°03' 44.3	Intermediate (Semi-protected)	NOAA Shorezone
Murk Bay (Graves Harbor), Alaska	58°17' 24, -136°44' 03	Intermediate (Semi-exposed)	NOAA Shorezone
Kasitsna Bay, Alaska	59°28' 10.09, -151°33' 00.5	Intermediate (Semi-protected)	NOAA Shorezone
Peterson Bay, Alaska	59°34' 28.95, -151°18' 38.56	Protected	NOAA Shorezone

Table S2.1. Collection sites with latitudinal and longitudinal coordinates, and wave-exposure classification (with the reference for wave exposure assignment)

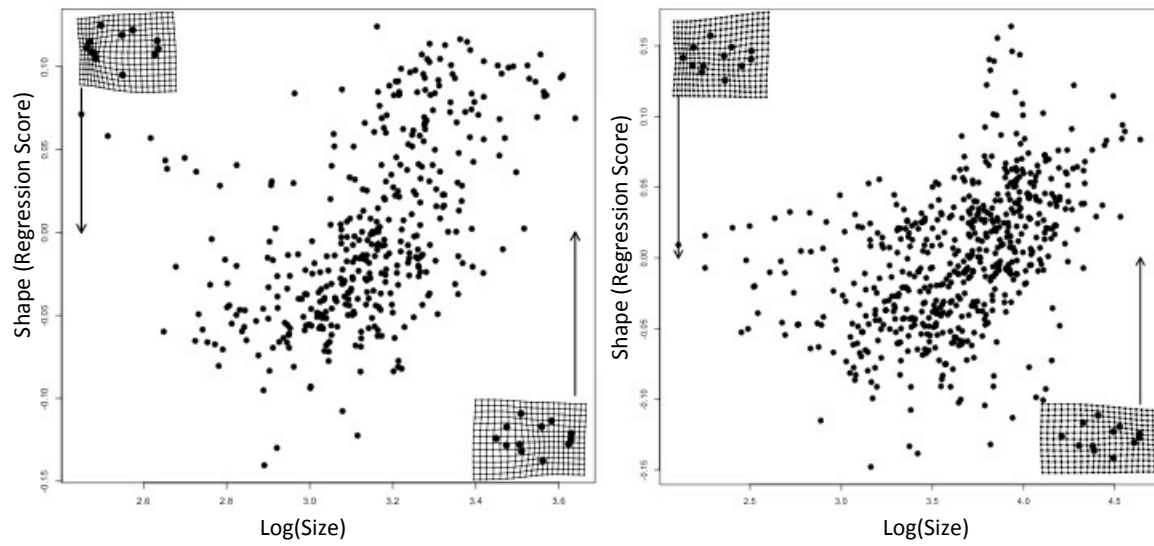


Figure S2.1: Allometric relationship between shape and centroid size in *Nucella ostrina* (left) and *Nucella lamellosa* (right). Deformation grids in upper left and lower right show how the shape of the shell changes across the morphospace.

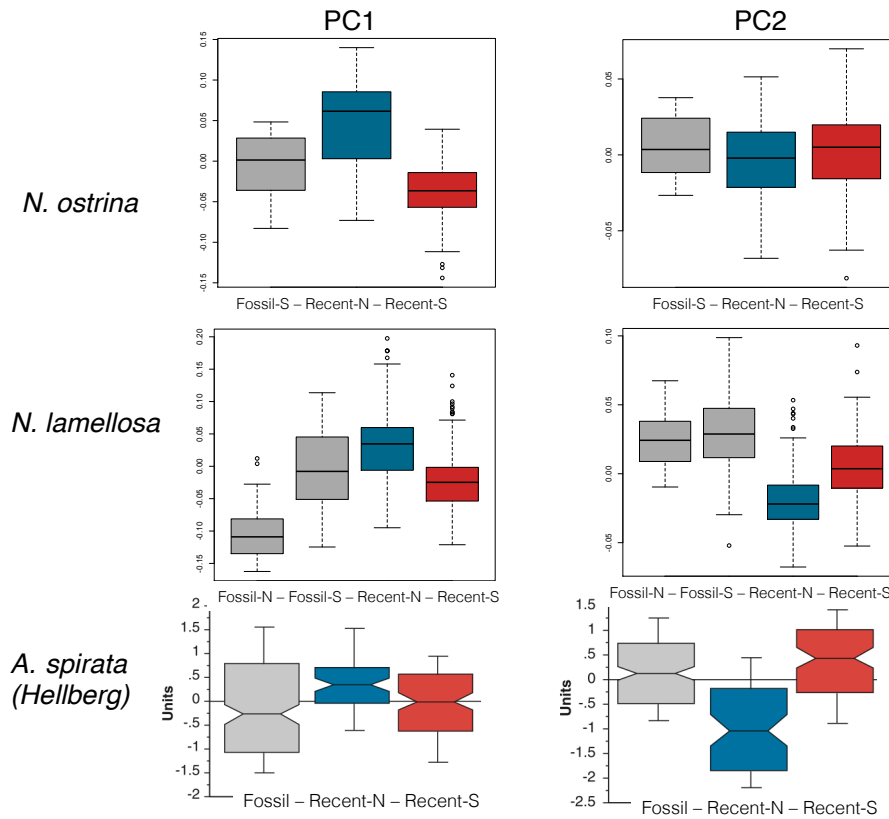


Figure S2.2. Box plots show the difference in PC scores for PC1 and PC2 between Fossil, Recent Northern, and Recent Southern sites. The top four panels (*N. ostrina* and *N. lamellosa*) are from the present study and the bottom two panels (*A. spirata*) are modified from Hellberg et al.. (2001). Results from Hotelling's T^2 tests show that all pairwise comparisons between groups within *N. ostrina* are significantly different and all pair-wise comparisons between groups within *N. lamellosa* are significantly different. Hellberg et al. (2001) find that all pair-wise comparisons between groups within *A. spirata* are significantly different except for Fossil to Recent South.

	F-Score	Distance between means	P-value
<i>N. ostrina</i>			
Recent-S vs. Recent-N	33.71	0.4186	<0.01
Fossil- S vs. Recent-S	11.09	0.3239	<0.01
<i>N. lamellosa</i>			
Recent-S vs. Recent-N	50.85	0.2569	<0.01
Fossil vs. Recent-S	17.99	0.1880	<0.01
Fossil vs. Recent-N	43.84	0.4764	<0.01

Table S2.2. Pairwise differences among groups shown in Figure S2.1 using a Hotelling's T^2 tests (IMP TwoGroup).

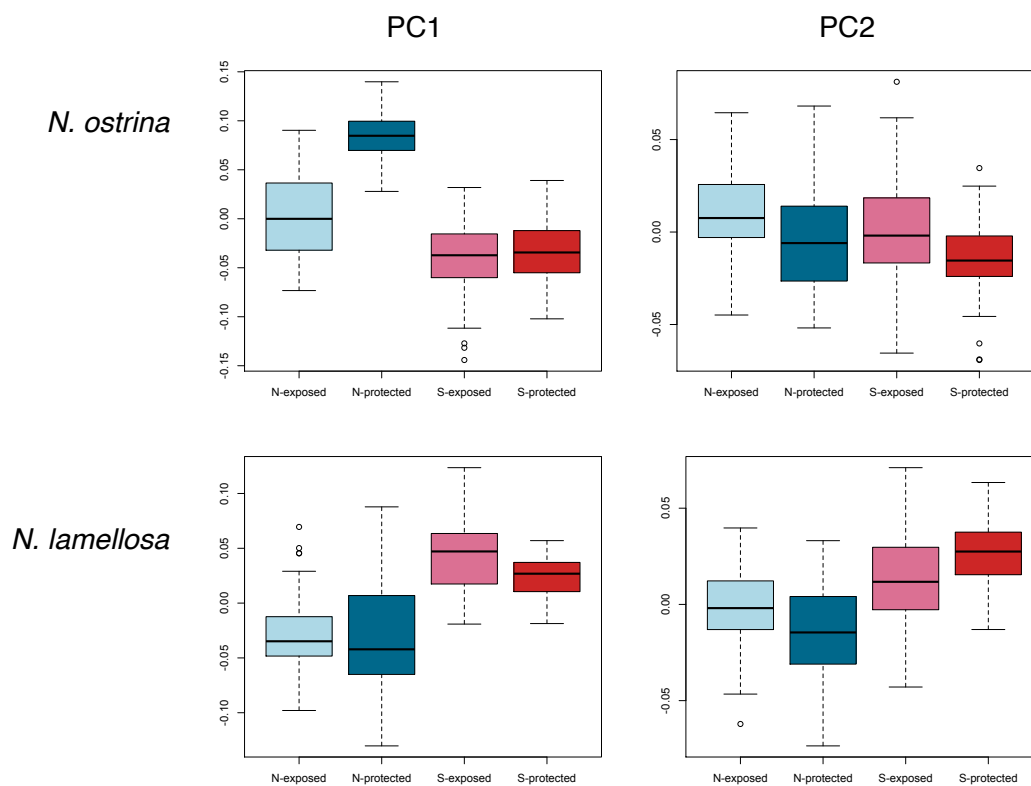


Figure S2.3: Box plots show the difference in PC scores for PC1 and PC2 between northern exposed, northern protected, southern exposed, and southern protected sites for *N. ostrina* (top two panels) and *N. lamellosa* (bottom two panels).

