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Plasticity in shell morphology and growth among deep-sea protobranch bivalves of the genus *Yoldiella* (Yoldiidae) from contrasting Southern Ocean regions

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Abstract

The ecology of Antarctic deep-sea fauna is poorly understood and few studies have gone beyond assessing biodiversity when comparing deep regions of the Southern Ocean. Protobranch bivalves are ubiquitous in the deep ocean and are widely distributed in the Southern Ocean. This paper examines the potential respon ses to environmental differences in the common protobranchs *Yoldiella valettei*, *Yoldiella ecaudata*, and *Yoldiella sabrina* from contrasting deep-sea environments of the Weddell Sea, Scotia Sea, Amundsen Sea, and South Atlantic. There are significant differences in morphology between deep-sea regions in all species and a significant difference in shell weight in *Y. valettei* between the Amundsen Sea and Weddell Seas. Growth rates of *Y. valettei* and *Y. ecaudata* in the Amundsen Sea are also higher than elsewhere and *Y. valettei* have heaviest shells in the Amundsen Sea, suggesting more favourable conditions for calcification and growth. The plasticity observed among deep-sea regions in the Southern Ocean is likely to be driven by different oceanographic influences affecting temperature and food fluxes to the benthos, and demonstrate the species' ability to differentially adapt between cold-stenothermal environments. This study suggests that subtle changes in the environment may lead to a divergence in the ecology of invertebrate populations and showcases the protobranch bivalves as a future model group for the study of speciation and radiation processes through cold-stenothermal environments.

1. Introduction

Despite an increase in sampling effort through international programmes of recent years, Antarctic deep-sea ecosystems remain, overall, poorly understood, with few studies investigating the ecology of deep benthic fauna beyond their taxonomic compositions (Brandt et al., 2007). A taxonomic group consistently found from the Antarctic shelf to the deep-sea are the protobranch bivalves (Cattaneo-Vietti et al., 2000; Arnaud et al., 2001; Linse, 2004) a subclass with a global distribution to depths below 6000m in all deep-sea basins (Allen, 1978; Allen and Saunders, 1996; Allen, 2008). The protobranchs are of interest to deep-sea biologists as they have a long evolutionary history and physiological characteristics, which enable them to thrive in high abundances. They also play an important role in the turnover of surface sediments (Allen, 1978). Key adaptations are a gill structure exclusively used for respiration, modified palps for feeding, and long digestive systems to process huge quantities of fine sediment in areas of impoverished food supply (Zardus, 2002; Allen, 2008). In the Antarctic, protobranch bivalves are well represented, although the ecology of the deep-water species remain unknown and only the common shallow water *Yoldia eightsii* has been studied in any detail (Davenport, 1988; Peck and Bullough, 1993; Peck et al., 2004)

Phenotypic plasticity is a common trait in marine intertidal molluscs (e.g. Vermeij, 1973; Nolan, 1991; Trussell, 2000; Bayne, 2004; Sousa et al., 2007) where adapting to different environmental conditions may increase their chances of survival and successful dispersal. In the deep sea, morphological analysis has been focussed on gastropods where species identification is often more reliable (Etter and Rex, 1990; Rex and Etter, 1990; Iguchi et al., 2005). However, the deep-sea protobranch bivalves make a good model group to examine morphological plasticity due to their large geographical ranges. Plasticity in protobranchs has been observed by changes in morphology over short geographical distances and bathymetry in the Rockall Trough (Fuiman et al., 1999) and can be evidence of distinct ecotypes or even cryptic species; however, sample sizes are often too low for morphological studies to be undertaken. The Antarctic remains an interesting place to study plasticity as much of the benthic environment is considered to be extreme in its thermal stability and highly seasonal pulsed food supply from phytoplankton blooms (Clarke, 1988; Barnes et al., 2006; Clarke et al., 2009). Assessing the extent whereby benthic fauna respond to subtle environmental differences between regions is helpful in the understanding of evolutionary processes that have maintained these populations in the Southern Ocean, and to predict the impacts of future environmental changes (Reed et al., 2012).

With the exception of chemosynthetic species, growth data of deep-sea bivalves are sparse. Some commonly found Atlantic species have been studied, such as *Nuculana pernula* and *Yoldia thraciaeformis* (Hutchings and Haedrich, 1984), *Tindaria callistiformis* (Turekian et al., 1975) and *Ledella pustulosa* (Gage, 1994), but only species that exhibit seasonal growth can be accurately studied. Many deep-sea protobranchs appear to have no obvious seasonal banding of their thin shells (Zardus, 2002) limiting analysis using traditional methods. Growth estimates suggest 5-12 years may be the normal lifespan for deep-sea protobranchs, although *T. callistiformis* may grow for up to 100 years (Turekian et al., 1975). Inconsistent food supply is likely to be a limiting factor for growth in many species (Gage and Tyler, 1991). The only growth data reported in an Antarctic protobranch are from the shallow water

Yoldia eightsii, which can live in excess of 50 years (Nolan and Clarke, 1993; Peck and Bullough, 1993; Peck et al., 2000).

The protobranch bivalves *Yoldiella sabrina* (Hedley, 1916)*, Yoldiella ecaudata* (Pelseneer, 1903), and *Yoldiella valettei* (Lamy, 1906), are commonly found from the Antarctic shelf to the deep-sea basins with a wide bathymetric range (200 – >5000m, Linse 2004), and known distributions from the east Weddell shelf, Scotia Sea, Antarctic Peninsula, and Amundsen Sea. In addition, *Y. sabrina* has a distribution into the South Atlantic (Linse et al., 2007) and all three species are likely to have circum-Antarctic distributions. Although all studied species are officially described as *Yoldiella*, the taxonomy of this genus is complex and has been described as a taxon 'waiting list' requiring revision (La Perna, 2004). However, for the purpose of this study, all species will be regarded as *Yoldiella*. This study aims to examine and compare the shell morphology, growth, and weight of *Yoldiella ecaudata, Yoldiella sabrina*, and *Yoldiella valettei* among Southern Ocean regions. Growth data will provide novel insights into the potential age and growth rates of deep-sea Southern Ocean protobranchs. Phenotypic plasticity is discussed in relation to the environmental constraints associated with the deep Southern Ocean.

2. Materials and Methods

Sample Collection

Yoldiella valettei, *Y. ecaudata*, and *Y. sabrina* were collected during a number of research expeditions to the Weddell Sea, Scotia Arc, Antarctic Peninsula, and Amundsen Sea between 2002 and 2008 (ANDEEP I&II (Fütterer et al., 2003); LAMPOS 2002 (Arntz and Brey, 2003); BENDEX 2003 (Arntz and Brey, 2005); ANDEEP III 2005 (Fahrbach, 2006); BIOPEARL 2006 (Linse, 2006); BIOPEARL II 2008 (Enderlein and Larter, 2008) (Figure 1). Benthic samples were collected primarily using an epibenthic sledge (EBS) (Brandt &

Barthel, 1995; Brenke, 2005) or Agassiz trawl (AGT), and the deployment methods are described in the relating reports. Samples containing the target protobranch species were taken in depths ranging from 192m to 4900m (but see below). Specimens collected by EBS were fixed immediately after coming on deck in 96% ethanol and later sorted while specimens collected by AGT were sorted alive and then fixed in 96% ethanol or 4% buffered formalin. Differences in fixing/sorting procedure were the consequence of different science priorities. Size frequency histograms of pooled data within each region were put together and Kolmogorov-Smirnov tests used to identify significant differences among regions within each species.

