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Differential adaptations between cold-stenothermal environments in the bivalve *Lissarca* cf. *miliaris* (Philobryidae) from the Scotia Sea islands and Antarctic Peninsula

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Abstract

The cold stenothermal nature of the Southern Ocean, and highly adapted fauna living within, raises the question of how much intra-specific variation there is among invertebrate populations, and how variation may have a role in speciation processes through ecological divergence, natural selection, and reproductive isolation. Despite decades of collecting biological material, this question remains largely unanswered, and many studies compare 'populations' of pooled material from wide geographic ranges to compensate for sampling constraints. In this study, variations in ecophysiological traits are explored by measuring growth, reproduction, and shell morphology among six populations of the small bivalve *Lissarca* cf. *miliaris* (Philippi, 1845) from the Southern Ocean, which experience subtle differences in temperature, disturbance, and food availability. There are significant differences in shell morphology and growth among different populations and slower growth rates at higher latitude populations. Prodissoconch sizes show an inverse 'U' shaped relationship with latitude, and are correlated with egg size at South Georgia and King George Island's Potter Cove. Higher brood sizes at the South Georgia population represent a trade-off with lower egg size, and correlate with shell morphology by offering lower internal capacity to brood young. Lower investment into offspring and morphological variations in *Lissarca* cf. *miliaris* highlight the importance of local scale environmental variations on species' ecology. These variations in physical traits appear to be underestimated in the Southern Ocean, but may be important drivers of ecological divergence and speciation, which should be considered in future genetic investigations on different invertebrate populations.

Keywords: Southern Ocean; Plasticity; Bivalve; Speciation; Reproduction; Morphology

1. Introduction

The ecological divergence of populations has an important role to play in speciation processes of terrestrial and aquatic ecosystems, globally (see Schuller, 2009 for review). It is the consequence of natural selection in populations between sufficiently contrasting environments, overcoming gene flow between them and encouraging reproductive isolation through local adaptation (Funk, et al. 2006; Schuller, 2009). For widespread species, ecological divergence can be the primary factor behind reproductive isolation, even in overlapping populations (Knowlton, 1993), while selection for particular traits is often observed as variation or plasticity in morphology, reproduction, physiology, or behaviour among populations (West-Eberhard, 1989). In the Southern Ocean, these traits have only occasionally been investigated, and to overcome the problems associated with small sample sizes, material has often been pooled from relatively wide geographic areas, under the assumption that the widespread cold-stenothermal environment, which prevails, is homogeneous in its selection pressure. For example, morphological differences in the bivalve *Lissarca notorcadensis* were examined among 48 stations between 159 and 910m, and yet pooled into just 14 sample locations representing the Scotia Arc, Weddell Sea, and Ross Sea (Cope and Linse, 2006), while ecophysiological plasticity (growth, reproduction, and somatic production) was measured in *L. notorcadensis* from 'Northern' and 'Southern' Weddell Sea locations, despite samples representing 65 stations covering a depth range of 80-1108m (Brey and Hain, 1992).

Morphological variation, commonly described as plasticity, is an easily measured trait in marine molluscs, usually determined by differences in the shape, size, and structure of the calcified shell in response to environmental differences (e.g. Vermeij, 1973; Seeley, 1986; Nolan, 1991; Fuiman et al., 1999; Trussell, 2000; Bayne, 2004; Sousa et al., 2007; Benaim et

al., 2011; Reed et al., 2013b). These adaptations may have important roles in survival and dispersal success, or promote more efficient energy partitioning. Morphological variations in shell shape can result from the physical effects of wave action or ice (Seed, 1968; de Wolf et al., 1998; Akester and Martel, 2000; Steffani and Branch, 2003; Harper et al., 2012), predation (Seeley, 1986; Trussell, 2000) or food availability (Appeldoorn, 1982), and are not necessarily representative of genetic structuring (de Wolf et al., 1998; Hoffman et al., 2010). Physiological plasticity, inferred by growth and reproductive output throughout a wide distribution, is poorly understood in the Southern Ocean, and yet can give important clues to the species response to changes in temperature (Morley et al., 2009; Reed et al., 2012), food availability (Peck et al., 2005), and even water chemistry (Reed et al., 2012). This is of particular interest in the Southern Ocean, because many species, which have wide distributions, are known to be sensitive to subtle variations in temperature (Peck et al., 2004; Clarke et al., 2004; Barnes and Peck, 2008; Reed et al., 2012).

Lissarca miliaris (Philippi, 1845) make a good model bivalve species in which to study differential adaptations to contrasting environments, with a geographic range from the Antarctic Peninsula, Scotia Sea, and Kerguelen Island to the Magellan region (Huber, 2010). They are relatively short lived (up to 7 years) with distinct growth increments, and brood their young for 18 months in the mantle cavity (Richardson, 1979; Reed et al., 2013a). While these brooding traits may limit their dispersal capability, their preferred macroalgal habitat makes rafting a likely successful dispersal mechanism within the circum-polar current and associated eddies (Highsmith, 1985; Martel and Chia, 1991; Helmuth et al., 1994; Higgs et al., 2009; Nikula et al., 2012).

This study aims to investigate the variation in morphology, growth, and reproduction in *Lissarca* cf. *miliaris* from six populations, spanning the Scotia Sea to the Antarctic Peninsula, and develop an ecological framework for future molecular studies. Although the studied areas are characteristically cold-stenothermal, all present subtly different environmental conditions, especially in respect to their temperature range and food availability. The wide geographic ranges of many Antarctic invertebrates may represent genetically distinct populations. However, variation driven by environmental differences can occur independently of genetic divergence (West-Eberhard, 1989), and conditions other than reproductive isolation, are not well discussed in the Southern Ocean. It is the common ancestry and not detailed molecular taxonomy of *L. cf. miliaris* populations in this study which makes variation important to understand, as it demonstrates how a species can respond to changes in the environment, and expand their geographic range over evolutionary time periods. Ecological divergence through local adaptations and variations driven by subtle environmental differences, may be a likely prerequisite to genetic divergence and speciation; a hypothesis which is discussed in an evolutionary context.

2. Materials and Methods

2.1 Bivalve Collection

Lissarca cf. *miliaris* were collected from macroalgae and rocks by hand (intertidally) or by SCUBA divers (subtidally) during a number of research expeditions to the Southern Ocean between 1972 and 2012 (Figure 1). Available for this study were specimens from South Georgia (Cumberland Bay, 54°17'S, 36°30'W, intertidal, 1972); Signy Island (South Orkney Islands, Shallow Bay, 60°42'S, 45°36'W, intertidal, 2002); King George Island (South Shetland Islands, Admiralty Bay, 62°10'S, 58°25'W, 10m, 1997; Potter Cove, 62°14'S, 58°42'W, 10m, 1994); Livingston Island (South Shetland Islands, Byers Peninsula, 62°38'S, 61°05'W,

intertidal, 2009), and Stepping Stones (Nr. Anvers Island, 64°47'S, 64°00W, 10m, 2012). All samples were fixed at collection in either 4% buffered formalin or 70% ethanol and subsequently all stored in 70% ethanol.