	F-Score	Distance between means	P-value
<i>N. ostrina</i>			
S-exposed vs. S-protected	8.13	0.1443	<0.01
N-exposed vs. N-protected	25.95	0.3206	<0.01
<i>N. lamellosa</i>			
S-exposed vs. S-protected	23.38	0.1341	<0.01
N-exposed vs. N-protected	7.43	0.1121	<0.01

Table S2.3: Table of pairwise differences among groups shown in Figure S2.2 using a Hotelling's T^2 tests (IMP TwoGroup).

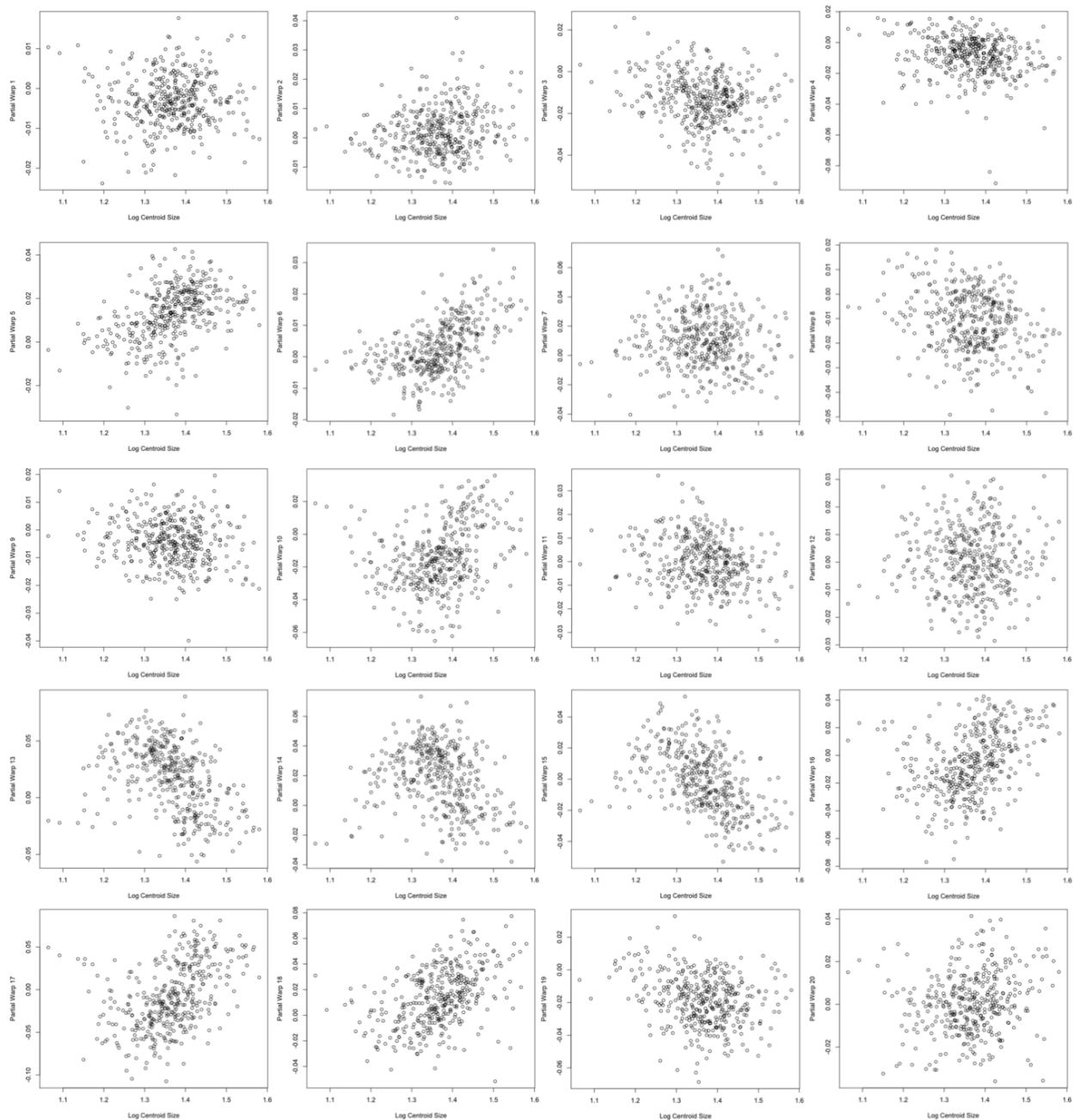


Figure S2.4. Partial warp scores generated from PCAGen in the Integrated Morphometrics Package (IMP) plotted by log centroid size for *N. ostrina* as a test for size-standardization.

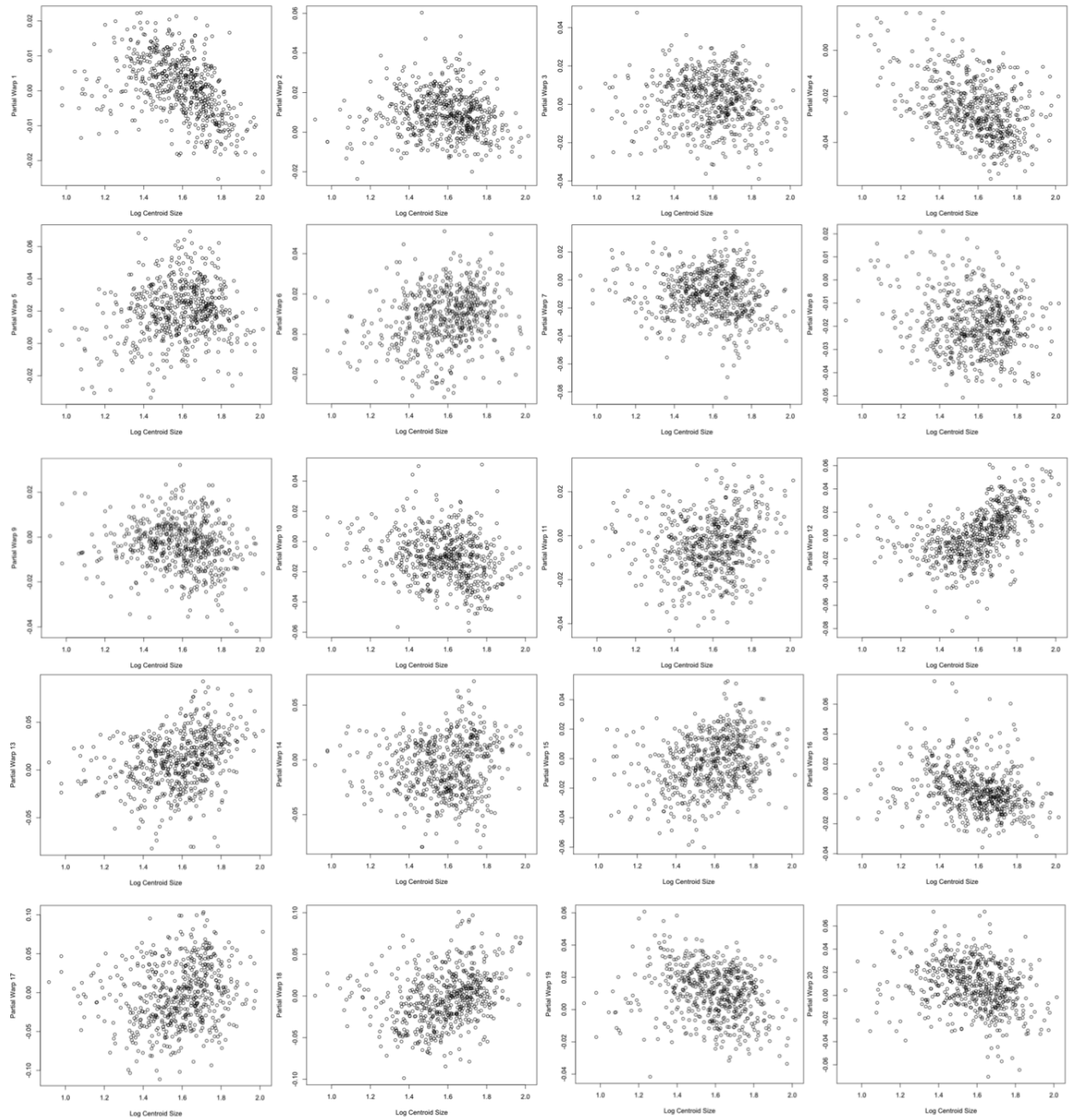


Figure S2.5. Partial warp scores generated from PCAGen in the Integrated Morphometrics Package (IMP) plotted by log centroid size for *N. lamellosa* as a test for size-standardization.