Morphometric Analysis

Shell length, height, and width of each individual were measured under a stereomicroscope to an accuracy of +/- 0.05mm using a micrometre lens. Shell length was defined as the maximum distance across the shell. In total 1050 individuals of *Y. valettei* were measured from the Scotia Sea (189-4679m), Weddell Sea (273-4655m), and Amundsen Sea (477-1473m), 636 *Y. ecaudata* from the Scotia Sea (496-3400m), Weddell Sea (2147m) and Amundsen Sea (477-1495m), and 506 *Y. sabrina* from the Scotia Sea (192-505m), Weddell Sea (600-4900m), Amundsen Sea (500m) and South Atlantic (4552-4730m). In all areas under investigation, highest abundances of bivalves were obtained from shelf depths (<500m). Morphology data were pooled between depths within areas when there was no significant difference in any of the characters studied found with depth. When the morphological data showed significant statistical differences across the depth gradient, only shelf depth samples (<500m) were used for comparisons. Reduced major axis regression of log transformed data was used to identify the relationships between length, height, and width. An analysis of covariance (ANCOVA) on normally distributed log transformed data was used to test for differences between areas, and a back transformation of mean corrected values used to display morphological differences. A Tukey test was performed to identify differences between populations.

Growth Analysis

Growth data for *Y. valettei* from the Weddell and Amundsen Seas at 500m and *Y. ecaudata* from the Scotia and Amundsen Seas at 500m were collected by counting growth lines under a stereomicroscope. Only lines that could be traced around the whole length of the shell were counted (Brey and Hain, 1992; Higgs et al., 2009). To confirm subtle growth lines, 20 individuals of each species from each area, covering the full size range of the sample, were selected for analysis using a Scanning Electron Microscope (SEM). Prior to the scans, each individual was blotted dry and mounted onto SEM stubs before being pulse sputter coated with a 40nm gold coat. Growth line counts from SEM analysis closely matched counts taken during stereomicroscope analysis and the rings resolved were assumed to represent seasonal growth increments (Gage, 1994). No growth data could be obtained for *Y. sabrina* as growth increments could not be observed with confidence. Size-at-age data were analysed using the von Bertalanffy growth function (vBGF);

$$S_t = S_\infty\ 1 - e^{-k(t-t0)}$$

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. This method, commonly used for fish growth analysis, has more recently been used for bivalve growth (Brey and Hain, 1992; Brey, 2001; Heilmayer et al., 2004; Brey et al., 2011; Higgs et al., 2009). As individual growth is non-linear, it is difficult to compare the overall growth between individuals. The derived parameters from vBGF can however, 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). The plotted values of OGP can act as a graphical representation of growth differences between populations.

Shell Weights

Shell weights were calculated by weighing specimens before and after decalcification in a rapid decalcification solution (HCl) for 5 minutes or until effervescence had stopped. Where possible at least 20 individuals were used for each location. *Yoldiella sabrina* from the Amundsen Sea (n=22, depth 500-548m), South Atlantic (n=15, depth 4730-4760m) and Scotia Sea (n=18, depth 211-3404); *Y. ecaudata* from the Amundsen Sea (n=26, depth 482-1477m) and Weddell Sea (n=22, 2097-3000m); and *Y. valettei* from the Amundsen Sea (n=22, depth 476-492m), Scotia Sea (n=22, depth 307m) and Weddell Sea (n=22, depth 296-910m). Depths were pooled within areas where no differences by depth could be found. Reduced major axis regression of log transformed data was used to identify the relationships between length and weight. An ANCOVA on normally distributed log transformed data was used to test for differences between areas and a Tukey test was performed to identify differences between populations where the ANCOVA found a significant result.

3. Results

Size Frequencies

The size frequency histograms show variability in population structure between sites (Figure 2). *Yoldiella ecaudata* size frequency distributions are significantly different between the Amundsen Sea and Scotia Sea (k-s, D=0.3785, p<0.001), and appear similar to *Y. valettei*, dominated by specimens at 1.2-1.3mm shell length (Figures 2a-b). The size frequency distributions of *Y. sabrina* show a smaller sized population in the Amundsen Sea compared to the Scotia Sea (Figures 2c-d) although no significant difference in frequency is found (k-s, D=0.173, p=0.19). Few specimens above 4mm are found in the Amundsen Sea samples and only one specimen above 8.5mm compared to specimens up to 11.2mm in the Scotia Sea. Populations of *Y. valettei* in the Scotia and Amundsen Seas were significantly different (k-s, D=0.283, $p<0.05$), have distributions with a peak at around 1mm length, and few specimens above 3.5mm length but maximum sizes of >5mm at each site (Figure 2e-f). The Weddell Sea population is dominated by 1.0-1.1mm specimens with few specimens above 2.5mm and no specimens greater than 3mm length (Figure 2g). There is a significant difference the Amundsen Sea and Weddell Sea (k-s, D=0.377, $p<0.001$), but not the Scotia Sea and Weddell Sea (k-s, 0.245, p=0.07).

Growth

When shell length is compared at the same interval of seven shell growth lines, *Y. valettei* grew faster (max. 5.2mm) than *Y. ecaudata* (3.3mm). Assuming growth increments represent a constant time increment, both species demonstrate slower growth than the three filter feeding philobryid bivalves *Adacnarca nitens* (Higgs et al. 2009), *Lissarca notorcadensis* (Brey and Hain 1992), and *Lissarca miliaris* (Richardson 1979) from the Ross Sea, Weddell Sea, and Scotia Sea, respectively (Figure 3a). The von Bertalanffy growth function parameters suggest both protobranch species show higher growth rates in the Amundsen Sea (Figure 3a; *Y. valettei* S_{oo}=4.87, k=0.293, n=91, *Y. ecaudata* S_{oo}=3.63, k=0.441, n=52) than in the Weddell Sea (*Y. valettei* S_{oo}=3.76, k=0.357, n=17) and Scotia Sea (*Y. ecaudata* S_{oo}=4.70, k=0.184, n=15). The overall growth performance (OGP) for *Y. valettei* and *Y. ecaudata*, derived from the calculated parameters of the von Bertalanffy growth function, is higher in the Amundsen Sea (OGP = 0.154 and 0.204 respectively) than the Weddell Sea and Scotia Sea (OGP = 0.127 and 0.063 respectively), and higher than the Antarctic philobryid bivalves

(Figure 3b). All OGP values in this study are lower however, than the similar sized North Atlantic, deep-sea protobranch *Ledella pustulosa* (OGP = 0.299; Gage 1994).

Shell Morphology

All three protobranch bivalves showed a significant positive linear relationship between log length and log height (Figures 4a-c) with r^2 values greater than 0.933 and demonstrated positive and negative allometry and isometry (Supplementary Table 1). A preliminary ANCOVA found significant differences with depth within some regions. *Yoldiella valettei* below 1000m in the Amundsen Sea (n=93) were significantly different to those collected at shelf depths above 538m (n=398) for both length/height ($F_{1,\ 488}=36.62$, $p<0.001$), and length/width ($F_{1,\ 486}=37.97$, $p<0.001$), and therefore were not used for the morphological comparisons. The deepest samples of *Y. sabrina* below 3404m (n=25) were also significantly different from specimens from the shelf, at 192-505m (n=156) in the Scotia Sea ($F_{1,\ 178}=7.52$, $p<0.05$) and were not used for length/height comparisons.

An analysis of covariance of length/height found a significant difference between areas for *Y. valettei* ($F_{2,\ 951}=15.66$, $p<0.001$) and a Tukey multiple comparison test found the Amundsen and Scotia Seas to be significantly different to the Weddell Sea ($p<0.05$) (Figure 4f). Significant differences were also found between areas in *Y. ecaudata* ($F_{2,\ 630}=26.40$, $p<0.001$) and *Y. sabrina* ($F_{3,\ 453}=5.22$, $p<0.001$), with the Scotia Sea being distinct from the Amundsen and Weddell Seas in *Y. ecaudata* ($p<0.05$) (Figure 4d), and Weddell Sea being distinct from the Amundsen Sea, Scotia Sea, and South Atlantic in *Y. sabrina* (Figure 4e) ($p<0.05$).