2.2 Shell Morphology

Shell length, height, and width of each bivalve were measured under a stereomicroscope to an accuracy of $\pm 0.05\text{mm}$, using an eye-piece micrometer calibrated with a stage micrometer. Shell length was defined as the maximum distance across the shell. In total 3665 *L. miliaris* were measured from South Georgia (n=626), Signy Island (n=460), King George Island's Admiralty Bay (n=117), King George Island's Potter Cove (n=2271), Livingston Island (n=58), and Stepping Stones (n=133). Reduced major axis regression of log transformed data were used to identify relationships between measured variables, and an analysis of covariance (ANCOVA) on normally distributed data used to test differences among populations. Back transformations of mean corrected values from the ANCOVA were used to visualise morphological differences, while a Tukey test was used to find statistical differences among populations. Sigmaplot v12.3, Minitab 16, and PAST analytical software were used for statistical analysis.

2.3 Growth

Growth data for *L. cf. miliaris* at South Georgia (n=558), Signy Island 2002 (n=458), King George Island's Admiralty Bay (n=117), King George Island's Potter Cove (n=1444), Livingston Island (n=58), and Stepping Stones (n=133), were collected by counting seasonally forming growth increments under a stereomicroscope (Richardson, 1979). Only lines that could be traced around the whole length of the shell were counted (Brey and

Hain, 1992; Higgs et al., 2009). Growth data were analysed using the von Bertalanffy growth function (vBGF);

$$S_t = S_\infty (1 - e^{-K(t - t_0)})$$

where S_t is length, S_∞ is asymptotic length, K is growth coefficient, t is age, and t_0 is age when size equals zero. The derived parameters from vBGF can be used further to compare the overall growth performance (OGP) of species of similar size;

$$P = \log(K * S_\infty)$$

where P is the overall growth performance, K is the growth coefficient and S_∞ is asymptotic length derived from vBGF (Pauly and Munro, 1984; Brey, 1999; Brey, 2001; Heilmayer et al., 2004; Reed et al., 2013b). An analysis of covariance and post-hoc Tukey test was used to identify significant differences in growth among populations.

2.4 Prodissoconch Sizes

Prodissoconch I (PI) length and height were measured on year 0-1 cohort shells, from microphotographs, processed using Adobe Photoshop CS5. Populations at South Georgia (n=99), Signy Island 2002 (n=47), King George Island's Admiralty Bay (n=26), and Stepping Stones (n=13) were measured. A general linear model Analysis of Variance with a post hoc multiple comparison test (Tukey test) was used to show significant differences among populations. Other populations were not used as too few year 0-1 cohort shells were available, and the poor condition of the prodissoconch on larger specimens make measurements impossible or inaccurate.

2.5 Egg Size and Brood size

Egg sizes were measured by dissection of vitellogenic eggs and image analysis from microphotographs using Sigmascan Pro 4 software. Eggs were removed and counted from the brood chamber of adult females or from the mature dorsal gonad from specimens at South Georgia, and King George Island's Potter Cove. All eggs were at the same stage of development (before observed blastula stage) and same time of year (January). Feret diameter was used to measure egg size; 125 eggs from 11 adults were measured from South Georgia while 845 eggs from 75 adults were measured from King George Island's Potter Cove. Egg counts per brood were taken from 16 adults from South Georgia and 150 adults from King George Island's Potter Cove. An analysis of covariance was performed on normally distributed data to identify significant differences between populations.

3. Results

3.1 Species Identification

Lissarca miliaris was originally described as *Pentaculus miliaris* from the Straits of Magellan by Phillippi (1845) and was suggested to be congeneric with *Lissarca rubro-fusca* by Smith (1879). Nicol (1966) synonymised the species after examining the morphology of both *miliaris* and *rubro-fusca* morphotypes but suggested that the two might be distinguished by a slightly more elongate shell form of *L. rubro-fusca*. Dell (1964) also included *Lissarca bennetti* (Preston, 1916) from the South Orkneys as a synonym. In this study, the different populations were identified as *Lissarca* cf. *miliaris* according to the description by Smith (1879) and Nicol (1966) (Figure 2). Key features include;

Shell size small, usually less than 5mm, robust, tumid, equivalve, subquadrate, distinctly inequilateral with beaks towards the anterior, anterior side rounded, outline oval, umbones project from dorsal line. Shell reddish brown to purple/pink, thick brown periostracum, thicker at margins. Valves with concentric striae, sometimes with radial striae. Hinge with

four or five strongly developed posterior chevron shaped teeth, three to four anterior. Ligament central to teeth, small, alivuncular indistinct, hinge line straight. Pallial line continuous without sinus, posterior adductor muscle scar large, slightly pear shape, anterior adductor muscle absent.

3.2 Morphology

The six populations of *L. cf. miliaris* from South Georgia, Signy Island, King George Island, Livingston Island, and Stepping Stones show positive relationships between shell length and shell height (Figure 3a) and shell length and shell width (Figure 3b) (length/height r^2 values all above 0.98, length/width r^2 values all above 0.93). An ANCOVA identified three distinct morphologies from log transformed length against height ($F_{5, 3654}=8.87$, $p<0.001$). A post hoc Tukey test ($p<0.05$) found King George Island (Admiralty Bay) and Stepping Stones to make up a distinct group (Figure 3c) by having more elongate shells than other populations (Figure 4a). South Georgia, King George Island's Potter Cove, Stepping Stones, and Livingston Island populations made up a second statistically distinct group (Figure 3c) being between the extremes of shell roundness and slenderness (Figure 4a), while Signy Island and Livingston Island made the third distinct group (Figure 3c), having the most discoid and inflated shell shapes (Figure 4a). Shells became more inflated with age but there was no trend in the length/height relationship with growth increment (Figure 4b). There was a significant difference between log transformed length and width among sites (ANCOVA, $F_{5, 2971}=25.75$, $p<0.001$), and a post hoc Tukey test ($p<0.05$) identified two distinct groups with only Livingston Island overlapping in both. South Georgia, King George Island's Admiralty Bay, and Stepping Stones made up a distinct group (Figure 3d) with the least inflated

morphologies (Figure 4a) while Signy Island and King George Island's Potter Cove made up a second group (Figure 3b) being most inflated (Figure 4a).

3.3 Growth

A von Bertalanffy growth curve for each population showed variations in the rate of growth among *L. cf. miliaris* (Figure 5a). The population from South Georgia showed the fastest growth, and had the largest observed adult at 6mm shell length after seven growth increments. In contrast, populations at Stepping Stones and Livingston Island had the slowest growth and smallest sizes at each age cohort; both populations only observed having up to five and six growth increments, respectively. An ANCOVA identified a significant difference in size-at-age among populations ($F_{5, 2763}=51.74$, $p<0.001$). A post-hoc Tukey test ($p<0.05$) of size-at-age measurements found the growth at South Georgia and both King George Island populations to be statistically indistinct, while populations at Signy Island, Livingston Island, and Stepping Stones all had significantly different and distinct growth. The overall growth performance (OGP), show higher values for South Georgia (0.443) and the King George Island populations (Admiralty Bay 0.437, Potter Cove 0.404), compared to Stepping Stones, Livingston Island, and Signy Island populations (Figure 5b). Calculated OGP was lowest at Signy Island (0.318), followed by Livingston Island (0.346), and Stepping Stones (0.373).

