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# The metabolic cost of developing under hydrostatic pressure: experimental evidence supports macroecological pattern

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ABSTRACT: Hydrostatic pressure is the most constant physical parameter on Earth. It increases linearly with water depth and is stable over evolutionary timescales. Despite this, bathymetric shifts in physiological adaptations that are observed in marine invertebrates (e.g. in metabolic rate and egg size) are currently interpreted to result predominantly from decreases in temperature. However, analyses of invertebrate egg size data presented here indicate an increase in egg volume with depth in the absence of a thermal gradient. This suggests hydrostatic pressure may also be important in determining resource allocation to offspring. To test the hypothesis that an increase in energy expenditure during development occurs with increasing hydrostatic pressure, we examined the effects of sustained exposure to pressure (1, 100, 200 and 300 atm) on development of a shallow-water marine gastropod, *Buccinum undatum*. Embryos developed successfully at 1, 100 and 200 atm, but the rate of development slowed with increasing pressure (by 3 d at 100 atm and 6 d at 200 atm). No development was observed at 300 atm. In embryos reared at 200 atm, veliger dry weight and carbon and nitrogen biomass were significantly reduced. These results indicate that high pressure significantly increases the metabolic cost associated with development, demonstrating a negative and ultimately critical effect. We hypothesise that pressure imposes increased metabolic cost on all physiological processes. This offers an additional explanation for physiological adaptations observed with increasing depth, indicating that hydrostatic pressure is an important and previously underestimated factor contributing to metabolic theory for most of our biosphere. Hydrostatic pressure may represent a critical physiological limit for the maximum depth distribution of shallow-water fauna.

KEY WORDS: Bioenergetics · *Buccinum undatum* · Development · Hydrostatic pressure · Metabolism · Egg size



## INTRODUCTION

Metabolism is crucial in determining the energy requirements necessary to sustain life. Consequently, physiological adaptations that affect metabolic rates are widely regarded as among the most important of evolutionary adjustments. Current hypotheses suggest such adaptations are governed primarily by temperature, and, to date, little attention has been given to the role of hydrostatic pressure. Hydrostatic pressure is, however, the only variable in the ocean to change linearly with depth. Over evolutionary periods of time it has remained the most stable environmental parameter in the aquatic environ-

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ment, which encompasses most of our biosphere (Schubel & Butman 2000).

In marine invertebrates, a reduction in metabolic rate with increasing water depth has been observed (Childress et al. 1990, Childress 1995, Seibel et al. 1997, Company & Sardà 1998, Seibel & Drazen 2007, Ikeda 2013), indicating a decrease in demand for energy in deep-water environments. Such shifts are generally thought to occur as a function of temperature (Childress et al. 1990, Childress 1995) or locomotory capacity (Childress et al. 1990, Company & Sardà 1998, Seibel & Drazen 2007) and only recently has water depth been considered important (see Ikeda 2013). Egg size, a proxy for energy investment per embryo, has been shown to increase with depth (King & Butler 1985, Gage & Tyler 1991, Van Dover & Williams 1991, Mauchline 1995, Morley et al. 2006, Scheltema & Williams 2009). Egg size is, in most cases, related to lipid content (Anger et al. 2002); larger eggs have greater lipid reserves, allowing offspring more energy for development (Anger 2001). These reserves facilitate longer larval duration and help sustain development through non-feeding periods (King & Butler 1985). A depth-associated increase in egg size has usually been attributed to the low temperature and intermittent food availability typical of the deep sea (King & Butler 1985, Gage & Tyler 1991, Van Dover & Williams 1991, Morley et al. 2006); increased lipid reserves help mediate these challenges.

In the oceans, food availability is greatest in surface waters, and at depths below 1000 m temperatures are relatively homogenous throughout (Gage & Tyler 1991). If egg size depended on temperature and productivity alone, then it would be expected to remain constant below approximately 1000 m; however, studies suggest that the depth-related increase in the allocation of lipids to offspring persists from shallow water to the abyss (Thatje & Mestre 2010). For example, egg size in lithodid crabs escalates with depth despite an overall isothermal water column at high southern latitudes (Morley et al. 2006), and egg size in other decapod crabs and neogastropod whelks has been found to continuously increase from surface waters to abyssal depths (see references in Table 1). Predictions considering only the effects of temperature and food availability would also anticipate species from hydrothermal vent environments to produce smaller eggs than related non-vent species, since vents are characteristically warm, productive habitats when compared to most of the deep sea (Gage & Tyler 1991). However, the limited data available indicate that closely related species produce eggs of a similar size in both deep-sea vent and non-vent habitats (Ramirez-Llodra et al. 2002). Consequently, these observations imply that factors other than temperature and food availability contribute to bathymetric patterns in egg size and consequently energy allocation.