The relationships between log length and log width also showed positive linear relationships (Figure 5a-c). *Y. valettei* length and width showed a significant difference between areas ($F_{2,\ 940}=3.57$, $p<0.05$) and a Tukey multiple comparison test identifying the Amundsen and Weddell Seas as being significantly different (Figure 5f). There was a significant difference between Amundsen Sea, Scotia Sea, and Weddell Sea for *Y. ecaudata* (ANCOVA, $F_{2, 629}=43.21$, $p<0.001$, post hoc Tukey test $p<0.05$) (Figure 5d) and *Y. sabrina* showed a significant difference between the Amundsen Sea, Weddell Sea, and Scotia Sea from the South Atlantic (ANCOVA. $F_{3, 477}=13.10$, $p<0.001$, post hoc Tukey test $p<0.05$) (Figure 5e).

Differences in morphology are visually represented by the corrected mean length/height against corrected mean length/width, derived from residuals of associated ANCOVA, and demonstrate variability among populations of species (Figure 6). *Yoldiella ecaudata* and *Y. sabrina* both have the most round and obese shell shape in the Weddell Sea, which contrasts to *Y. valettei* with the thinnest elongated shell shape in the Weddell Sea. The Scotia Sea has the thinnest elongate shells of all the *Y. ecaudata* sampled. All *Y. sabrina* in the Southern Ocean are more obese in shell shape than the specimens from the South Atlantic although vary in elongation, while *Y. valettei* from the Scotia and Amundsen Seas are the most rounded and obese.

Shell Weight

Yoldiella valettei show a significant positive relationship between log shell length and log shell weight (Figure 7c) (Scotia Sea $r^2=0.969$, Amundsen Sea $r^2=0.916$, Weddell Sea $r^2=0.944$) and have heavier shells in the Amundsen Sea making up 62.1% of total wet weight compared to 52% in the Scotia Sea and 37.1% in the Weddell Sea. Shell weight was isometric in all populations with a RMA slope of 3.19 (Amundsen Sea), 3.02 (Scotia Sea) and 2.74 (Weddell Sea). An analysis of covariance (ANCOVA) shows a significant difference between the regions ($F_{2, 60} = 8.40$, $p=0.001$) with a post hoc multiple comparison test showing no significant difference between the Weddell and Scotia Seas while having a significant difference when compared separately to the Amundsen Sea (Figure 7f, Tukey test, $p<0.05$).

Yoldiella ecaudata in the Amundsen Sea were observed to have thicker and stronger sculptures in their shells compared to specimens from the Weddell and Scotia Seas. There was a significant positive relationship between shell length and log weight (Figure 7.6a) (Weddell Sea r^2=0.981, Amundsen Sea r^2=0.984) with both populations showing positive allometric regressions of 3.30 (Amundsen Sea) and 3.61 (Weddell Sea). There was however, no significant difference between the Weddell Sea and Amundsen Sea (ANCOVA $F_{1, 42}$ = 0.51, p=0.479, Figure 7d). Scotia Sea specimens were not studied because of lower sample 'n' number and unsuitable size distribution of shell lengths for analysis. *Yoldiella sabrina* also show significant positive relationships between shell weight and length (Scotia Sea r^2=0.938, Amundsen Sea r^2=0.950, South Atlantic r^2=0.954) (Figure 7b). All populations showed an isometric relationship between length and weight with RMA slope values of 2.98 (Amundsen Sea), 2.81 (Scotia Sea) and 2.88 (Weddell Sea). There was no significant difference between the three areas (ANCOVA $F_{2, 56}$ = 2.31, p = 0.109, Figure 7e) despite shell weight in the Scotia Sea making up only 45.3% of total weight compared to 56.6% and 62.0% in Amundsen Sea and South Atlantic, respectively.

4. Discussion

Phenotypic plasticity is well reported globally in molluscs and has been described in the Southern Ocean lamellibranch bivalve *Lissarca notorcadensis* (Cope and Linse, 2006) and deposit feeding *Laternula elliptica* (Harper et al., 2012). In the Southern Ocean deep-sea, protobranch bivalve plasticity is important for our understanding of how species have come to radiate over large geographic distances and bathymetric ranges. This can also provide evidence of diverging ecologies, distinct ecotypes, and clues to potential speciation processes. The numbers of bivalve specimens used in this study are a considerable collection for the Southern Ocean, representing ten years of deep-sea sampling effort. Representing a wide geographic range, this study highlights three distinct Southern Ocean regions, which are under contrasting oceanographic and biological influences. These influences are the likely drivers of observed plasticity and ecophysiological responses (through growth and shell production), and represent how the studied species can adapt to contrasting conditions.

Previous studies on small deep-sea protobranchs have discovered modest genetic structuring over large geographic distances at abyssal depths with evidence of restricted gene flow in the more heterogeneous bathyal depths or vast geographic distances in excess of 8000km (Etter et al., 2005; Zardus et al., 2006; Etter et al., 2011). The unique free-swimming lecithotrophic pericalymma larval form of protobranch bivalves is suggested to be capable of dispersing over long distances (Allen and Sanders, 1996; Zardus, 2002). This may be further pronounced in the cold Antarctic where larval development can be considerably slower (Pearse and Bosch, 1986; Bosch and Pearse, 1990), allowing longer times for dispersal. Strong currents associated with the Antarctic circum-Polar current and deeper water counter currents, may also enable significant dispersal potential in free-swimming larvae (for discussion see Thatje, 2012). However, to fill a new niche and thrive in that environment, it is important to adapt under the selection pressures presented at settlement, and in the Antarctic, contrasting differences in selection may represent only subtle differences in the environment.

Growth and shell development are commonly dependent on food availability, temperature, and disturbance events (Appeldoorn, 1982; Brey et al., 2011; Harper et al, 2012), and in the Antarctic deep-sea, the ability to extract calcium from seawater at low temperatures (Harper, 2000). Food availability in the deep Southern Ocean can be highly variable (Gutt et al., 1998) and although data from the sea floor are very patchy, there is strong evidence for high levels of seasonal supply to the benthos (Smith et al., 2008). The deep Weddell Sea can have a moderate to high seasonal flux of phytodetritus depending on distance from ice shelf edge and seasonal ice melt (Gutt et al., 1998; Diaz, 2004). Open water polynyas are possible sources of local deep-water food supply for deposit feeding organisms, especially from the Maudheim polynya (71°01’S, 10° 88°W) in the east Weddell Sea and the Pine Island Bay polynya (73° 16’S, 104° 25’W) in the Amundsen Sea (Arrigo and Dijken, 2003; Yager et al., 2012). Availability of such primary production hot-spots in the form of coastal and open ocean polynyas was reduced during glacial periods, likely affecting the ecology of populations over time (Thatje et al., 2008). Today, the Scotia Sea is also variable with regards to phytoplankton on both a spatial and temporal scale and is largely dependent on the mixing of water masses (Holm-Hansen et al., 2004).