Appendix B: Supplementary Materials for Chapter 3

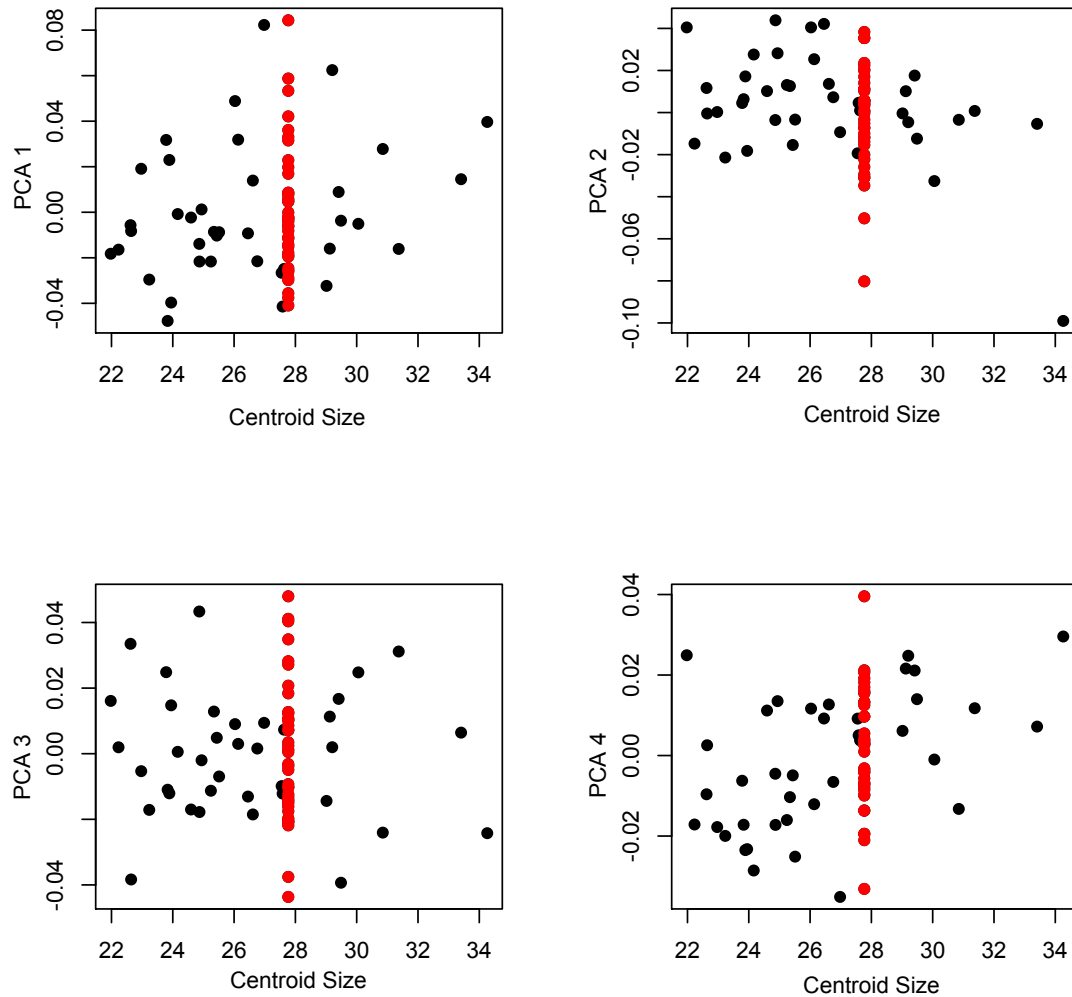


Figure S3.1. Size-standardized (red) versus non-size-standardized PC scores by centroid size for Bodega Bay *N. ostrina* parent population.

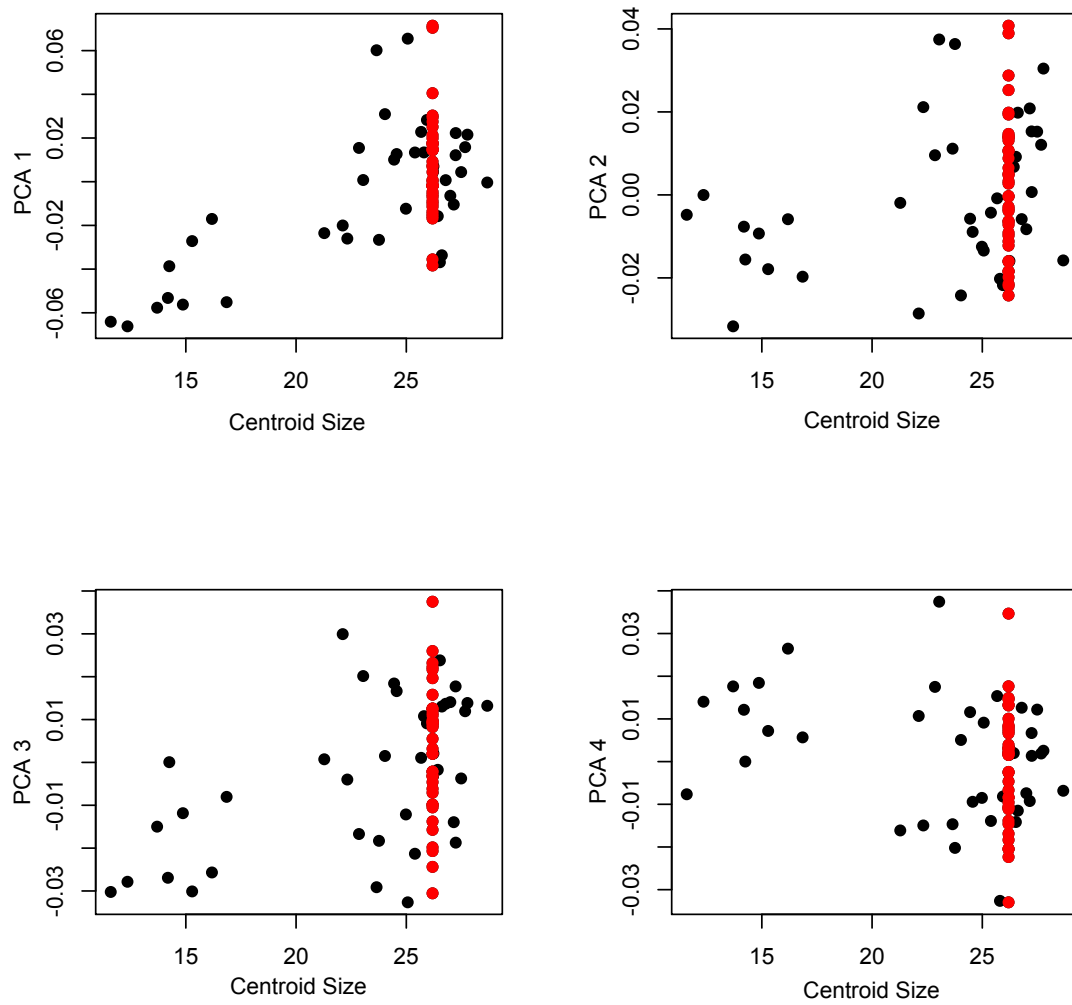


Figure S3.2. Size-standardized (red) versus non-size-standardized PC scores by centroid size for Graves Harbor *N. ostrina* parent population.