Here, we advocate that the physiological impacts of pressure are of significant ecological and evolutionary consequence for marine invertebrates (Brown & Thatje 2014). Understanding the effects of pressure may therefore increase our knowledge of the drivers of both modern and historical adaptation. Acute exposure of invertebrates to high pressure (≤50 h) has revealed a slow-down in developmental rate (e.g. Mestre et al. 2009), but the effects of pressure on the metabolic cost of development have never been examined. In the present study, we carry out an analysis exploring trends in egg size with depth for 2 families of gastropod and 2 families of crustacean with food-independent (lecithotrophic) larval development. We then use a shallow-water neogastropod, the common whelk *Buccinum undatum*, as a model organism to, for the first time, investigate the effects of sustained pressure throughout early, lecithotrophic development. We test the hypothesis that energy expenditure during development increases with increasing pressure, even when variables like food availability and temperature are held constant.

## MATERIALS AND METHODS

### Analysis of trends in egg size with depth

We conducted an analysis of invertebrate egg size literature in order to examine the relationship between egg size and depth in the marine environment. Literature searches were carried out using the database ISI Web of Science (www.apps.webofknowledge.com) and the search engine Google Scholar (www.scholar.google.com). Comparisons were restricted to marine invertebrates with lecithotrophic larval development; for these species the amount of energy available for larval development can be inferred directly from egg size, as no additional food source is used during development. The searches were conducted using the keywords 'invertebrate', 'marine', 'lecithotroph*', 'egg' 'oocyte' 'size', 'diameter', 'volume' and 'depth'. In Web of Science, topic searches were carried out; this covers the complete Web of Science database, including titles, abstracts, author key words and Web of Science 'KeyWords

Plus'. We completed our topic searches using 3 fields; the first field contained 'size OR diameter OR volume', the second contained 'egg OR oocyte', and the third contained 'invertebrate AND marine AND lecithotroph* AND depth'. In Google Scholar we conducted a basic search using all of the above keywords. Google Scholar searches cover entire articles including title, abstract, keywords, document text and references. The literature search initially focused on all marine invertebrates. Data were only included if egg size (diameter or volume) and sample depth were expressed in the article. To provide statistical robustness only families with data for ≥10 species were analysed. All taxa were classified according to the World Register of Marine Species (www.marinespecies.org).

Sufficient data were only available for the gastropod families Buccinidae and Muricidae and the crustacean families Munidopsidae and Chirostylidae. Egg size was recorded as volume ($mm^3$); where only egg diameter (spherical shaped eggs) or egg length and width (ellipsoid shaped eggs) were stated in the literature, egg volume was determined using standard mathematical equations for sphere and ellipsoid volume. In crustaceans, resources are typically allocated to each egg upon production, and the volume of one egg is representative of the amount of energy available to one offspring. In gastropods, in contrast, resources are typically provided as nurse eggs available for consumption by developing embryos. For gastropods, egg volume was therefore determined from the number of nurse eggs consumed by each embryo and the volume of each nurse egg. Here, the total volume of nurse egg consumed by an individual embryo was estimated by multiplying the number of nurse eggs consumed and the volume of one nurse egg. These values were determined for each species from the referenced literature. To examine the relationship between egg volume and depth for each phylum investigated, non-linear regression analyses were performed using a power function ($a \cdot x^b$). Prior to analysis, homoscedasticity was confirmed for all data (Levene's test, $p > 0.05$).

### Experimental analysis of the effects of sustained pressure on development

Existing high-pressure technology does not permit controlled feeding during sustained experimental exposures (see Thatje & Robinson 2011). This restricts potential investigations of development under pressure to species with a lecithotrophic developmental mode, such as *Buccinum undatum*. Studying hyperbaric effects during lecithotrophic development allows relative metabolic expenditure to be assessed following a comparative approach without quantifying energy inputs.