3.4 Prodissoconch Size

There was a significant difference among mean *L. cf. miliaris* prodissoconch length (PI) at South Georgia, Signy Island, King George Island's Admiralty Bay, and Stepping Stones (ANCOVA $F_{3, 180}=5.6$, $p<0.001$) with a Tukey test ($p<0.05$) identifying those at South Georgia and Stepping Stones to be statistically grouped with smaller PI lengths of $687.72\mu\text{m} \pm 1.57 \text{ SE}$

and $680.52 \mu\text{m} \pm 6.71 \text{ SE}$, respectively (Figure 6a). Signy Island and King George Island populations (both sites) were also statistically grouped together with larger PI lengths of $699.21 \mu\text{m} \pm 4.96 \text{ SE}$ and $701.13 \mu\text{m} \pm 5.41 \text{ SE}$, respectively.

The ratio of prodissoconch length and height were also significantly different (ANCOVA $F_{3,180}=64.99$, $p<0.001$) and a Tukey test identified South Georgia and Stepping Stones populations to be distinct with ratios of $1.44 \pm 0.0046 \text{ SE}$ and $1.70 \pm 0.0240 \text{ SE}$ respectively. Specimens from Signy Island and King George Island's Admiralty Bay were grouped together with ratios of $1.53 \pm 0.013 \text{ SE}$ and $1.49 \pm 0.016 \text{ SE}$ (Figure 6b).

3.5 Egg Size and Brood Size

Brooded eggs of the same developmental stage, measured at King George Island's Potter Cove and South Georgia, were significantly different in size and number. An ANCOVA found a significant difference between King George Island and South Georgia egg sizes ($F_{1,82}=75.64$, $p<0.001$) with corrected mean Feret diameters of $355.3 \mu\text{m} \pm 3.64 \text{ SE}$ and $263.0 \mu\text{m} \pm 9.98 \text{ SE}$, respectively (Figure 7a). The number of eggs brooded was correlated with shell size (King George Island $r^2=0.390$, $p<0.001$, $n=150$; South Georgia $r^2=0.215$, $p<0.05$, $n=16$) (Figure 7b) and was significantly different between populations. King George Island's Potter Cove population had significantly lower numbers per cohort than the South Georgia population (ANCOVA $F_{1,163}=74.85$, $p<0.001$) with corrected mean brood sizes of $32.95 \text{ eggs} \pm 0.97 \text{ SE}$ and $60.00 \text{ eggs} \pm 2.97 \text{ SE}$, respectively (Figure 7c).

4. Discussion

The populations of *L. cf. miliaris* studied were identified by the anatomical and shell characteristics, which have defined them as a species since their original descriptions were published (Phillippi, 1845; Smith, 1879; Figure 1). Whether these populations are one

continuous species with distinct morphologies, or a selection of cryptic species, cannot be determined from this study alone, and should be subject to future molecular analysis. Unfortunately, such analyses were not appropriate in this study, as many samples were previously fixed in formalin due to differing research priorities. In the context of this study, a detailed classification by molecular markers is not required, as we define differences among populations of a species, likely derived from a single common type *Lissarca miliaris*. If future studies find speciation processes to be occurring in the studied *L. cf. miliaris*, it would support the hypothesis that variation, and the ecological divergence of populations, allows radiation and speciation within cold stenothermal environments. Phenotypic plasticity observed within a single population of *L. miliaris* over few decades in response to atmospheric warming (Reed et al., 2012), emphasises the potential importance of plasticity in determining the resilience of a species to rapid change, and the flexibility of the species in both morphology and physiology. However, variation and the expression of plastic traits do not require a change in genotype, and may even constrain evolution by buffering the need for genetic change (West-Eberhard, 1989). Over time, distinct phenotypes can become genetically canalised, even when faced with moderate levels of gene flow (Knowlton, 1993; Schluter, 2009). This may be particularly true for brooding species where life history traits prevent genetic transfer between populations, as studied in the genus *Lasaea* (Crisp and Standen, 1988; Ó Foighil and Smith 1996; Li et al., 2013).

Despite the cold stenothermal conditions of the Southern Ocean, *L. cf. miliaris* demonstrate morphological and reproductive variation among populations of close geographic proximity, highlighting how data may remain hidden within previous studies, which pooled together material from wider regions. However, subtle environmental differences become important

in the Antarctic context at the local scale, by the selection of traits with population-specific benefits. Additionally, evidence for reproductive trade-offs associated with variation in the Southern Ocean may be a driver for ecological divergence in *L. miliaris*, and there is potential for reproductive isolation, despite the likelihood of dispersal by passive rafting of macroalgae (Highsmith et al., 1985; Helmuth et al., 1994; Higgs et al., 2009; Nikula et al., 2012; Thatje, 2012). The demonstration of variation among populations presented here could therefore be significant in understanding the radiation of *L. miliaris* and that of other taxa in the Southern Ocean.

4.1 Morphological variants

Morphological variations in molluscs are often attributed to the physical environment to which they are exposed (Seed, 1968; De Wolf et al., 1998; Akester and Martel, 2000; Steffani and Branch, 2003; Reed et al., 2013b). Each population of *L. cf. miliaris* studied lives in a subtly contrasting environment (see below), collected either intertidally (South Georgia, Signy Island, and Livingston Island) or subtidally (King George Island and Stepping Stones). However, this difference alone cannot explain all of the morphological differences among populations. The two King George Island populations, geographically closest together and collected by SCUBA divers at 10m water depth, are significantly different by their length/height and depth relationships, and similar only by growth rate. Meanwhile, significant differences exist in the morphology of adult shell, larval shell, and growth between intertidal populations at Signy Island and South Georgia.

Exposure to wave action also appears to have little effect on shell morphology; specimens from Livingston Island were collected at the rocky Byers Peninsula and yet show no significant differences in morphology to the Signy Island population collected on the

sheltered intertidal mud flats at Shallow Bay. Both of these populations show a more discoid and inflated morphology, previously associated with wave-exposed areas (Seed, 1968; Akester and Martel, 2000), in comparison to the elongate shells at King George Island, South Georgia, and Stepping Stones.

Differences in population density can also force shell morphology variations (Seed, 1968). *Lissarca miliaris* usually live in dense clumps (Dell, 1964; Richardson, 1979; personal observation) and population density is known to have been high at Signy Island, King George Island, Livingston Island, and Stepping Stones. Recruitment of Antarctic brooding bivalves to the immediate environment is usually high (Richardson, 1979; Brey and Hain, 1992; Brey et al., 1993; Higgs et al., 2009), and this factor may be assumed to be constant among all populations studied. Harper et al. (2012) found phenotypic plasticity in the infaunal *Laternula elliptica* related to geographic variations in ice scour disturbance between Hangar Cove at Rothera, and McMurdo Sound, with no genetic differences identified among populations. Although ice cover and disturbance varies among all populations of *L. cf. miliaris* studied, their small size and epifaunal settlement reduce the impacts of ice scour, and populations are perhaps more likely to be dislodged rather than crushed or damaged by ice.