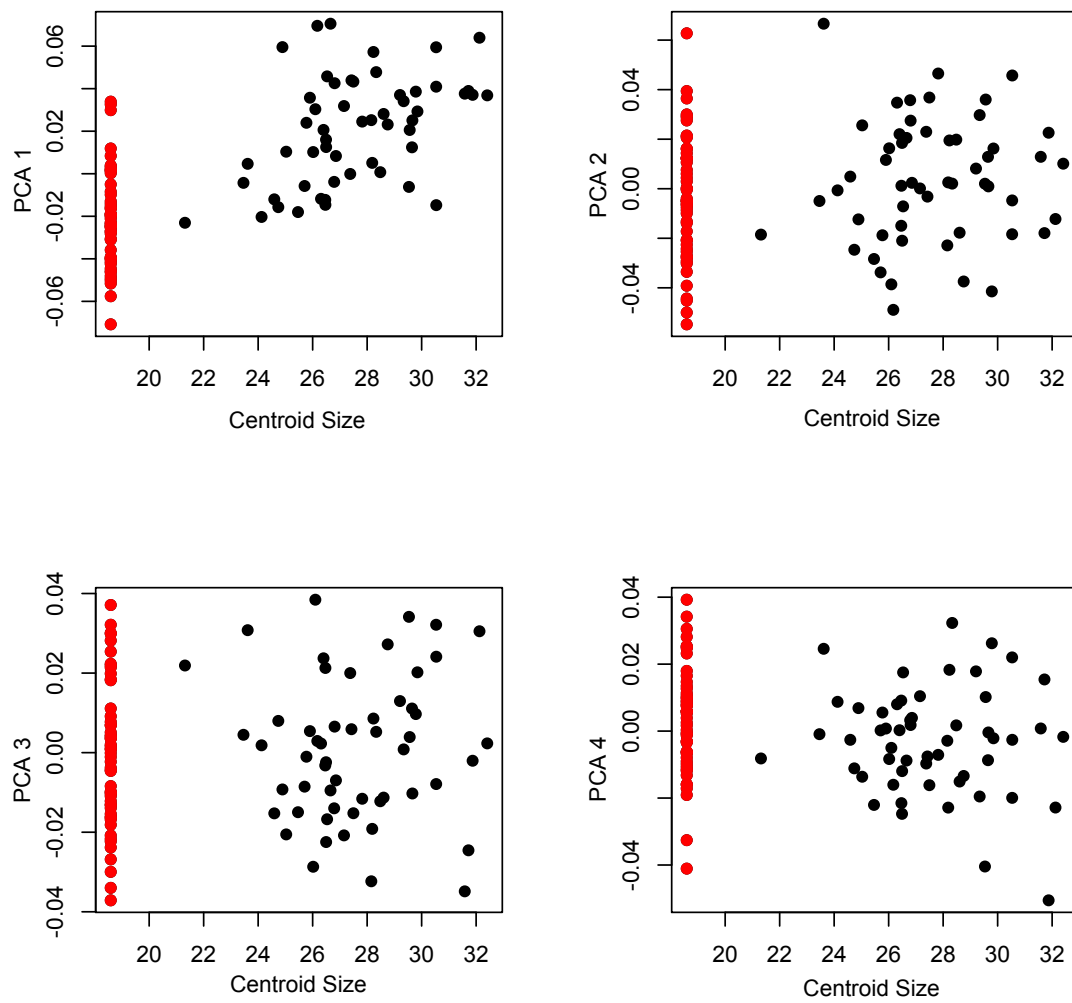


Figure S3.3. Size-standardized (red) versus non-size-standardized PC scores by centroid size for Sitka *N. ostrina* parent population.

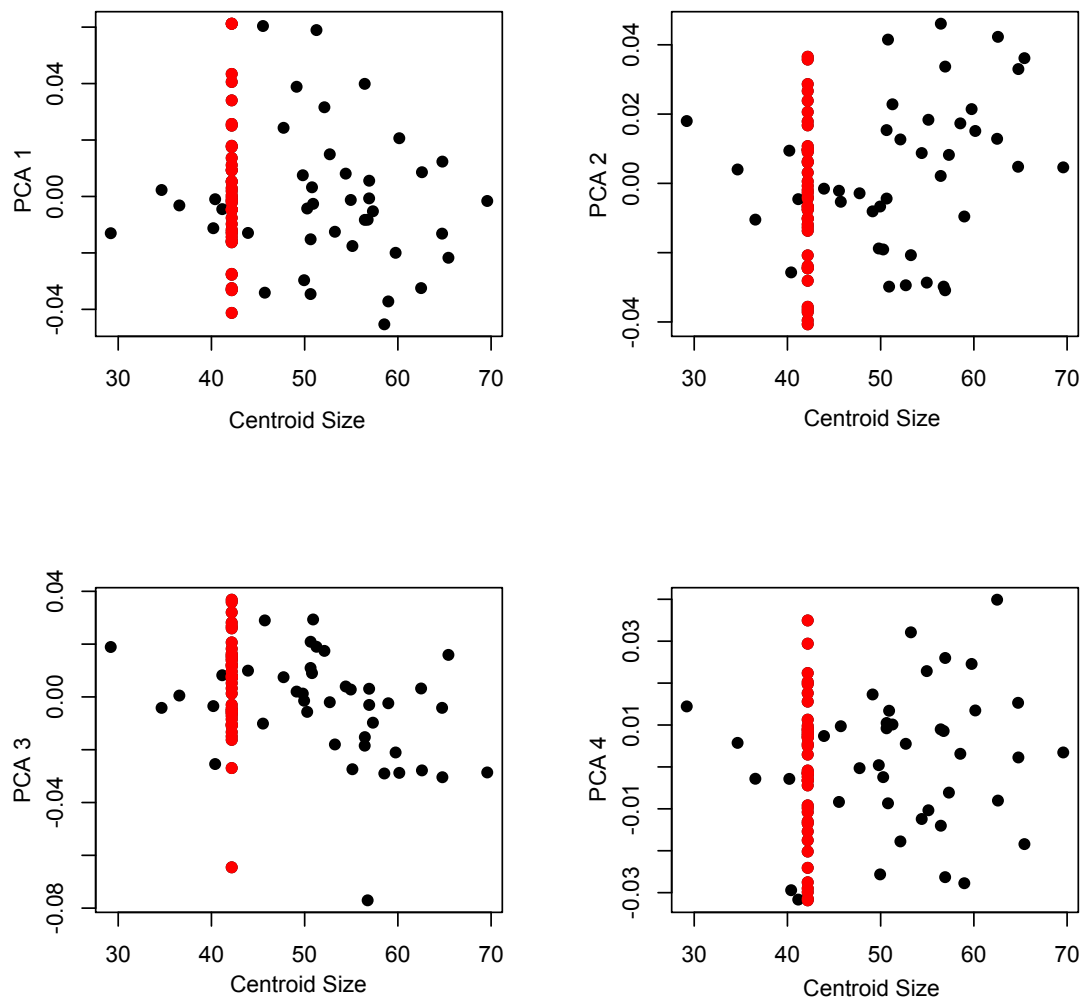


Figure S3.4. Size-standardized (red) versus non-size-standardized PC scores by centroid size for Friday Harbor *N. lamellosa* parent population.

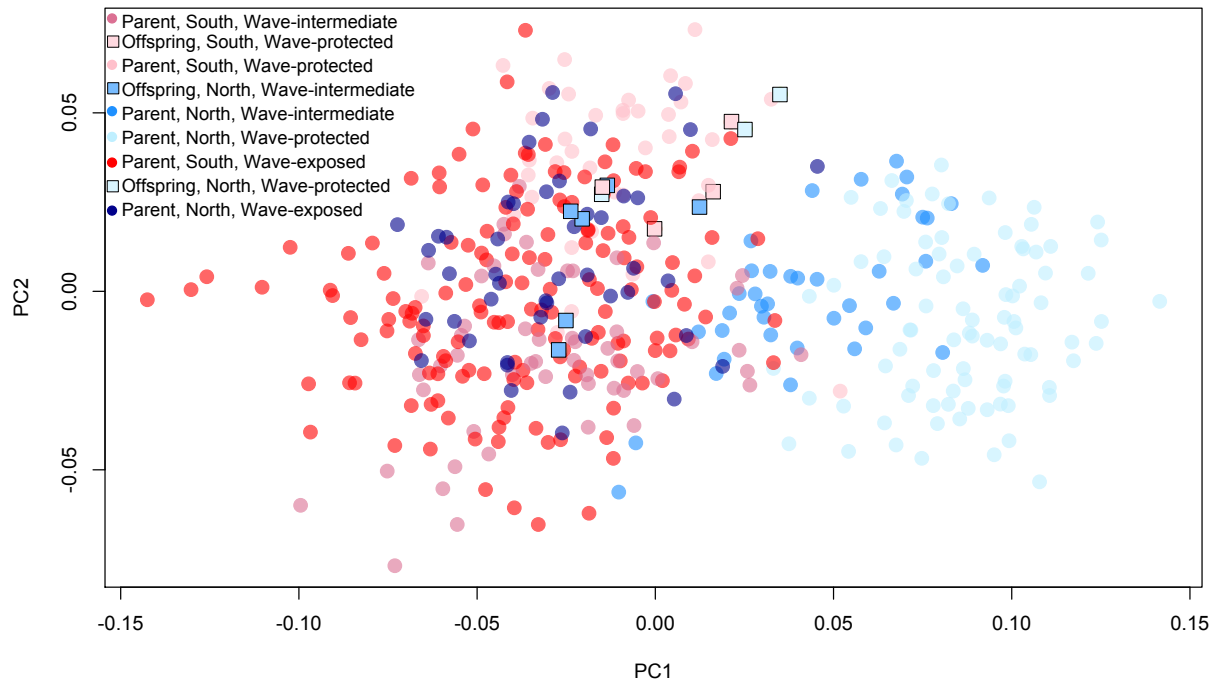


Figure S3.5. *Nucella ostrina* morphospace plot with *N. ostrina* populations from common-garden experiment and from field collections across the species geographic range to give additional morphological context. Points are colored according to geography and wave-exposure category. Offspring populations are shown in square points, colored by the geography and wave-exposure of the parent population. PC1 is strongly influenced by shell spire height, and PC2 by aperture shape. PC1 represents 49.4% of the variance, PC2: 11.7%, PC3: 7.1%, PC4: 6.7%, PC5: 4.5%.