Protobranch bivalves are specially adapted to living in food-poor conditions and despite evidence of food being limiting to growth in deep water (Gage and Tyler, 1991), the differing fluxes of phytodetritus from the surface to the deep sea are likely to be insufficiently contrasting between regions to affect differences in growth and shell development (Allen, 2008). Additionally, cold Southern Ocean deep-sea conditions can result in the persistence of organic matter in sediments and act as a year round food supply to deposit feeding fauna, dampening the effects of strong seasonal pulses of food (Mincks et al., 2005; Glover et al., 2008). When compared to the similarly sized deep-sea protobranch *Ledella pustulosa* (Gage, 1994), the Antarctic species have lower overall growth performances, although this is not expected to be related to food availability. The similarity of growth and OGP to other Southern Ocean bivalves strengthens the assumption of seasonality of growth in the Southern Ocean protobranchs. Assuming food resource to be indifferent between study areas (although perhaps even greater in the Antarctic compared to elsewhere), temperature is expected to have the strongest influence on growth and morphology in the deep-Southern Ocean protobranchs.

Oceanographic influences on bottom temperature create different conditions between areas and this can affect the benthic fauna (Clarke et al., 2009). The Southern Ocean is influenced by unique oceanographic conditions that are likely to play key roles in species distribution by larval dispersal, and creating heterogeneity of temperature. As well as feeding the world’s oceans by circulating cold bottom water, the Weddell Sea produces some of the coldest deep waters in the world. Weddell Sea Bottom Water is highly influential in the Weddell and Scotia Seas as a stable, dense and extreme cold water mass as low as -1.88°C (Carmack and Foster, 1975; Fahrbach et al., 1995; Smith et al., 1999). Flowing west into the Scotia Sea, bottom water acts as an important counter current to the powerful Antarctic Circumpolar Current. The lack of differentiation in shell weights between the Weddell Sea and Scotia Sea in *Y. valettei* and *Y. ecaudata* may be a consequence of the similar bottom water temperature effect on calcification and shell formation in these regions. West of the Antarctic Peninsula to the Amundsen Sea, warmer circumpolar deep water (>1°C) can flood the deep (>500m) continental shelf accelerating the melting of ice along the West Antarctic Ice Shelf (Jacobs et al., 1996; Lowe and Anderson, 2002; Thorma et al., 2008). These turbulent and complex oceanographic processes increase heterogeneity in a system that may otherwise be considered highly stenothermal and stable (Barnes et al., 2006; Clarke et al., 2009). Small changes in temperature are known to cause drastic changes in metabolic rates of Antarctic benthic invertebrates in shallow water (Peck et al., 2002; Peck et al., 2004) but to date there is no published work on metabolic rates of deep-sea Antarctic invertebrates.

The differences in shell weights between the Scotia Sea and Weddell Sea with the Amundsen Sea are also likely to result from spatial heterogeneity in temperature, with the warmer Amundsen Sea temperatures increasing growth and shell weights. Low temperatures increase the cost of calcification and reduce metabolic rates (Peck et al., 2004), and increasing temperatures have been shown to directly increase growth rates of Southern Ocean bivalves (Nolan and Clarke, 1993; Brey et al., 2011). The effect of temperature can also be observed with a decrease in shell thickness with latitude in buccinid gastropods and echinoids while increasing shell thickness in the bivalve genus *Laternula* (Watson et al., 2012), where mechanical damage and associated shell repair increases calcification (Harper et al., 2012) at the cost of increased metabolic activity (Phillip et al., 2011). Heavier shells and faster growth observed in *Y. valettei* and *Y. ecaudata* in the Amundsen Sea may therefore be a consequence of temperature effects on metabolic activity, lower energetic cost of calcification or an adaptation to disturbance events afforded by energy reallocation. Increased shell weights in the Amundsen Sea may also offer extra protection against invasive predators associated with regional warming or ice scouring (Aronson et al., 2007, 2011; Harper et al., 2012). No significant differences with depth were found within or between regions, despite comparing shallow shelf depths (from 211m) with abyssal depths in *Y. sabrina* (South Atlantic >4500m) and *Y. ecaudata* (Weddell Sea 2097-3000m).

Significant differences in morphology with depth (*Y. valettei* and *Y. sabrina*) and between regions suggest adaptations to contrasting conditions, which are key to the wide dispersal of a circum-Antarctic species and highlights the success of the protobranch bivalves in deep-sea ecosystems. Increased growth rates and overall growth performance for *Y. valettei* and *Y. ecaudata* in the Amundsen Sea over the Scotia and Weddell Seas are also evidence of environmental conditions being more favourable for growth (Heilmayer et al., 2004; Brey et al., 2011). The morphological variations found in this study demonstrate distinct ecotypes within species and although the degree of connectivity between these deep populations is still unknown, showcase the protobranch bivalves as a group for future molecular and ecological studies in the Antarctic, with special regard to likely cryptic speciation processes. Trade-offs associated with increased growth and calcification rates under different temperature regimes are also important in our understanding of the evolutionary history of the Antarctic benthos and to predict the response to regional warming.

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Figure Legends

Figure 1. Map of the study areas showing presence/absence of *Yoldiella valettei, Y. ecaudata*, and *Y. sabrina* at the Antarctic stations of the research cruises ANDEEP I&II, LAMPOS, BENDEX, ANDEEP III, BIOPEARL I&II between 2002 and 2008.

Figure 2. Size (shell length) frequency histograms for *Yoldiella ecaudata, Y. sabrina*, and *Y. valettei* in the Southern Ocean. a-b) *Yoldiella valettei* from a) Scotia Sea; b) Amundsen Sea; c-d) *Yoldiella sabrina* from c) Scotia Sea; d) Amundsen Sea; e-g) *Yoldiella valettei* from e) Scotia Sea; f) Amundsen Sea; g) Weddell Sea.

Figure 3. Growth and overall growth performance in Southern Ocean protobranchs compared to filter feeding Antarctic lamellibranch bivalves *Lissarca notorcadensis* (Brey and Hain, 1992), *Lissarca miliaris* (Richardson, 1979), and *Adacnarca nitens* (Higgs et al., 2009). a) von Bertalanffy growth curves for *Yoldiella valettei* from the Weddell Sea (S_{oo}=3.76, k=0.357, n=17), and Amundsen Sea *Y. valettei* (S_{oo}=4.87, k=0.293, n=91) *Y. ecaudata* from the Scotia Sea (S_{oo}=4.70, k=0.184, n=15), and Amundsen Sea (S_{oo}=3.63, k=0.441, n=52); b)

Overall growth performance of *Yoldiella valettei* from the Weddell Sea and Amundsen Sea and *Yoldiella ecaudata* from the Scotia Sea and Amundsen Sea compared to Antarctic lamellibranch bivalves and North Atlantic protobranch *Ledella ultima* (Gage, 1994).

Figure 4. a-c) Reduced major axis regression of length and height in *Yoldiella ecaudata* and *Y. valettei* in the Amundsen Sea, Scotia Sea and Weddell Sea, and *Y. sabrina* in the Amundsen Sea, Scotia Sea, Weddell Sea, and South Atlantic; d-f) Adjusted means from ANCOVA of length/height in d) *Yoldiella ecaudata* from the Amundsen Sea, Scotia Sea, and Weddell Sea; e) *Yoldiella sabrina* from the Amundsen Sea, Scotia Sea, Weddell Sea, and South Atlantic; f) *Yoldiella valettei* from the Amundsen Sea, Scotia Sea, and Weddell Sea. Circles represent significantly different groups (Tukey test, $p<0.05$).

Figure 5. a-c) Reduced major axis regression of length and width in *Yoldiella valettei* and *Y. ecaudata* in the Amundsen Sea, Scotia Sea, and Weddell Sea, and *Y. sabrina* from the Amundsen Sea, Scotia Sea, Weddell Sea, and South Atlantic; d-f) Adjusted means from ANCOVA of length and width in d) *Yoldiella ecaudata* in the Amundsen Sea, Scotia Sea, and Weddell Sea; e) *Yoldiella sabrina* in the Amundsen Sea, Scotia Sea, Weddell Sea, and South Atlantic; f) *Yoldiella valettei* from the Amundsen Sea, Scotia Sea, and Weddell Sea. Circles represent significantly different groups (Tukey test, $p<0.05$).