*B. undatum* is commonly found in soft-bottomed areas of the north Atlantic and Arctic oceans from the shallow subtidal down to approximately 250 m water depth (Rosenberg 2009). Each female lays large egg masses comprising of approximately 140 egg capsules (for images see Smith & Thatje 2013a,b). Within each egg capsule multiple veligers develop. *B. undatum* egg masses were collected from depths of approximately 10 m in the Solent, UK (50° 47' N, 001° 15' W) during January and February in 2011 and 2012. Collection took place using a beam trawl deployed from on board the University of Southampton's research vessels RV 'Bill Conway' and RV 'Callista'. Egg masses were taken to the National Oceanography Centre, Southampton. Three capsules from each egg mass were dissected and their contents were examined using a microscope to establish developmental stage (according to Smith & Thatje 2013a). Only egg masses without discernible embryonic development (i.e. at the egg stage) were used in the investigation.

Each egg mass was carefully dissected into halves down the centre, from the point at which it was attached to hard substrate. Since egg masses are laid from the point of attachment upward, this ensured that both halves contained egg capsules of equal age. Each egg mass half was then exposed to either the control or the experimental treatment.

Experimental treatments were carried out using the IPOCAMP pressurised incubator, previously described by Shillito et al. (2001). In brief, the IPOCAMP is a flow-through pressure system, allowing continuous water exchange to the incubator whilst maintaining both experimental pressure and temperature. The IPOCAMP was run at 10°C for 24 h prior to the start of incubations to ensure the temperature was stable. Following this, each experimental egg mass half was loosely attached by cable tie to the inside of one leg of a tripod frame placed inside the IPOCAMP. The cable tie was attached to the egg mass by insertion through gaps between capsules. Once attached to the frame, each egg mass sat below a viewing port, allowing it to be monitored using an endoscope camera. In total, 3 egg masses were used for each treatment. The IPOCAMP was then run at atmospheric pressure (1 atm) or pressurised to 100, 200 or 300 atm. In high-pressure treatments, pressure was increased stepwise by 10 atm every 10 min

until experimental pressure was achieved. Each week, 10 l of pre-incubated, 1 µm filtered seawater was added to the system, following the removal of an equal amount; the whole system held a total of 60 l.

Control treatments were maintained independently at 10°C (1.8 l incubation tank containing aerated, 1 µm filtered seawater at 10°C; 100% water change 3 times per week). Each control egg mass half was examined non-invasively each day in order to establish development. In *B. undatum* the egg capsule walls are semi-transparent, meaning the capsule content can be observed without dissection (Smith & Thatje 2013a). *B. undatum* egg capsules contain both developing embryos and nurse eggs that are consumed by the embryos during development. Control egg capsules were maintained until all nurse eggs had been consumed and only developing embryos remained. Once all of the nurse eggs had been consumed in the capsules in all 3 control egg masses the treatment was ended. The 1 atm experimental treatment was carried out to establish that incubation in the IPOCAMP had no direct effect on development. Since the exact age of each egg mass was unknown, and based only on developmental stage, experimental duration varied, from 20 d at 1 atm, to 18 d at 100 and 200 atm, to 14 d at 300 atm.

To end the experimental treatment, pressure was released from the IPOCAMP at the same rate at which it had been pressurised (10 atm pressure decrease every 10 min). Following depressurisation, the experimental egg masses were removed from the IPOCAMP and the control and experimental halves of each egg mass were compared. Ten randomly selected capsules were dissected from each half and their contents examined; this provided a total of 30 capsules per treatment. For each capsule, the number of embryos (normal and abnormal) was counted, and their developmental stage was assessed. From this, the proportion of embryos at each stage was calculated. The developmental age of each egg mass was then estimated relative to known developmental rates for *B. undatum* at 1 atm, 10°C (see Smith et al. 2013).

Dry weight (DW) and bioenergetics content of embryos was established for both control and experimental samples using embryos at the veliger stage of development. From the 10 dissected capsules from each condition, 20 veligers (2 from each capsule) were individually sampled at random to determine DW, giving a total of 60 veligers from each control and experimental treatment. Each veliger was placed individually in a pre-weighed (6 mm × 4 mm) tin capsule and stored at –80°C. These samples were later freeze-dried over 24 h and DW was established (accurate to 1 µg).

To examine embryo bioenergetics, elemental analysis was carried out on 10 veligers from each control and experimental treatment. These veligers were randomly selected from the 60 veligers from each treatment that were used to assess DW. Samples were selected randomly from the freeze-dried individuals. Analysis was carried out using a Fison Elemental Analyser (1108, Carlo Erba), calibrated using chitin as a standard (% C = 44.71;% N = 6.79). Percentages of C and N were determined during analysis. The C and N biomass for each individual was then calculated from the C:N ratio and the DW.