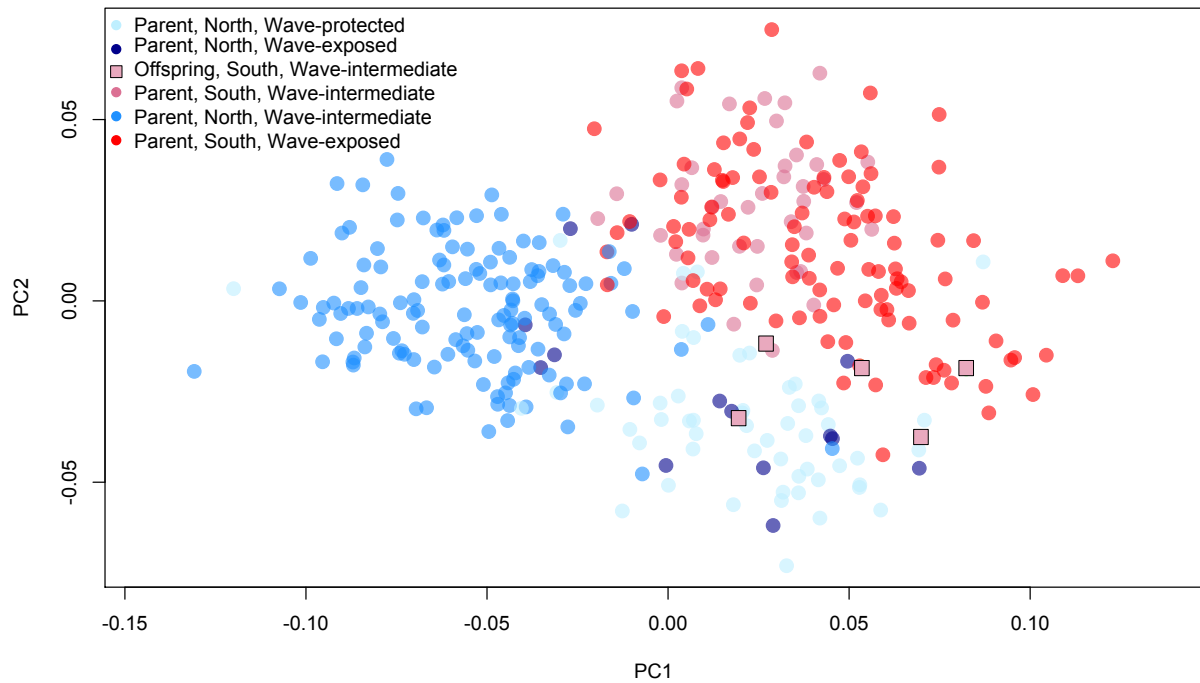


Figure S3.6. *Nucella lamellosa* morphospace plot with *N. lamellosa* populations from common-garden experiment and from field collections across the species geographic range to give additional morphological context. Points are colored according to geography and wave-exposure category. The offspring population (Friday Harbor) is shown in square points, colored by the geography and wave-exposure of the parent population. PC1 is strongly influenced by shell spire height, and PC2 by aperture shape. PC1 represents 46.1% of variance, PC2: 12.5%, PC3: 9%, PC4: 6.9%, PC5: 4.1%.

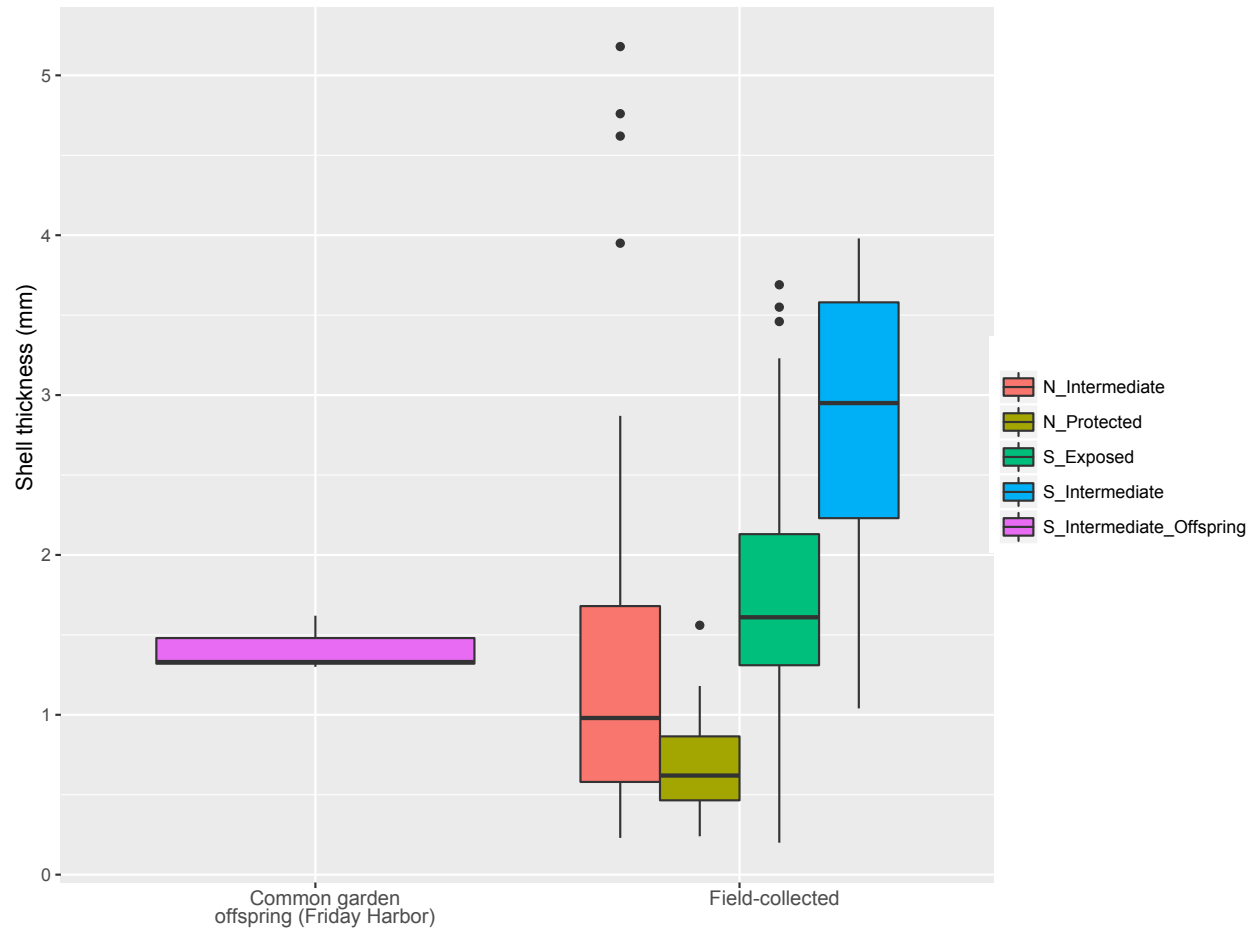


Figure S3.7. Shell thickness of *N. lamellosa* plotted by geography and wave-exposure, including the common-garden offspring population from Friday Harbor (a southern wave-intermediate site).