Figure 6. Relative morphology of *Yoldiella ecaudata, Yoldiella sabrina*, and *Yoldiella valettei*. Corrected mean length/height v corrected mean length/width among populations identifying different shell shapes.

Figure 7. Reduced major axis regression of shell length and log shell weight with back transformed mean shell weights. a, d) *Yoldiella ecaudata* from the Amundsen Sea (n=26) and Scotia Sea (n=35); b, e) *Yoldiella sabrina* from the Amundsen Sea (n=16), Scotia Sea (22),

and South Atlantic (n=15); c, f) *Yoldiella valettei* from the Amundsen Sea (n=22), Scotia Sea (n=22), and Weddell Sea (n=22). Circles represent significant differences ($p<0.05$).

Highlights

- We examine plasticity in protobranch bivalves from the deep Southern Ocean.
- We find differences in shell morphology among contrasting deep-sea environments.
- Contrasting growth and shell weights between Scotia/Weddell and Amundsen Seas.
- Protobranchs demonstrate differential adaptation between stenothermal environments.
- Subtle environmental differences between regions may lead to ecological divergences.

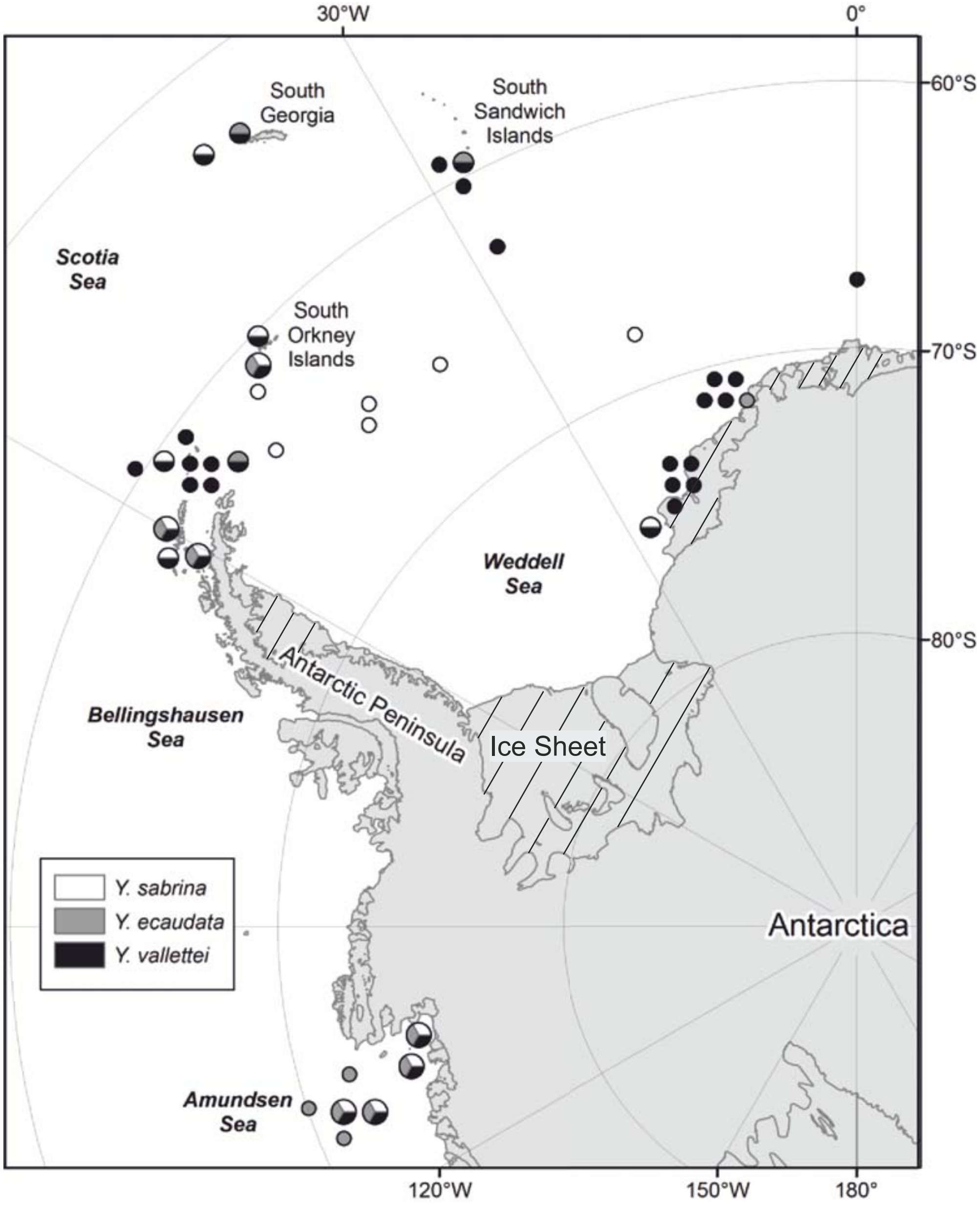

30°W
0°
60°S
70°S
80°S
120°W
150°W
180°
South Georgia
South Sandwich Islands
Scotia Sea
South Orkney Islands
Weddell Sea
Bellingshausen Sea
Antarctic Peninsula
Ice Sheet
Antarctica
Amundsen Sea
Y. sabrina
Y. ecaudata
Y. vallettei