Although predation of bivalves in the Southern Ocean is documented, to date the effects of predation are poorly known. Predatory shell boring gastropods such as *Trophon longstaffi* and *Neobuccinum eatoni*, and the asteroids *Odontaster validus*, and *Cryptasterias turqueti* (Dayton et al., 1974; Stockton, 1984; Zamorano et al., 1986; Harper and Peck, 2003) are known consumers of larger infaunal bivalve species *Laternula elliptica*, *Yoldia eightsii*, and *Adamussium colbecki*. Also found in the guts of fish, small bivalves can survive ingestion,

and may use consumption by fish as a method of dispersal (Domaneschi et al., 2002). Of the *L. cf. miliaris* collected in this study, few empty shells were observed and no evidence of shell boring occurred at any site; the effects of predation on shell morphology are likely to be negligible.

4.2 Growth

The growth and adult sizes of *L. cf. miliaris* demonstrate a decreasing trend with latitude, contrasting with previous growth work on bryozoan and limpet growth in the Southern Ocean (Barnes and Arnold, 2001; Clarke et al., 2004). Brey and Hain (1992) found no significant differences in growth rates of *L. notorcadensis*, but shells were distinctly larger from lower latitudes. Growth rate and shell characteristics are commonly dependant on food availability and temperature (Appeldoorn, 1982; Brey et al., 2011; Harper et al., 2012; Reed et al., 2012; Reed et al., 2013a) and the ability to extract calcium from sea-water at low temperature (Harper, 2000), but species sensitivity to these factors is likely complex.

Food availability in the Southern Ocean is often limiting with respect to short durations of highly seasonal primary productivity (Clarke et al., 1988; Clarke and Leaky, 1996), and has a close association to the inter-annual variation in sea ice formation (Whitaker, 1982; Lizotte, 2001). The length and concentrations of blooms among the studied populations are variable (Table 1), and relate to the heterogeneity of hydrographic conditions, which prevail in the Southern Ocean. The exposed shores of Livingston Island are in contrast to the sheltered Potter Cove at King George Island, which although deep, is protected from open water by a 30m sill at the entrance to the inner cove (Klöser et al., 1994; Schloss et al., 2002). Admiralty Bay, meanwhile, is a large embayment with a maximum depth of 500m and a high freshwater input from glacial melt (Rajusa-Suszczewski, 1980).

Peak chlorophyll-*a* ranges from 50.9 mg m⁻³ at Signy Island (Clarke et al., 1988) to peaks of just 1.7 mg m⁻³ at King George Island Admiralty Bay (Lange et al., 2007) and 7 mg m⁻³ at Cumberland Bay, South Georgia (Whitehouse et al., 1996). The populations studied at King George Island are contrasting in primary production with peaks of up to 25 mg m⁻³ at Potter Cove (Tatian et al., 2002; Schloss et al., 2002) but only up to 1.7 mg m⁻³ within Admiralty Bay (Brandini, 1993; Lange et al., 2007), while the population at Stepping Stones, near Palmer Station, may receive peaks between 20.9 – 35 mg m⁻³ from nearby waters (Holm-Hansen et al., 1989; Baker et al., 1996), but often with high inter-annual variability (Baker et al., 1997).

There are also subtle variations in temperature range among populations (Table 1); the most northern population of South Georgia being the warmest with water temperatures reaching 4.4°C (Whitehouse et al., 1996). Signy Island is comparatively cold with water temperatures from freezing (-1.8°C) to only 0.3°C (Clarke et al., 1988), which may have impacted on the lower than expected OGP value (Figure 5b), while King George Island populations have water temperatures from freezing (-1.8°C) to 1.76 and 1°C in Admiralty Bay and Potter Cove, respectively (Rakusa-Suszczewski, 1980; Klöser et al., 1994). At the highest latitude studied, surrounding waters of Stepping Stones have surface water temperatures between -1.8°C and 1.5°C, but within this upper range for fewer months (Baker et al., 1997; see Barnes et al., 2006).

The high growth rates, overall growth performance, and larger adult sizes of *L. cf. miliaris* at South Georgia are likely to be in response to higher water temperatures and longer periods of phytoplankton availability within Cumberland Bay. Both King George Island populations have similar growth and overall growth performance despite contrasting peaks in chlorophyll levels. This suggests that low temperature may be limiting the growth of adult *L.*

cf. *miliaris* at King George Island over food availability. High levels of seasonal melt water from retreating glaciers, creating high sedimentation rates, particularly impact both of these ecosystems, and fluctuating salinities (Klöser et al., 1994; Lange et al., 2007) may further affect growth.

The low water temperatures of Signy Island, and extreme variance in air temperature when exposed at low tide (Walker, 1972; Reed et al., 2012; Kuklinski and Balazy, 2013) could also result in overall growth performance.. Populations at Livingston Island and Stepping Stones with the smallest sizes are perhaps more restricted by food availability, lower average temperatures, and greater impacts of ice. Given the intertidal ecology of *L. miliaris*, short-term acute thermal tolerance might be of importance to survival, but care should be taken in comparing inter- and subtidal populations as physiological responses to emersion may differ (Weihe and Abele, 2008).

Prodissoconch development in *L. miliaris* occurs within the maternal brood chamber and is largely protected from the physical disturbances of predators, ice, and wave action. Extended periods of protected brood care in *L. cf. miliaris* occur during a critical time of larval shell secretion, and while protected, other environmental stressors may affect larval shell characteristics (Ó Foighil et al., 1986). The potential for energetic differences in egg content affecting overall size and morphology cannot be ruled out, and the effects of energy availability on early shell secretion not known in the Southern Ocean. However, decreasing prodissoconch size and changing morphology correlated with rapid atmospheric warming in *L. miliaris* at Signy Island (Reed et al. 2012), indicates that temperature is likely to be the driver of morphological differences in larval shells presented in this study. This is observed

by the most contrasting morphologies at South Georgia and Stepping Stones being most contrasting in maximum temperature range.

4.3 Reproduction

Few studies have investigated reproductive plasticity throughout a species range, although plasticity in egg size over a latitudinal gradient has been described in serolid isopods (Wägele, 1987; Clarke and Gore, 1992) and the caridean decapod *Notocrangon antarcticus* (Lovrich et al., 2005). Reproductive output and variation in *L. cf. miliaris* can be discussed in relation to growth rate and the energetic trade-off between large adult size and large eggs/juveniles. Morphology can have a significant impact on the reproductive output in brooding species, as typically brood size is limited by the females' capacity to carry young (Strathmann and Strathmann, 1982; Reed et al., 2013a). Linse et al. (2006) also demonstrated that differences in body size of the gastropod *Margarella antarctica* across populations in the Southern Ocean were reflected in their reproductive output.