### Data analysis for the effects of sustained pressure on development

Between egg masses, age varied to some degree and capsule size was not standardised due to availability of material; the latter factor impacts number of offspring and may affect offspring size (Smith & Thatje 2013b). The content of individual egg capsules from one female are, however, typically equal in their number of nurse eggs per embryo and their bioenergetic content (Smith & Thatje 2013a). For each experimental treatment, egg masses were therefore only directly comparable to the related control (1 atm) treatment. Data for each pressure were therefore analysed independently.

A paired *t*-test (two-tailed) was used to compare number of embryos per capsule and veliger DW, C biomass, N biomass, and C:N ratio, of control and experimental treatments. For number of embryos per capsule, n = 30 for each *t*-test. For veliger DW, n = 60 for each *t*-test. For veliger C biomass, N biomass, and C:N ratio, n = 10 for each *t*-test. Prior to analysis homoscedasticity was confirmed for all data (Levene's test, $p > 0.05$). No statistical analysis was carried out on data for developmental age.

## RESULTS

### Analysis of trends in egg size with depth

In total, we obtained data from 43 articles that could be included in the analysis. Data were obtained for 36 species of Neogastropoda from 2 families (Buccinidae and Muricidae) and 79 species of Decapoda from 2 families (Munidopsidae and Chirostylidae) (Table 1). Data were identified across a

depth range of 1 to 2200 m for molluscs and 1 to 4670 m for crustaceans. Regression analysis indicated a significant relationship between egg volume and depth for both neogastropods ($r^2 = 0.494$; $p < 0.001$) and decapods ($r^2 = 0.542$; $p < 0.001$) (Fig. 1).

### Experimental analysis of the effects of sustained pressure on development

Embryos developed successfully at pressures of 1, 100, and 200 atm (equivalent to 1, 1000 and 2000 m depth respectively) and all nurse eggs were consumed. No development was observed at 300 atm (equivalent to 3000 m) (Fig. 2, Table 2). Where development occurred, the number of embryos developing per capsule was not affected by pressure (Table 3). However, development proceeded more slowly with increasing pressure. Development was delayed by approximately 3 d at 100 atm and 6 d at 200 atm, relative to expected developmental rates at 1 atm (Smith et al. 2013) (Fig. 2). Analysis of the DW and elemental (C and N) composition of veliger larvae from each treatment allowed us to determine the remaining energy available to the larvae in each pressure treatment and infer the metabolic cost the larvae had incurred (Anger 2001, Evjemo et al. 2001, Anger et al. 2002, García-Guerrero et al. 2003, Lovrich et al. 2003, Smith et al. 2013). At 1 and 100 atm, pressure did not affect veliger DW, C biomass, N biomass or C:N ratio (Fig. 3, Table 3). At 200 atm, however, we observed a significant reduction in the DW, C biomass, and N biomass of veligers ($p \leq 0.01$), despite no significant change in C:N ratio (Fig. 3, Table 3).

Table 1. Egg volumes and depth of sampling for 2 molluscan families (Buccinidae, Muricidae) and 2 crustacean families (Munidopsidae and Chirostylidae). All examples included show lecithotrophic development. Where applicable, egg volumes per embryo were calculated from cited nurse egg volumes and numbers of nurse eggs per embryo