Figure 2.pdf

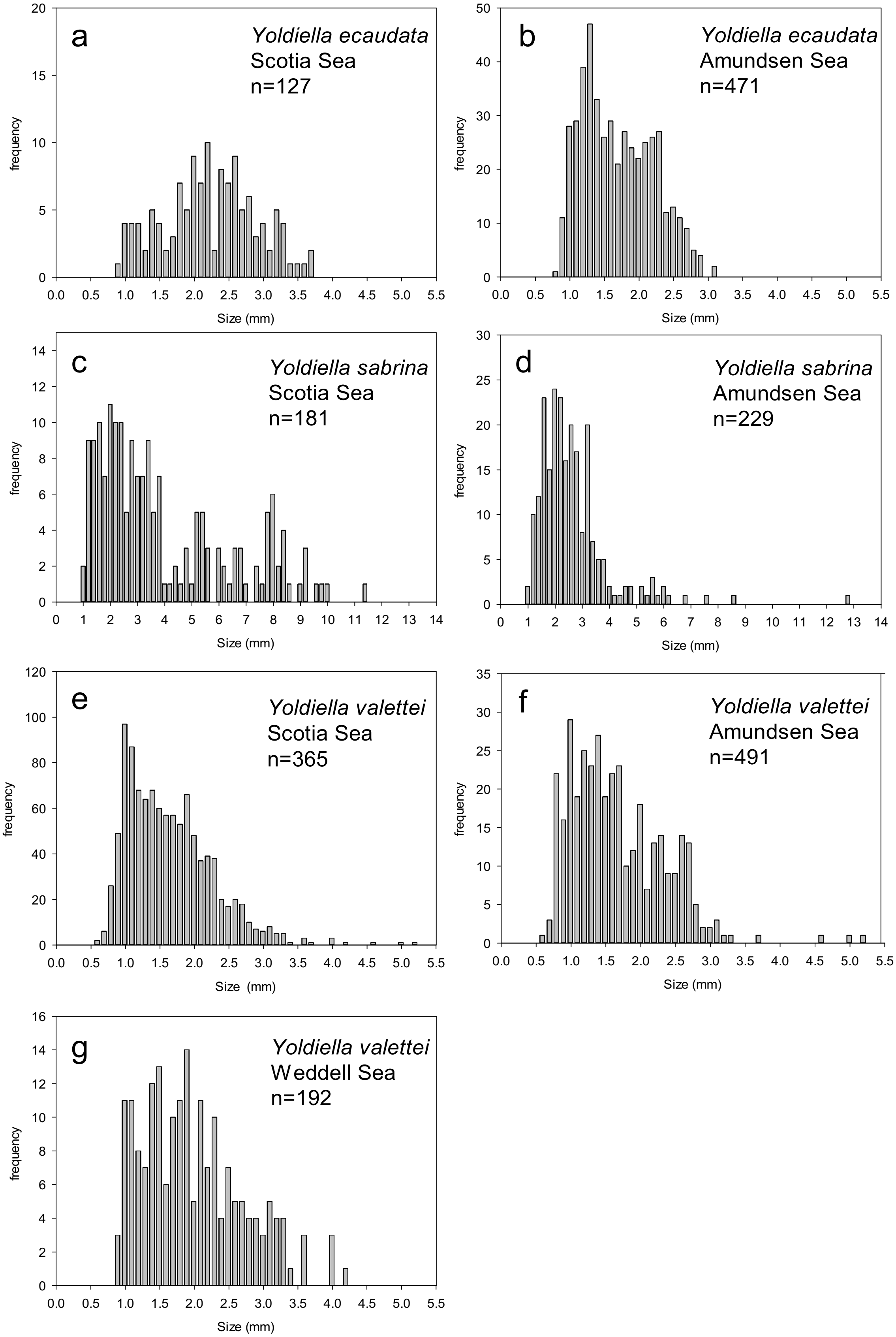
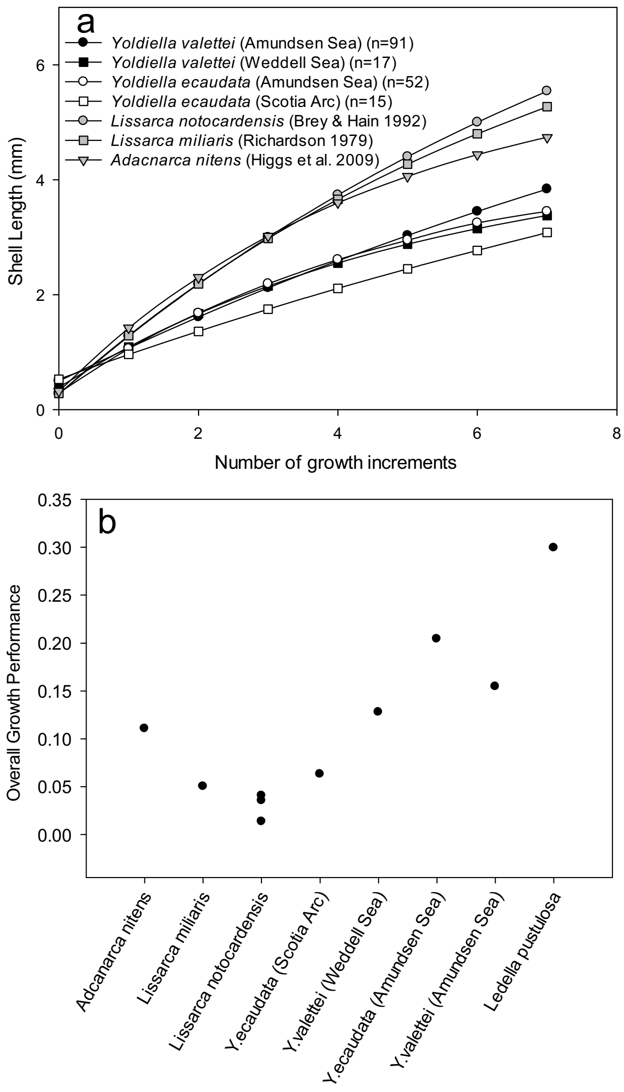
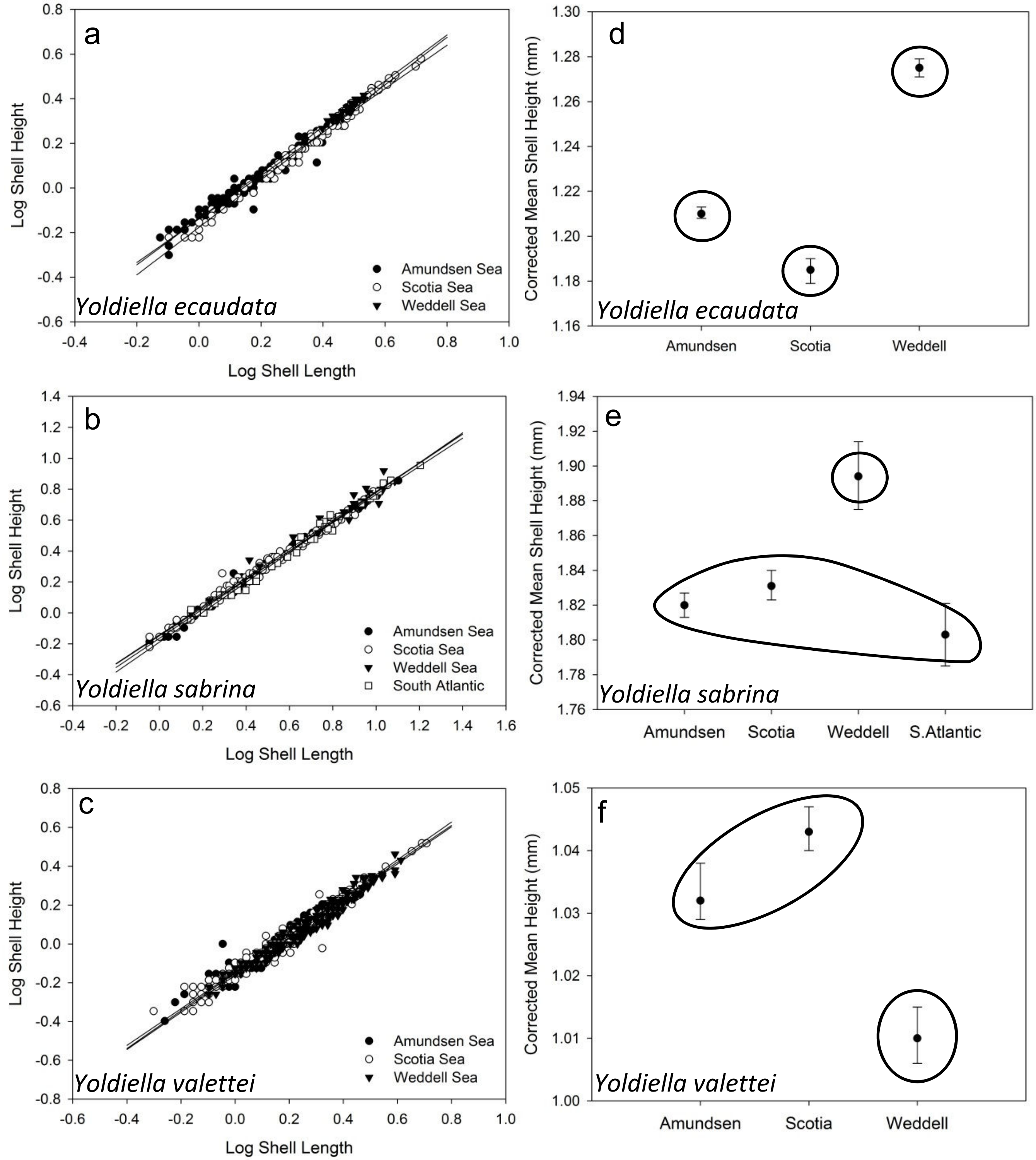

a
Yoldiella ecaudata
Scotia Sea
n=127
b
Yoldiella ecaudata
Amundsen Sea
n=471
c
Yoldiella sabrina
Scotia Sea
n=181
d
Yoldiella sabrina
Amundsen Sea
n=229
e
Yoldiella valettei
Scotia Sea
n=365
f
Yoldiella valettei
Amundsen Sea
n=491
g
Yoldiella valettei
Weddell Sea
n=192
frequency
Size (mm)
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0 4.5 5.0 5.5
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
0 5 10 15 20
0 10 20 30 40 50
0 2 4 6 8 10 12 14
0 5 10 15 20 25 30
0 20 40 60 80 100 120
0 5 10 15 20 25 30 35
0 2 4 6 8 10 12 14 16