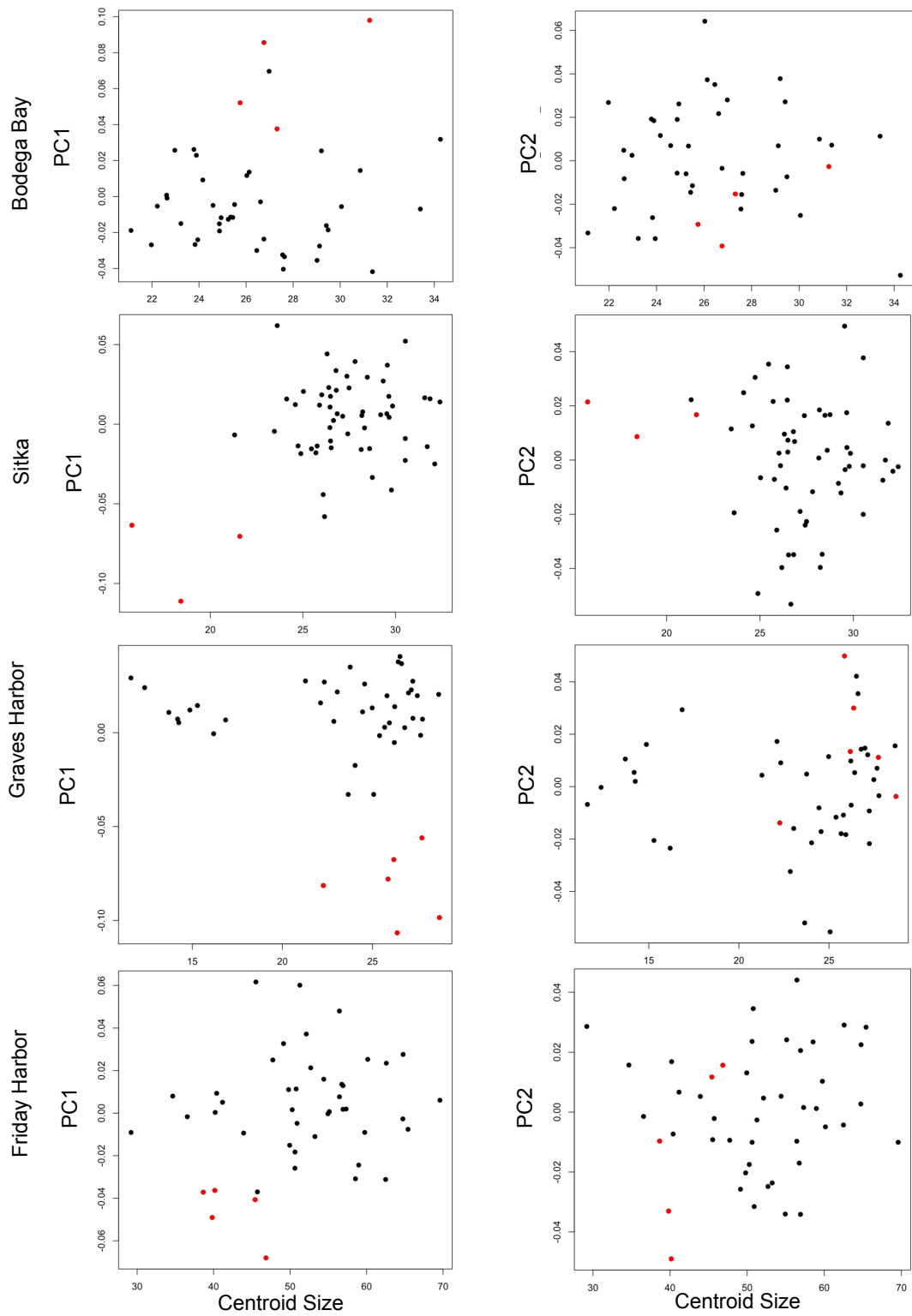


Figure S3.8. PC1 and PC2 plotted by centroid size for each site showing the difference between size-standardized parental forms (in black) and offspring forms (in red).

Appendix C: Supplementary Materials for Chapter 4

Table S4.1. List of alien marine bivalves used in this study with native and invasive range, date of introduction, highly invasive and niche expansion classifications, and references for the dates, vectors, and classifications. References, including all used for non-native occurrence records, are provided as supplementary references.

Family	Genus	Species	Native Range	Invasive Range	Date	Vector	Highly invasive	Niche Expansion	References for date, vector, and invasiveness (if highly invasive); citations in Appendix
Glycymerididae	<i>Tucetilla</i>	<i>adenensis</i>	Indo-West Pacific	Mediterranean	1966	Lessepsian	No	No	Galil 2007
Carditiidae	<i>Centrocardita</i>	<i>akabana</i>	Indo-West Pacific	Mediterranean	2005	Shipping	No	Yes	Ceviker and Albayrak 2006
Mytilidae	<i>Semimytilus</i>	<i>algosus</i>	Southern Eastern Pacific (Ecuador to Chile)	Atlantic coast of Africa	1931	Shipping	No	Yes	Bigatti 2014
Corbulidae	<i>Potamocorbula</i>	<i>amurensis</i>	Western Pacific	Eastern Pacific	1986	Shipping	Yes	No	Carlton et al 1990, http://www.psp.wa.gov/downloads/ANS/MISM_Online.pdf
Laternulidae	<i>Laternula</i>	<i>anatina</i>	Indo-West Pacific	Mediterranean	1905	Lessepsian	No	No	Galil 2006, 2007
Ostreidae	<i>Crassostrea</i>	<i>angulata</i>	Western Pacific	Eastern Atlantic	1550	Shipping	No	Yes	Huvet et al 2000
Lucinidae	<i>Divalinga</i>	<i>arabica</i>	Indo-West Pacific	Mediterranean	1966	Lessepsian	No	Yes	Barash & Danin 1977, Galil 2007

Table S4.1 continued

Hiattellidae	<i>Hiattella</i>	<i>arctica</i>	Western Atlantic, Eastern Atlantic, Mediterranean	Hawaii	1920	Shipping	No	Carlton & Eldredge 2009
Myidae	<i>Mya</i>	<i>arenaria</i>	Western Atlantic; Eastern Atlantic; Western Pacific	Mediterranean ; Eastern Pacific	1500	Multiple	Yes	Strasser 1991, Streflaris and Zenetos 2006
Mytilidae	<i>Leiosolenus (Myoforceps)</i>	<i>aristatus</i>	Western Atlantic	Southern Western Atlantic	2004	Shipping	No	Simone & Goncalves 2006
Chamidae	<i>Chama</i>	<i>asperella</i>	Indo-West Pacific	Mediterranean	2002	Multiple	No	Ovalis and Zenetos 2007, Galil 2007
Mytilidae	<i>Modiolus</i>	<i>auriculatus</i>	Indo-West Pacific	Mediterranean	1935	Lessepsian	No	Galil 2007
Cardiidae	<i>Fulvia</i>	<i>australis</i>	Indo-West Pacific	Mediterranean	1948	Lessepsian	No	Galil 2007
Neilonellidae	<i>Neilo</i>	<i>australis</i>	New Zealand	Tasmania	1965	Aquaculture Byproduct	No	Greenhill 1965, Australia Coastal Estuarine & Marine Report
Ungulinidae	<i>Diplodonta</i>	<i>bogii</i>	Indo-West Pacific	Mediterranean	1982	Lessepsian	No	Galil 2007
Chamidae	<i>Chama</i>	<i>chinensis</i> (includes <i>C. brassica</i> Reeve 1847)	Indo-West Pacific	Mediterranean	2003	Shipping	No	Galil 2007
Arcidae	<i>Scapharca</i>	<i>broughtonii</i>	Indo-West Pacific	Mediterranean	2002	Shipping	No	Ceviker and Albayrak 2002, Cinar et al 2005
Mytilidae	<i>Mytella</i>	<i>charruana</i>	S. Western Atlantic	N. Western Atlantic	1986	Shipping	Yes	Spinuzzi et al 2013

Table S4.1 continued

Ostreidae	<i>Ostrea</i>	<i>chilensis</i>	South America; New Zealand	Eastern Atlantic; Tasmania	1960	Aquaculture	No	Yes	Morgan and Richardson 2012
Anomiidae	<i>Anomia</i>	<i>chinensis</i>	Indo-West Pacific	Eastern Pacific	1924	Aquaculture Byproduct	No	No	Carlton 1994
Veneridae	<i>Constellipitar</i>	<i>chordatum</i>	Indo-West Pacific	Eastern Mediterranean	2014	Lessepsian	No	No	Van Aarsten et al 2015
Veneridae	<i>Gouldiopa (Microcirce)</i>	<i>consternans</i>	Indo-West Pacific	Eastern Mediterranean	2011	Lessepsian	No	Yes	Van Aarsten et al 2015
Chamidae	<i>Pseudochama</i>	<i>corbierei</i>	Indo-West Pacific	Mediterranean	1946	Lessepsian	No	No	Zenetos et al 2005
Myidae	<i>Sphenia</i>	<i>coreanica</i>	Western Pacific	Hawaii	1996	Shipping	No	No	Coles et al 1999
Ostreidae	<i>Dendostrea</i>	<i>crenulifera</i>	Indo-West Pacific	Mediterranean	2005	Lessepsian	No	No	Mienis 2005, Galil 2007
Ostreidae	<i>Lopha</i>	<i>cristagalli</i>	Indo-West Pacific	Hawaii	1971	Shipping	No	No	Gregory 2009
Ostreidae	<i>Saccostrea</i>	<i>cucullata</i>	Indo-West Pacific	Mediterranean ; Western Atlantic	1999	Shipping	No	No	CIESM, Cinar et al 2011
Pharidae	<i>Ensiculus</i>	<i>cultellus</i>	Indo-West Pacific	Eastern Mediterranean	2008	Lessepsian	No	No	Bogi & Galil 2009
Macluridae	<i>Rangia</i>	<i>cuneata</i>	Western Atlantic	Eastern Atlantic	1956	Shipping	Yes	Yes	Hopkins and Andrews 1970, Sousa et al 2009
Gastrochaenidae	<i>Gastrochaena</i>	<i>cymbium</i>	Indo-West Pacific	Mediterranean	1954	Lessepsian	No	No	Galil 2007
Veneridae	<i>Venerupis (Ruditapes)</i>	<i>decussata</i>	Mediterranean	Gulf of Suez	1927	Anti-Lessepsian	No	Yes	Parisi et al 2012
Mytilidae	<i>Gaukensia</i>	<i>demissa</i>	N. Western Atlantic	Eastern Pacific; S. Western Atlantic	1850	Multiple	Yes	Yes	Torchin et al 2005, Sousa et al 2009