The difference in egg size observed between South Georgia and King George Island's Potter Cove may be related to differences in temperature and food availability, but also shows a strong relationship with adult shell obesity. The significantly larger number of eggs per brood may be associated with the faster growth and larger sizes of *L. cf. miliaris* (South Georgia), but the trade-off is a reduction in mean egg size. Kraeuter et al. (1982) found that small differences in the egg size of the bivalve *Mercenaria mercenaria* and *Argopecten irradians* are important for survival, and smaller sizes may reflect a lower energy store, although may not always correlate with energy content (Byrne et al., 2008; McAlister and Moran, 2012). Several studies have identified differences in egg size and quality between populations of invertebrates attributed to food availability in echinoderms (George, 1994,

1996; Bertram and Strathmann, 1998) and bivalves (Barber and Blake, 1983; Phillips, 2007). The small egg sizes at South Georgia relate to the small prodissoconch sizes measured, indicating smaller juveniles. Morphological differences in adult shells are particularly striking however, as both populations show the same length/height relationship yet are significantly different in shell inflation; the South Georgia population being less inflated than the Potter Cove specimens (Figure 4a).

Measurements of prodissoconch maximum length at four of the populations revealed an inverse 'U' shape trend with increasing latitude. Secreted by the larval form, prodissoconch I (PI) sizes are directly linked to egg size (Ockelmann, 1965; Scheltema and Williams, 2009) and differences in egg size as small as 10µm can be reflected in significant differences in PI length (Goodsell and Eversole, 1992). The largest prodissoconch sizes, statistically grouped together, were measured at Signy Island and King George Island's Admiralty Bay, suggesting largest egg and juvenile size. Parental shell morphology is however, most morphologically dissimilar with Signy Island having a discoid shell to Admiralty Bays elongated shell. Prodissoconch lengths at South Georgia and Stepping Stones are the shortest with Stepping Stones having the smallest overall morphology. Both populations have adult shells of similar shape; more flattened and oval in shape with potentially reduced capacity to brood.

Increased volumes from differing morphologies in *L. cf. miliaris* affecting juvenile size cannot be conclusive from prodissoconch measurements alone; however the smallest egg sizes of South Georgia and small prodissoconch sizes of Stepping Stones do correlate to restricted internal volume. This also relates to an increase in growth rate and thinner shell shapes found at Signy Island over 40 years, and decreasing offspring size (Reed et al., 2012). The larger prodissoconch sizes at King George Island's Admiralty Bay, despite space limiting

adult morphology, may be related to an unmeasured trade-off with brood size. Evolutionary implications of differences in reproductive output are potentially significant, but would require further analysis of energetic contents of eggs to interpret. Investment of energy into eggs can affect larval fitness of marine invertebrates with consequences for future adult fitness (Vance, 1973; Emler and Hoegh-Guldberg, 1997). Smaller offspring sizes, inferred from prodissoconch sizes at South Georgia and Stepping Stones, would suggest a lower investment of energy per offspring, with a reduction in larval fitness, ability to disperse long distances, and mortality. Such ecological divergence and selection, may act against these individuals, and resulting reproductive isolation eventually influencing speciation processes.

5. Conclusions

Lissarca cf. *miliaris* demonstrate a wide range of plastic traits over its distribution south of the Polar Front including significant differences in growth, morphology, and reproduction, but there are trade-offs between morphology (potential volume to brood), growth, egg size, and fecundity. These differences are occurring despite only subtle environmental differences, and highlight the importance of local scale variations in ecology when comparing populations, especially in relation to food and temperature ranges. The intertidal ecology of *L. cf. miliaris* may indicate a wider tolerance to extremes in temperature and food supply, which have helped this species to survive a radiation north and south of the Polar Front. Distinct ecotypes also suggest a possibility for resilience to current challenges, particularly the rapid warming of the Antarctic Peninsula, which may rival climatic events since the origin of *Lissarca* in the Southern Ocean (Vaughan et al., 2003; Turner et al., 2005).

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Figure Legends

Figure 1. Map showing relative location of islands studied in relation to the Antarctic Peninsula.

Figure 2. *Lissarca miliaris* shell types from six Antarctic populations used in this study. a) South Georgia, Cumberland Bay, 1972; b) Signy Island, Shallow Bay, 2002; c) King George Island, Potter Cove, 1994; d) King George Island, Admiralty Bay, 1997; e) Livingston Island, Byers Peninsula, 2009; f) Stepping Stones, 2011.

Figure 3. Reduced major axis regressions of morphometric measurements in *Lissarca cf. miliaris* from different populations. a) log shell length against log shell height; b) log shell length against log shell width; c,d) Significant differences among populations marked by circled groupings, Tukey Test $p < 0.05$. KGI = King George Island.

Figure 4. Morphology of *Lissarca cf. miliaris* by populations and with age. a) corrected mean length/height v corrected mean length/width among populations identifying differing shell shapes; b) shell morphology with age among populations. Black line shell length/shell width,

grey line shell length/shell height. Decreasing ratio value indicates increasing obesity or roundness, respectively.

Figure 5. Growth parameters of *Lissarca cf. miliaris* among populations. a) von Bertalanffy growth function from age-at-size data of *Lissarca cf. miliaris* from different populations; b) overall growth performance of *Lissarca cf. miliaris* from different populations derived from residuals of von Bertalanffy growth function. Separate circles represent significantly different growth, $p < 0.001$. KGI = King George Island.

Figure 6. Mean prodissoconch sizes for *Lissarca cf. miliaris* at South Georgia, Signy Island, King George Island Admiralty Bay, and Stepping Stones. a) mean prodissoconch length (μm); b) ratio of prodissoconch length and height. Circles represent significant differences ($p < 0.05$). KGI = King George Island.

Figure 7. Mean egg size and number of eggs per brood in *Lissarca cf. miliaris* from King George Island Potter Cove and South Georgia. a) Mean egg size (Ferret Diameter μm) and standard error for Potter Cove (filled circle) and South Georgia (open circle). Solid line represents corrected mean egg size for Potter Cove, dashed line corrected mean egg size for South Georgia; b) Log. egg number against log. length for South Georgia (open circle) and Potter Cove (filled circle); c) Number of eggs per brood against shell length at Potter Cove (filled circle) and South Georgia (open circle). Solid line represents corrected mean egg number for Potter Cove. Dashed line represents corrected mean egg number for South Georgia. Egg Counts - Potter Cove, King George Island sample $n=150$; South Georgia sample $n=16$. Egg Sizes – 845 eggs from 75 adults from Potter Cove, King George Island; 125 eggs from 11 adults South Georgia.

Table 1. Environmental parameters for South Georgia, Signy Island, King George Island, Livingston Island, and Stepping Stones derived from published literature (references within).