Figure 3.pdf


a
Yoldiella valettei (Amundsen Sea) (n=91)
Yoldiella valettei (Weddell Sea) (n=17)
Yoldiella ecaudata (Amundsen Sea) (n=52)
Yoldiella ecaudata (Scotia Arc) (n=15)
Lissarca notocardensis (Brey & Hain 1992)
Lissarca miliaris (Richardson 1979)
Adacnarca nitens (Higgs et al. 2009)
Shell Length (mm)
0
2
4
6
0
2
4
6
8
Number of growth increments
b
Overall Growth Performance
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Adcanarca nitens
Lissarca miliaris
Lissarca notocardensis
Y.ecaudata (Scotia Arc)
Y.valettei (Weddell Sea)
Y.ecaudata (Amundsen Sea)
Y.valettei (Amundsen Sea)
Ledella pustulosa


a
Log Shell Height
Log Shell Length
Amundsen Sea
Scotia Sea
Weddell Sea
Yoldiella ecaudata
d
Corrected Mean Shell Height (mm)
Amundsen
Scotia
Weddell
Yoldiella ecaudata
b
Log Shell Height
Log Shell Length
Amundsen Sea
Scotia Sea
Weddell Sea
South Atlantic
Yoldiella sabrina
e
Corrected Mean Shell Height (mm)
Amundsen
Scotia
Weddell
S.Atlantic
Yoldiella sabrina
c
Log Shell Height
Log Shell Length
Amundsen Sea
Scotia Sea
Weddell Sea
Yoldiella valettei
f
Corrected Mean Height (mm)
Amundsen
Scotia
Weddell
Yoldiella valettei

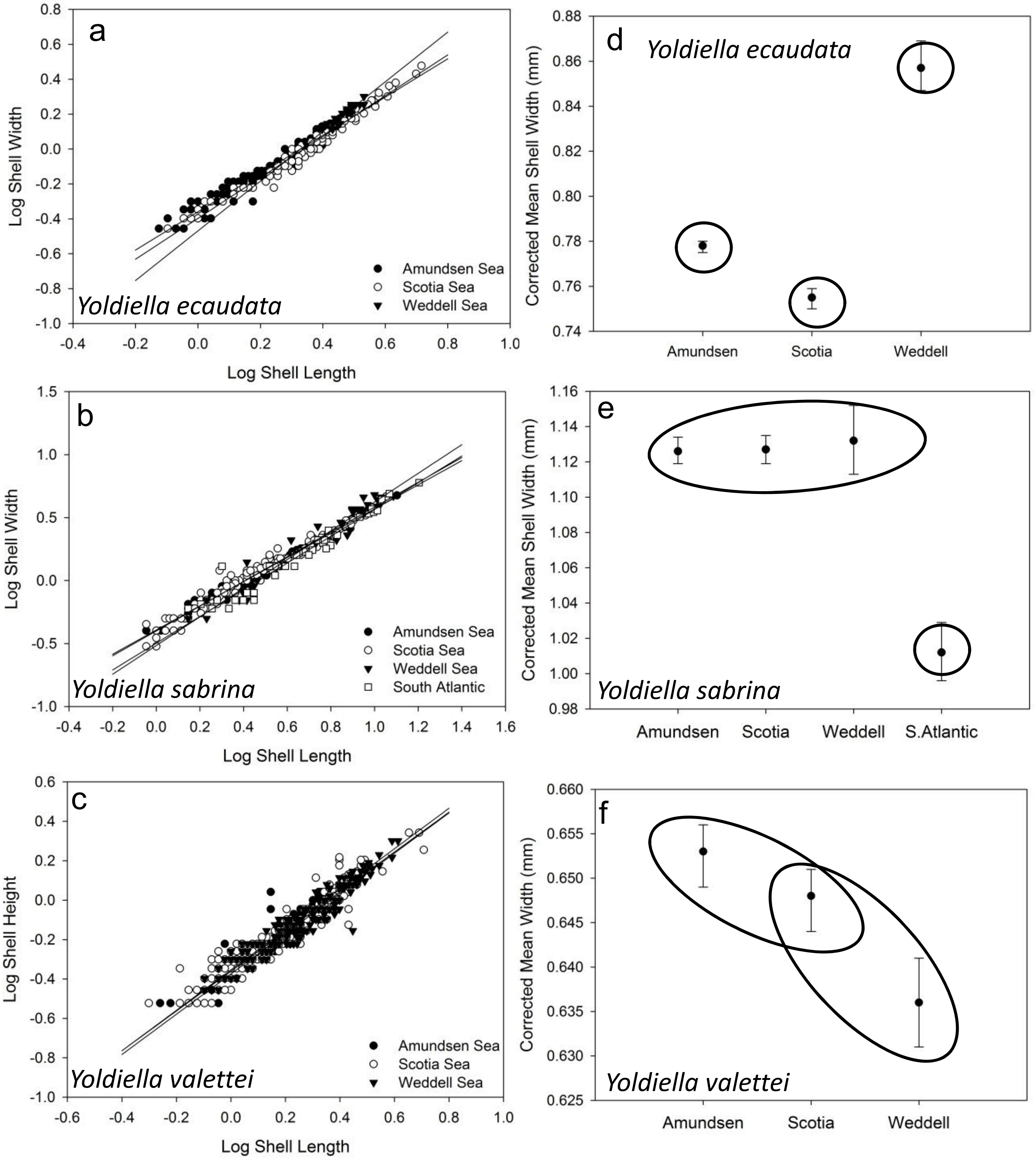

a
Yoldiella ecaudata
Log Shell Width
Log Shell Length
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
● Amundsen Sea
○ Scotia Sea
▼ Weddell Sea
d
Yoldiella ecaudata
Corrected Mean Shell Width (mm)
0.88
0.86
0.84
0.82
0.80
0.78
0.76
0.74
Amundsen
Scotia
Weddell
b
Yoldiella sabrina
Log Shell Width
Log Shell Length
1.5
1.0
0.5
0.0
-0.5
-1.0
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
● Amundsen Sea
○ Scotia Sea
▼ Weddell Sea
□ South Atlantic
e
Yoldiella sabrina
Corrected Mean Shell Width (mm)
1.16
1.14
1.12
1.10
1.08
1.06
1.04
1.02
1.00
0.98
Amundsen
Scotia
Weddell
S.Atlantic
c
Yoldiella valettei
Log Shell Height
Log Shell Length
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
● Amundsen Sea
○ Scotia Sea
▼ Weddell Sea
f
Yoldiella valettei
Corrected Mean Width (mm)
0.660
0.655
0.650
0.645
0.640
0.635
0.630
0.625
Amundsen
Scotia
Weddell