Table S4.1 continued

Pharidae	<i>Ensis</i>	<i>directus</i> (=E. leei Huber 2015)	Western Atlantic	Eastern Atlantic	1978	Shipping	Yes	Yes	Arias and Anadon 2012, http://www.europe-alien.org/speciesTheWorst.do
Veneridae	<i>Timoclea</i>	<i>djiboutiensis</i>	Indo-West Pacific	Mediterranean	1997	Lessepsian	No	No	Galil 2007
Mytilidae	<i>Mytilus</i>	<i>edulis</i>	Arctic; Mediterranean; Western Atlantic; Eastern Atlantic; Western Pacific	Eastern Pacific	1980	Multiple	No	No	Alexandrov and Berlinsky 2005
Ostreidae	<i>Ostrea</i>	<i>edulis</i>	Eastern Atlantic; Mediterranean	Eastern Pacific; Western Atlantic	1949	Aquaculture	Yes	Yes	Carlton 1992, Vercaemer et al 2006, http://massbay.mit.edu/resources/pdf/case-studies.pdf
Isognomonidae	<i>Isognomon</i>	<i>ephippium</i>	Indo-West Pacific	Eastern Mediterranean	2004	Shipping	No	No	Mienis 2004
Donacidae	<i>Dosinia</i>	<i>erythraea</i>	Indo-West Pacific	Mediterranean	1905	Lessepsian	No	Yes	Tzomos et al 2012
Veneridae	<i>Petricola</i>	<i>fabagella</i>	Indo-West Pacific	Mediterranean	1900	Lessepsian	No	No	Ceviker & Albayrak 2006, Crocetta et al 2013
Veneridae	<i>Lioconcha</i>	<i>fastigiata</i>	Indo-West Pacific	Hawaii	1985	Shipping	No	No	Carlton & Eldredge 2009

Table S4.1 continued

Chamidae	<i>Chama</i>	<i>asperella</i> (includes <i>C. fibula</i> Reeve 1847)	Indo-West Pacific	Hawaii	1920	Shipping	No	No	Coles et al 1999, Ray 2005
Tellinidae	<i>Tellina</i>	<i>flacca</i>	Indo-West Pacific	Mediterranean	1997	Lessepsian	No	No	Galil 2007
Veneridae	<i>Callista</i>	<i>florida</i>	Indo-West Pacific	Mediterranean	1945	Multiple	No	No	Mienis 2005, Tzomos et al 2012
Ostreidae	<i>Dendostrea</i>	<i>folium</i>	Indo-West Pacific	Mediterranean	2010	Lessepsian	No	No	Crocetta et al 2013 suggests that the likely vector of invasion is spreading via the Suez Canal, but the native range is not in the Red Sea
Mytilidae	<i>Septifer</i>	<i>forskali</i>	Indo-West Pacific	Mediterranean	1999	Lessepsian	No	Yes	Nawrot et al 2015
Cardiidae	<i>Fulvia</i>	<i>fragilis</i>	Indo-West Pacific; Eastern Atlantic	Mediterranean	1939	Multiple	Yes	No	Goud & Mifsud 2009, Crocetta et al. 2008
Mytilidae	<i>Mytilus</i>	<i>galloprovincialis</i>	Western Atlantic; Mediterranean	Eastern Pacific; Indo-West Pacific	1940	Multiple	Yes	Yes	https://www.cbd.int/invasive/doc/marine-menace-iucn-en.pdf
Veneridae	<i>Gemma</i>	<i>gemma</i>	Western Atlantic	Eastern Pacific	1893	Aquaculture Byproduct	Yes	Yes	Zhang et al 2014, Sousa et al 2009
Corbulidae	<i>Varicorbula</i>	<i>gibba</i>	Eastern Atlantic; Mediterranean	Australia	1987	Shipping	No	No	Bogi & Galil 2007

Table S4.1 continued

Ostreidae	<i>Crassostrea</i>	<i>gigas</i>	Western Pacific	Mediterranean ; N. Eastern Pacific; S. Eastern Pacific, S. Western Atlantic; South Africa; Australia	1964	Aquaculture	Yes	Yes	Leffler & Greer 1991, Streflaris and Zenetos 2006
Cardiidae	<i>Cerastoderma</i>	<i>glaucum</i>	Mediterranean	Red Sea	1905	Anti-Lessepsian	No	Yes	Barash & Danin 1987, Por 2012
Ostreidae	<i>Saccostrea</i>	<i>glomerata</i>	Indo-West Pacific	Pacific Islands; Hawaii	1984	Aquaculture	No	No	Ruesink et al 2005
Arcidae	<i>Telligarca</i>	<i>granosa</i>	Indo-West Pacific	Mediterranean	2006	Shipping	No	No	Zenetos et al 2009
Spondylidae	<i>Spondylus</i>	<i>groschi</i>	Indo-West Pacific	Mediterranean	1998	Multiple	No	No	Galil 2007
Chamidae	<i>Chama</i>	<i>gryphoides</i>	Eastern Atlantic; Mediterranean	Western Atlantic	1902	Anti-Lessepsian	No	Yes	Barash & Danin 1987, Por 2012
Tellinidae	<i>Psammacoma</i>	<i>gubernaculum</i>	Indo-West Pacific	Mediterranean	1992	Shipping	No	No	Cinar et al 2001
Mytilidae	<i>Leiosolenus</i>	<i>hanleyanus</i>	Indo-West Pacific	Eastern Mediterranean	2003	Shipping	No	Yes	Galil 2007
Gryphaeidae	<i>Hyotissa</i>	<i>hyotis</i>	Indo-West Pacific	Mediterranean ; Western Atlantic	2003	Shipping	No	No	Galil 2007
Pteriidae	<i>Pinctada</i>	<i>imbricata</i>	Indo-West Pacific; Western Atlantic	Western Atlantic	2014	Shipping	No	No	Marques & Braves 2014

Table S4.1 continued

Pectinidae	<i>Argopecten</i>	<i>irradians concentricus</i>	Western Atlantic	N. Western Atlantic; Western Pacific	1991	Aquaculture	No	Yes	Fan et al 2015, Huber 2015
Arcidae	<i>Scapharca</i>	<i>kagoshimensis</i>	Indo-West Pacific	Mediterranean	1966	Shipping	No	Yes	Lipej et al 2012
Veneridae	<i>Antigona</i>	<i>lamellaris</i>	Indo-West Pacific	Mediterranean	1992	Lessepsian	No	No	Nunes 2014
Veneridae	<i>Ruditapes</i>	<i>largillierii</i>	New Zealand	Tasmania	1950	Aquaculture Byproduct	No	No	Maguire 2005
Chamidae	<i>Chama</i>	<i>lazarus</i>	Indo-West Pacific	Hawaii	1950	Shipping	No	No	Carlton and Eldredge 2009
Mytilidae	<i>Lioborus</i>	<i>ligneus</i>	Indo-West Pacific	Mediterranean	1999	Lessepsian	No	No	Nunes 2014
Macluridae	<i>Maclura</i>	<i>lilacea</i>	Indo-West Pacific	Mediterranean	1972	Lessepsian	No	No	Galil 2007
Mytilidae	<i>Mytilaster</i>	<i>lineatus</i>	Western Atlantic; Mediterranean	Mediterranean	1918	Shipping	No	No	Karpinsky 2010
Trapezidae	<i>Trapezium</i>	<i>liratum</i>	Western Pacific	Eastern Pacific	1935	Aquaculture Byproduct	No	Yes	Wonham & Carlton 2005
Pectinidae	<i>Scaevola</i>	<i>livida</i>	Eastern Australia	Western Australia	1989	Shipping	No	No	McDonald & Wells 2009
Semellidae	<i>Theora (Endopleura)</i>	<i>lubrica</i>	Western Pacific	Australia; NZ; Mediterranean ; Eastern Pacific	1958	Shipping	No	Yes	Bogi & Galil 2007, McDonald & Wells 2009
Chamidae	<i>Chama</i>	<i>macrophylla</i>	Western Atlantic	Hawaii	1996	Shipping	No	No	Godwin 2003
Pteriidae	<i>Pinctada</i>	<i>margaritifera</i>	Indo-West Pacific	Mediterranean ; Western Atlantic	1974	Aquaculture	No	No	Galil 2007
Laternulidae	<i>Exolaternula</i>	<i>liataudi</i> (incl. records of E. marilina Reeve 1860)	Western Pacific	Eastern Pacific	1990	Shipping	No	No	Miller et al 1999