Population	Water Temperature Range (°C)	Chlorophyll Peak (mg m⁻³)	Chlorophyll Peak duration	References
South Georgia	-0.95 to 4.4	4 to 7	5 months	Whitehouse et al. 1996
Signy Island	-1.8 to 0.3	50.9	3 months	Clarke et al. 1988
King George Island Admiralty Bay	-1.8 to 1.76	0.1 to 1.7	4 months	Rakusa-Suszczewski 1980 Lange et al. 2007
King George Island Potter Cove	-1.0 to 1.0 (Summer)	25	4 months	Tatian et al. 2002; Schloss et al. 2002 Klöser et al. 1994
Stepping Stones	-1.8 to 1.5	15 to 35	unknown	Holm-Hansen et al. 1989 Baker et al. 1996

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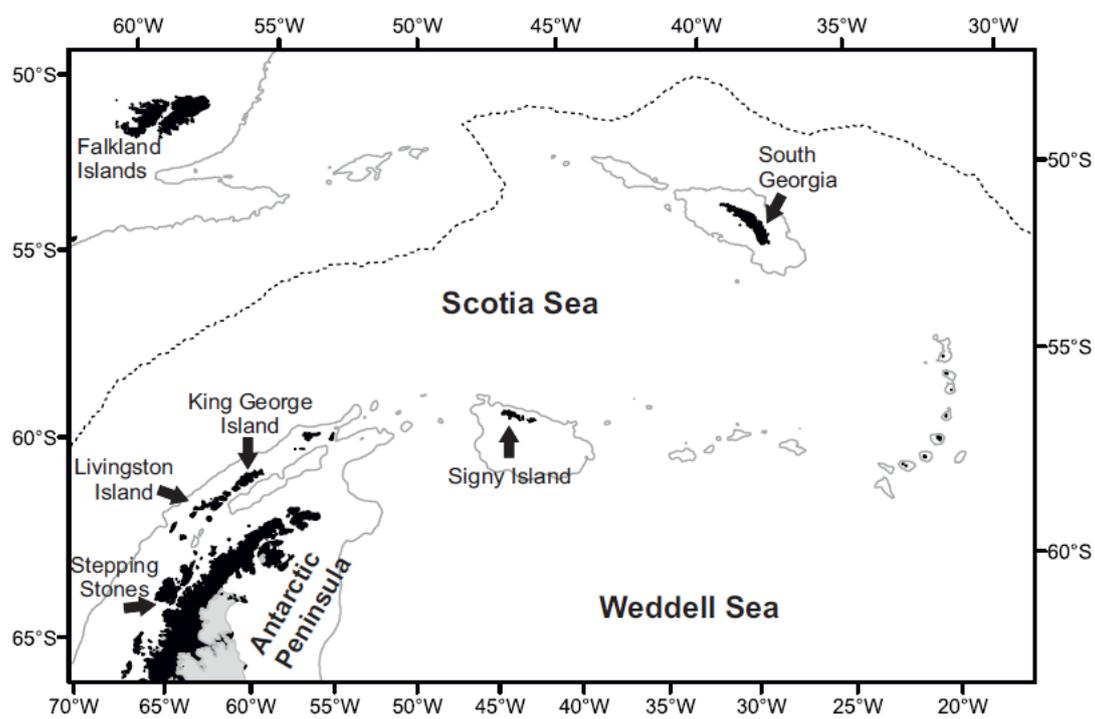