Figure 6.pdf

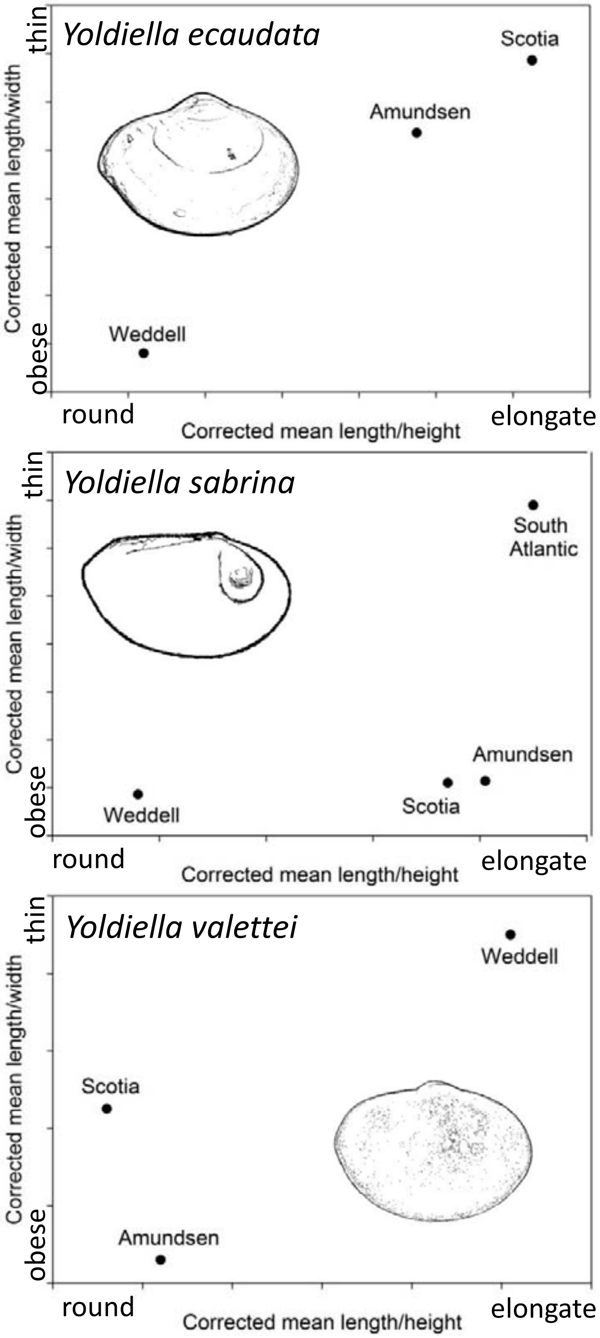
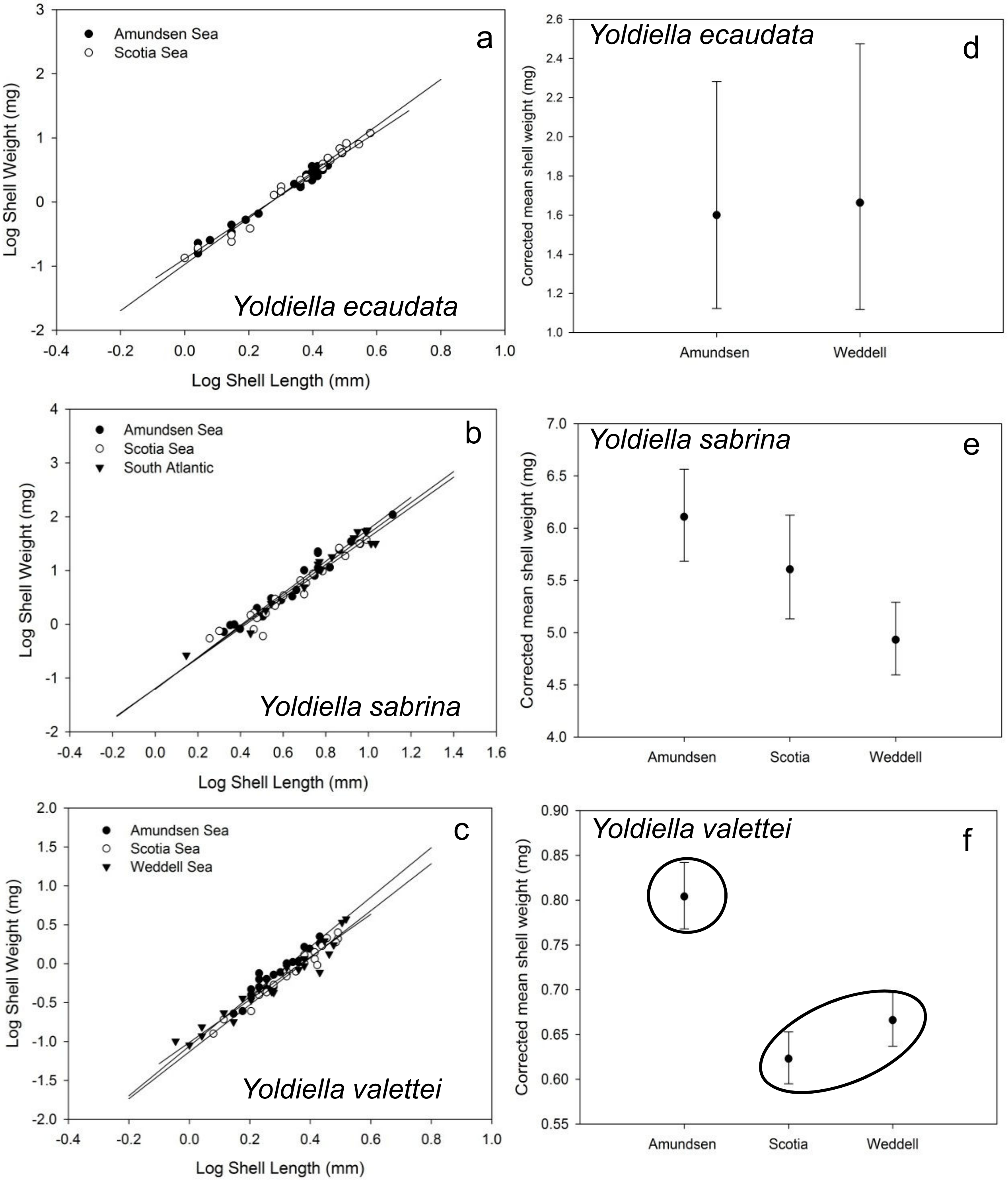

Yoldiella ecaudata
Scotia
Amundsen
Weddell
thin
obese
Corrected mean length/width
round
elongate
Corrected mean length/height
Yoldiella sabrina
South Atlantic
Amundsen
Scotia
Weddell
thin
obese
Corected mean length/width
round
elongate
Corrected mean length/height
Yoldiella valettei
Weddell
Scotia
Amundsen
thin
obese
Corrected mean length/width
round
elongate
Corrected mean length/height

Figure 7.pdf


a
Amundsen Sea
Scotia Sea
Log Shell Weight (mg)
Log Shell Length (mm)
Yoldiella ecaudata
3
2
1
0
-1
-2
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
d
Yoldiella ecaudata
Corrected mean shell weight (mg)
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
Amundsen
Weddell
b
Amundsen Sea
Scotia Sea
South Atlantic
Log Shell Weight (mg)
Log Shell Length (mm)
Yoldiella sabrina
4
3
2
1
0
-1
-2
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
e
Yoldiella sabrina
Corrected mean shell weight (mg)
7.0
6.5
6.0
5.5
5.0
4.5
4.0
Amundsen
Scotia
Weddell
c
Amundsen Sea
Scotia Sea
Weddell Sea
Log Shell Weight (mg)
Log Shell Length (mm)
Yoldiella valettei
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
f
Yoldiella valettei
Corrected mean shell weight (mg)
0.90
0.85
0.80
0.75
0.70
0.65
0.60
0.55
Amundsen
Scotia
Weddell