Table S4.1 continued

Veneridae	<i>Mercenaria</i>	<i>mercenaria</i>	Western Atlantic	Eastern Atlantic; Mediterranean; Eastern Pacific; Western Pacific	1925	Aquaculture	Yes	Yes	Grosholz and Ruiz 2003, Wonham & Carlton 2005, Grosholz et al 2015
Limopsidae	<i>Limopsis (Oblimopa)</i>	<i>multistriata</i>	Indo-West Pacific	Mediterranean	1965	Lessepsian	No	No	Galil 2007
Arcidae	<i>Scapharca</i>	<i>natalensis</i>	Indian Ocean	Mediterranean	1935	Lessepsian	No	No	Galil 2007
Spondylidae	<i>Spondylus</i>	<i>nicobaricus</i>	Indo-West Pacific	Mediterranean	1988	Shipping	No	No	Mienis 2004, Galil 2007
Trapezidae	<i>Trapezium</i>	<i>oblongum</i>	Indo-West Pacific	Mediterranean	1980	Lessepsian	No	No	Mienis 1980
Psammobiidae	<i>Nuttallia</i>	<i>obscurata</i>	Western Pacific	Eastern Pacific	1991	Shipping	Yes	Yes	Chan 2013, http://www.psp.wa.gov/download/ANS/MISM_Online.pdf
Macluridae	<i>Maclura</i>	<i>olorina</i>	Indo-West Pacific	Mediterranean	1876	Lessepsian	No	No	Por 1971
Limidae	<i>Limaria</i>	<i>orientalis</i>	Indo-West Pacific	New Zealand	1972	Shipping	No	No	Cranfield 1998
Chamidae	<i>Chama</i>	<i>pacifica</i>	Indo-West Pacific	Mediterranean	1905	Lessepsian	Yes	Yes	Nawrot et al 2015, Tillier and Bavay 1905, Streftaris and Zenetos 2006
Veneridae	<i>Clementia</i>	<i>papyracea</i>	Indo-West Pacific	Mediterranean	1937	Lessepsian	No	No	Galil 2007
Pectinidae	<i>Zygochlamys</i>	<i>patagonica</i>	South America	Mediterranean	1985	Shipping	No	Yes	Crocetta & Renda 2008
Veneridae	<i>Gafrarium</i>	<i>pectinatum</i>	Indo-West Pacific	Mediterranean	1880	Lessepsian	No	No	Por 1971

Table S4.1 continued

Pteriidae	<i>Pteria</i>	<i>penguin</i>	Indo-West Pacific	Pacific Islands	1975	Aquaculture	No	No	Teitelbaum and Fale 2008
Mytilidae	<i>Arcuatula (Musculista)</i>	<i>perfragilis</i>	Indo-West Pacific	Mediterranean	1960	Lessepsian	No	No	Galil 2007
Mytilidae	<i>Perna</i>	<i>perna</i>	Indo-West Pacific; Eastern Atlantic; Mediterranean; S. Western Atlantic	N. Western Atlantic	1990	Shipping	Yes	No	Holland 2001, Sousa et al 2009
Ostreidae	<i>Planostrea</i>	<i>pestigris</i>	Indo-West Pacific	Eastern Mediterranean	2003	Shipping	No	No	Galil 2007
Veneridae	<i>Meretrix</i>	<i>petechialis</i>	Western Pacific	N. Western Pacific?	1997	Aquaculture	No	Yes	Yamakawa and Imai 2012
Mytilidae	<i>Brachidontes</i>	<i>pharaonis</i>	Indo-West Pacific	Mediterranean	1876	Multiple	Yes	Yes	Galil 2007, Streflaris and Zenetos 2006
Veneridae	<i>Ruditapes</i>	<i>philippinarum</i>	Indo-West Pacific	Mediterranean ; Eastern Atlantic; Eastern Pacific	1936	Aquaculture	Yes	Yes	Toupoint et al 2008, Streflaris and Zenetos 2006
Veneridae	<i>Petricolaria</i>	<i>pholidiformis</i>	Western Atlantic	Eastern Atlantic; Mediterranean ; Eastern Pacific	1927	Shipping	Yes	Yes	NOBANIS
Arcidae	<i>Acar (Barbatia)</i>	<i>plicata</i>	Indo-West Pacific	Mediterranean	1978	Lessepsian	No	No	Galil 2007
Plicatulidae	<i>Plicatula</i>	<i>plicata</i>	Indo-West Pacific	Mediterranean	2003	Shipping	No	No	Crocetta et al 2015, Mienis 2012
Macluridae	<i>Raetella</i>	<i>pulchella</i>	Indo-West Pacific	Australia	1991	Shipping	No	No	Cohen et al 2001

Table S4.1 continued

Pteriidae	<i>Pinctada</i>	<i>radiata</i>	Indo-West Pacific	Mediterranean	1874	Multiple	Yes	No	Galil 2007, Lodola et al 2013, Streftaris and Zenetos 2006
Malleidae	<i>Malleus</i>	<i>regulus</i>	Indo-West Pacific; Eastern Pacific	Mediterranean	1900	Lessepsian	No	No	Por 1971
Cardiidae	<i>Afrocardium (Fragum)</i>	<i>richardi</i>	Indo-West Pacific	Mediterranean	1997	Lessepsian	No	No	Galil 2007
Veneridae	<i>Timoclea</i>	<i>roemeriana</i>	Indo-West Pacific	Mediterranean	1997	Lessepsian	No	Yes	Galil 2007
Psammobiidae	<i>Soletellina</i>	<i>rosea</i>	Indo-West Pacific	Mediterranean	1905	Lessepsian	No	No	CIESM
Myidae	<i>Sphenia</i>	<i>rueppellii</i>	Indo-West Pacific	Mediterranean	1978	Multiple	No	Yes	Galil 2007
Pectinidae	<i>Mimachlamys</i>	<i>sanguinea</i>	Indo-West Pacific	Mediterranean	2012	Lessepsian	No	No	Shefer et al 2012
Semelidae	<i>Ervilia</i>	<i>scaliola</i>	Indo-West Pacific	Mediterranean	2014	Shipping	No	No	Zenetos & Ovalis 2014
Veneridae	<i>Circe</i>	<i>scripta</i>	Indo-West Pacific	Mediterranean	2007	Shipping	No	No	Zenetos et al 2008
Mytilidae	<i>Xenostrobus</i>	<i>securis</i>	Australia	Mediterranean; Western Atlantic; Western Pacific	1992	Aquaculture	Yes	Yes	Streftaris and Zenetos 2006
Mytilidae	<i>Arcuatula (Musculista)</i>	<i>senhousia</i>	Indo-West Pacific	Mediterranean; Eastern Pacific; Australia; Southern Indian Ocean	1960	Multiple	Yes	Yes	Galil 2007, Streftaris and Zenetos 2006
Spondyliidae	<i>Spondylus</i>	<i>spinosis</i>	Indo-West Pacific	Mediterranean	1988	Multiple	Yes	No	Galil 2007, Streftaris and Zenetos 2006

Table S4.1 continued

Mesodesmatidae	<i>Atactodea</i>	<i>striata</i>	Indo-West Pacific	Mediterranean	1973	Lessepsian	No	Galil 2007
Pholadidae	<i>Martesia</i>	<i>striata</i>	Global	Hawaii; Mediterranean	1915	Shipping	No	Carlton & Eldredge 2009
Pteriidae	<i>Pinctada</i>	<i>sugillata</i>	Indo-West Pacific	South Australia	1980	Shipping	No	Rutherford & Miller 2011
Veneridae	<i>Redicirce</i>	<i>sulcata</i>	Indo-West Pacific	Mediterranean	1970	Shipping	No	Galil 2007
Veneridae	<i>Paratapes</i>	<i>textile</i>	Indo-West Pacific	Mediterranean	1939	Lessepsian	No	Galil 2007
Arcidae	<i>Scapharca</i>	<i>transversa</i>	Western Atlantic	Mediterranean	1972	Shipping	Yes	Lipej et al 2012, Streftaris and Zenetos 2006
Arcidae	<i>Barbatia</i>	<i>trapezina</i>	Indo-West Pacific	Mediterranean	2004	Shipping	No	Mienis 2004
Tellinidae	<i>Tellina</i>	<i>valtonis</i>	Indo-West Pacific	Mediterranean	1970	Lessepsian	No	CIESM, Cinar et al 2011
Veneridae	<i>Circenita</i>	<i>varia</i>	Indo-West Pacific	Mediterranean	1972	Lessepsian	No	Galil 2007
Pteriidae	<i>Electroma</i>	<i>vexillum</i>	Indo-West Pacific	Mediterranean	2002	Multiple	No	Nawrot et al 2015
Pectinidae	<i>Bracteochlamys</i>	<i>vexillum</i>	N. Australia	Mediterranean	2000	Shipping	No	WGITMO 2006
Ostreidae	<i>Crassostrea</i>	<i>virginica</i>	Western Atlantic	Eastern Pacific	1869	Aquaculture	Yes	Sousa et al 2009
Mytilidae	<i>Perna</i>	<i>viridis</i>	Indo-West Pacific	Western Atlantic; Pacific Islands; Mediterranean ; Australia	1989	Multiple	Yes	Spinuzzi et al 2013

	Model	AIC	Predictors with p<0.05
Niche expansion among alien bivalves	RS + D	106.58	D, RS
	S + RS + D	107.43	RS, D
	S + RS + D + F + V + Sub + M + Fix + Fe	149.04	RS
Invasiveness among alien bivalves	S + RS + D	108.88	RS, D
	RS + D	111.08	D
	S + RS + D + F + V + Sub + M + Fix + Fe	142.55	
Non-native establishment among all bivalves	S + RS + Sub	937.31	S, RS
	S + RS	962.68	S, RS
	S + RS + F + Sub + M + Fix + Fe	1011.3	S, RS, Sub

Table S4.2. Results from logistic regression. Predictors: S, size; RS, geographic range size; D, date of introduction; F, family; V, vector; Sub, substrate; M, mobility; Fix, fixation; Fe, feeding

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Perna viridis ???

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