Figure 1

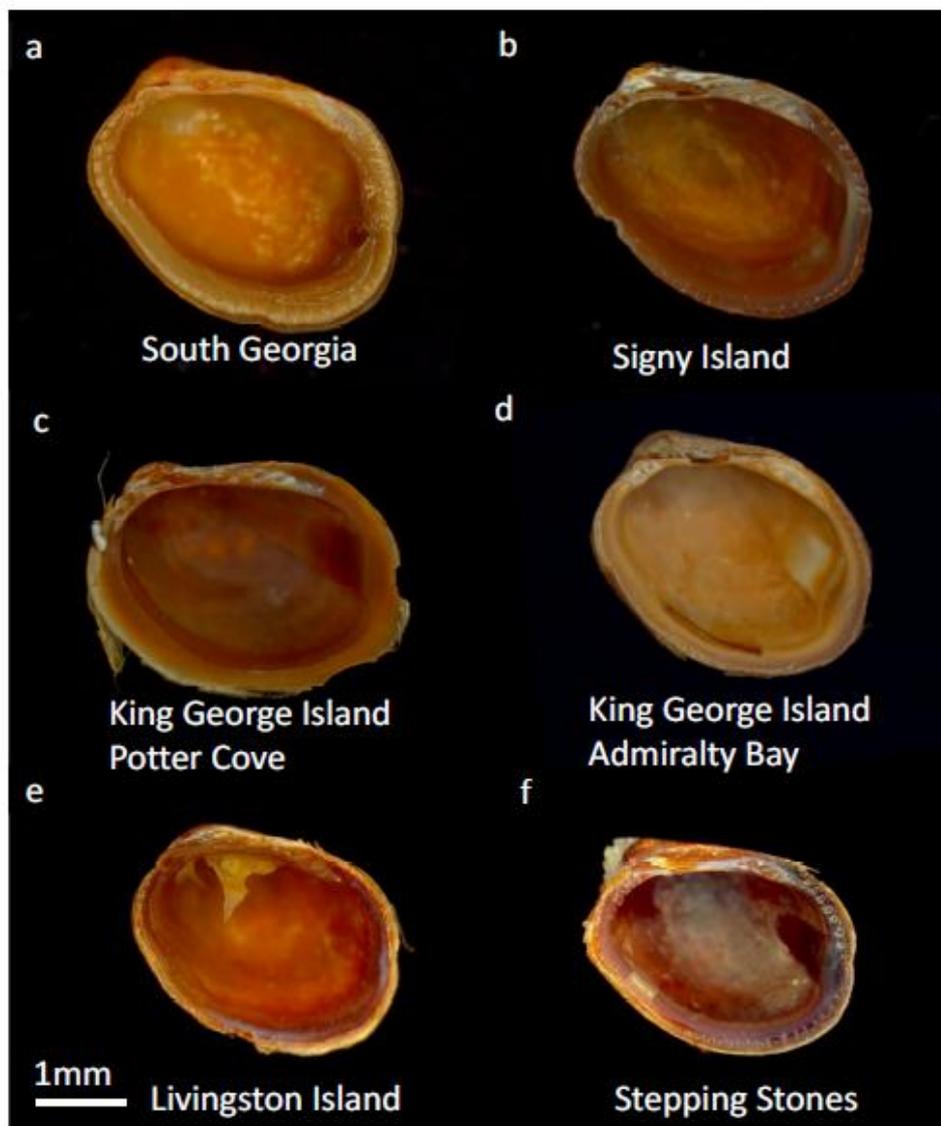


Figure 2

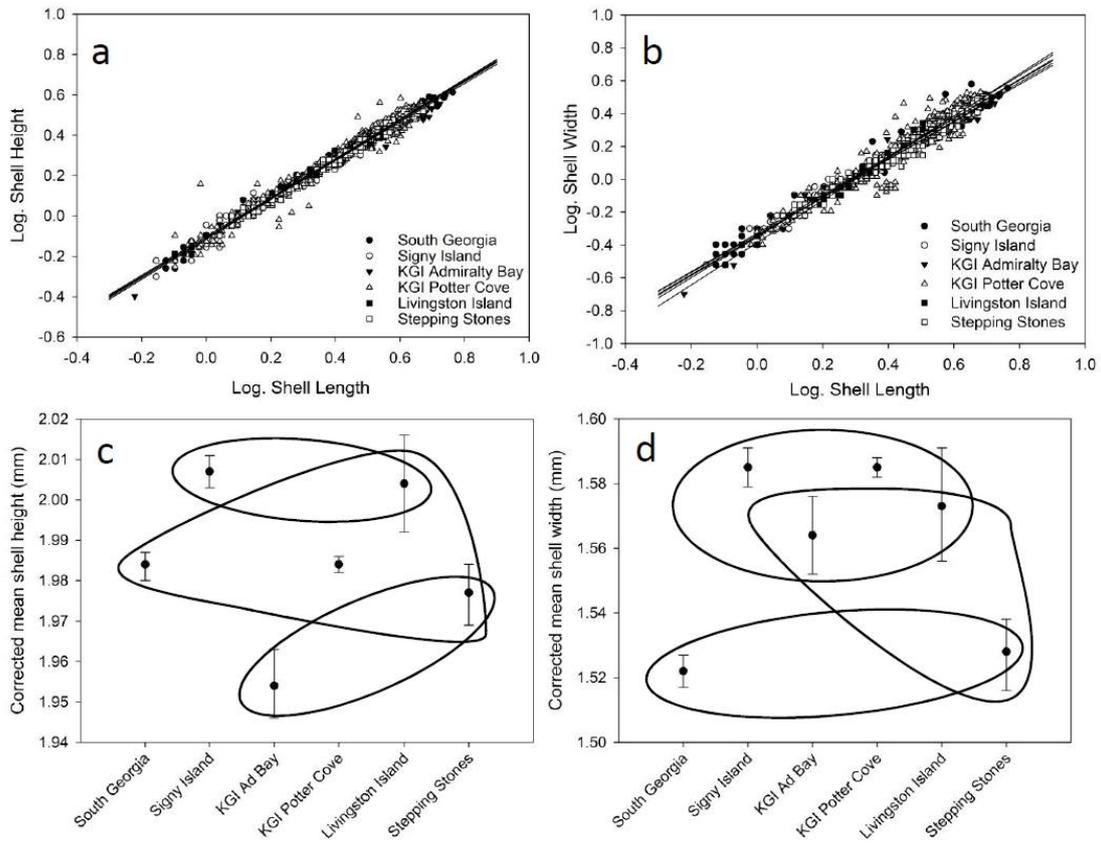


Figure 3

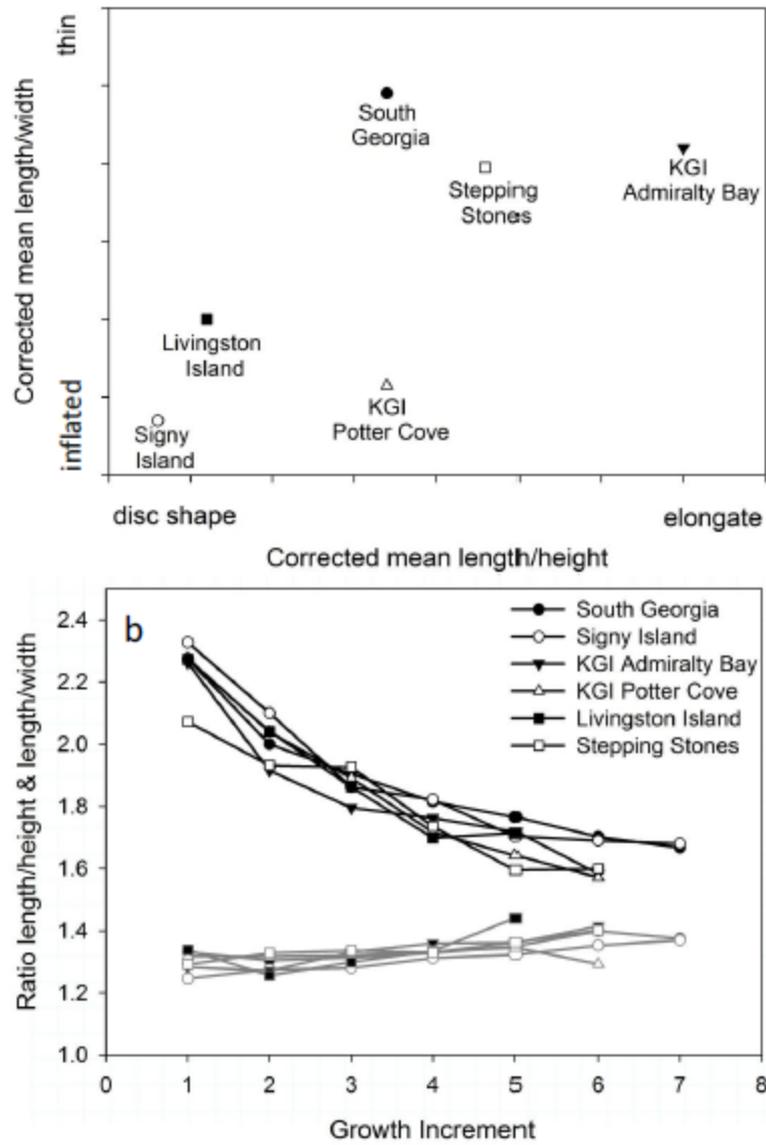


Figure 4

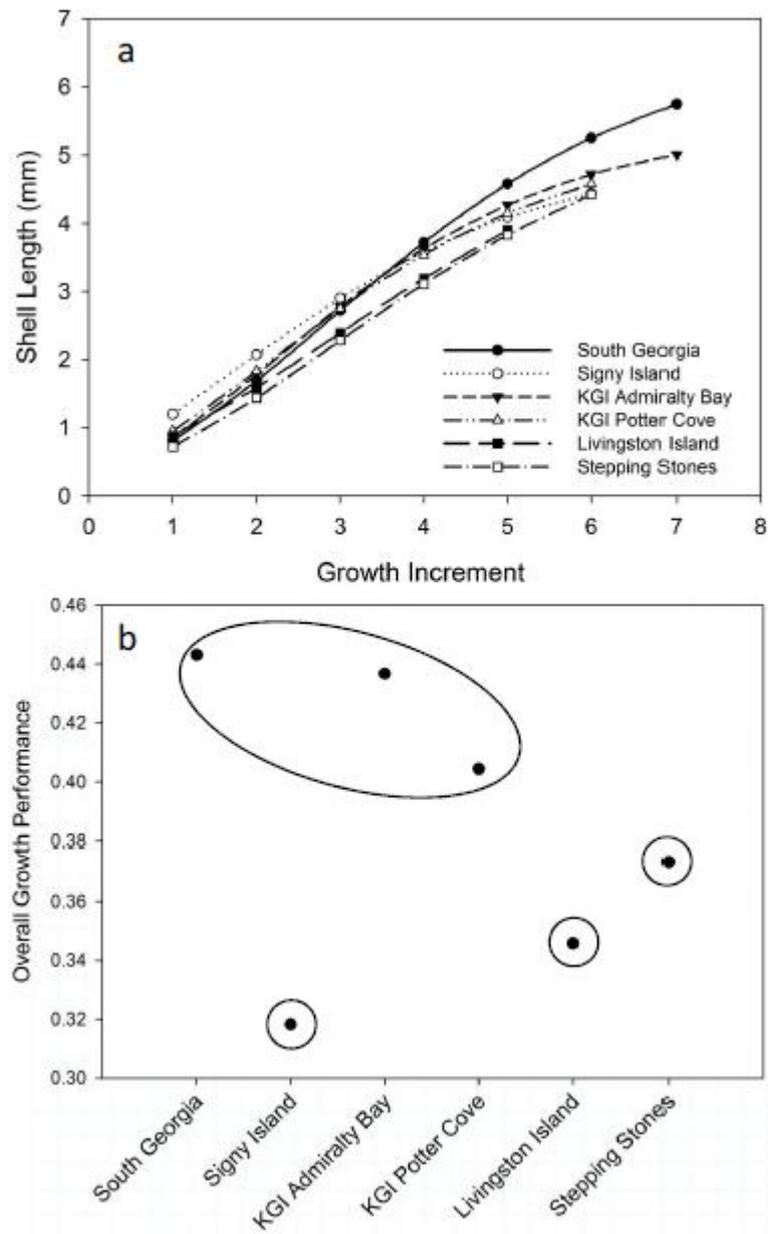


Figure 5

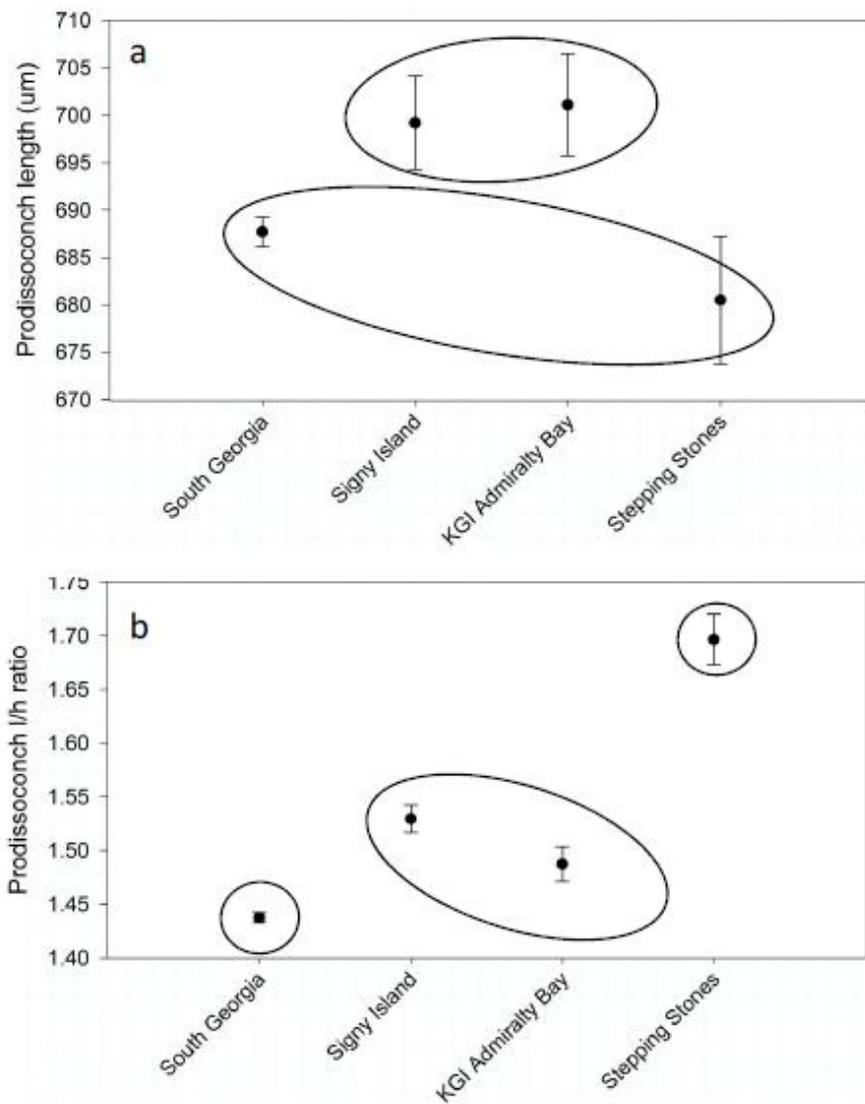


Figure 6

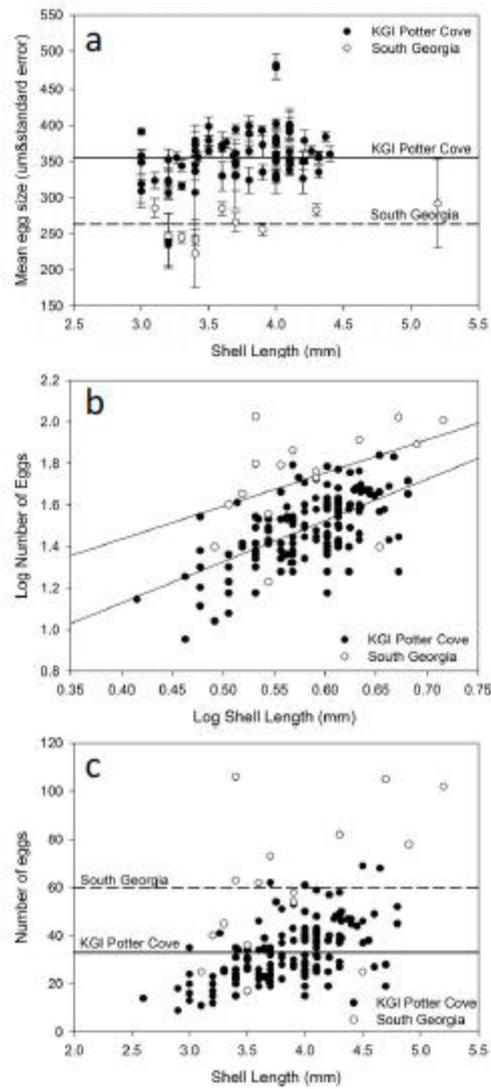


Figure 7

Highlights

- Our study explores Southern Ocean plasticity and its role in ecological divergence
- There are variations in bivalve morphology and maximum size among populations
- Slower growth rates with increasing latitude linked to lower temperatures
- Egg/larval size and number show trade-offs and relationship with latitude
- We provide evidence for ecological divergence for future molecular investigations

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