| Species | Depth (m) | Egg volume ($mm^3$ $embryo^{-1}$) | Reference |
|---|---|---|---|
| **Phylum Mollusca** | | | |
| **Class Gastropoda** | | | |
| **Order Neogastropoda** | | | |
| **Family Buccinidae** | | | |
| *Cominella virgate* | ~1 | 0.006 | Carrasco & Phillips (2014) |
| *Lirabuccinum dirum* | 5 | 0.13 | Rivest (1983) |
| *Buccinum isaotakki* | 10 | 0.03 | Ilano et al. (2004) |
| *Buccinum undatum* | 10 | 0.73 | Smith & Thatje (2013a) |
| *Buccinum cyaneum* | 30 | 1.52 | Miloslavich & Dufresne (1994) |
| *Colus islandicus* | 383 | 10.26 | Thorson (1935) |
| *Colus stimpsoni* | 551 | 3.73 | West (1973) |
| *Mohnia mohni* | 1772 | 1.44 | Bouchet & Warén (1979) |
| *Mohnia danielsseni* | 2076 | 7.72 | Bouchet & Warén (1979) |
| *Colus jeffreysianus* | 2200 | 8.27 | Colman & Tyler (1988) |
| **Family Muricidae** | | | |
| *Acanthinucella spirata* | ~1 | 0.02 | Spight (1976a) |
| *Haustrum scobina* | ~1 | 0.15 | Carrasco & Phillips (2014) |
| *Nucella crassilabrum* | ~1 | 0.09 | Gallardo (1979) |
| *Nucella emarginata* | ~1 | 0.15 | Spight (1976a) |
| *Nucella lamellosa* | ~1 | 0.11 | Spight (1976b) |
| *Thais calcar* | ~1 | 0.13 | Spight (1976b) |
| *Trophon geversianus* | ~1 | 0.50 | Cumplido et al. (2011) |
| *Chicoreus capucinus* | ~5 | 0.38 | Spight (1976b), Knudsen (1950) |
| *Chicoreus torrefactus* | ~5 | 0.39 | Cernohorsky (1965) |
| *Eupleura caudata* | ~5 | 0.02 | Mackenzie (1961) |
| *Favartia cellulosa* | ~5 | 0.002 | Lebour (1945), Raeihle (1966) |
| *Nucella lapillus* | ~5 | 0.08 | Thorson (1950), Fioroni (1966) |
| *Nucella lima* | ~5 | 0.41 | Spight (1976b) |
| *Ocenebra* sp. | ~5 | 0.14 | Spight (1976b), Fioroni (1966) |
| *Ocenebra japonica* | ~5 | 0.29 | Spight (1976b), Amio (1963) |
| *Siratus senegalensis* | ~5 | 0.15 | Spight (1976b), Knudsen (1950) |
| *Ceratostoma foliatum* | ~7 | 0.20 | Spight (1976b) |
| *Urosalpinx cinerea* | ~8 | 0.02 | Hancock (1959) |
| *Bolius brandaris* | 18 | 0.28 | Spight (1976b), Fioroni (1966) |
| *Bedeva hanleyi* | ~10 | 0.03 | Anderson (1965) |
| *Hexaplex trunculus* | 10 | 0.11 | Lahbib et al. (2010) |
| *Stramonita caniculata* | 25 | 0.12 | Spight (1976b) |
| *Boreotrophon truncatus* | 40 | 0.03 | Thorson (1946) |
| *Trophonopsis muricatus* | 115 | 0.06 | Lebour (1936) |
| *Trophonella scotiana* | 700 | 0.52 | Hain & Arnaud (1992) |
| *Trophonella shackletoni* | 700 | 0.22 | Hain & Arnaud (1992) |
| **Subphylum Crustacea** | | | |
| **Class Malacostraca** | | | |
| **Order Decapoda** | | | |
| **Family Munidopsidae** | | | |
| *Munidopsis polymorpha* | 1 | 0.62 | Van Dover & Williams (1991) |
| *Munidopsis robusta* | 520 | 1.23 | Kilgour & Shirley (2014) |
| *Munidopsis galabra* | 566 | 1.23 | Kilgour & Shirley (2014) |
| *Galacantha spinosa* | 627 | 3.59 | Kilgour & Shirley (2014) |
| *Munidopsis polita* | 689 | 0.27 | Kilgour & Shirley (2014) |
| *Munidopsis andamanica* | 706 | 0.92 | Van Dover & Williams (1991) |
| *Munidopsis longimanus* | 713 | 0.61 | Kilgour & Shirley (2014) |
| *Munidopsis quadrata* | 714 | 0.54 | Van Dover & Williams (1991) |
| *Munidopsis depressa* | 760 | 0.62 | Van Dover & Williams (1991) |

(Table continued on next 2 pages)

## DISCUSSION

During lecithotrophic development in marine invertebrates, a shift in C:N ratio is typically observed, as nutritional reserves are depleted and structure and metabolic machinery develop. The C:N ratio usually declines throughout development as C is preferentially metabolised while N reserves are minimally depleted (Anger 2001). Once the C available from the lipid pool is exhausted, however, N reserves may be metabolised as an alternative. Under this scenario, the C:N ratio will fall during initial development, but will then rise as N reserves are metabolised (Harms et al. 1991). The mass of the organism, however, is reduced when compared to an individual that has not depleted its N reserves (Harms et al. 1991). The absence of a shift in C:N ratio, as presented in our study, indicates that the depletion of C and N is not consistent across the pressure spectrum. Instead, the reduction in DW, C and N shows greater reserves (both C and N) are being used under increased hydrostatic pressure, but without a simultaneous increase in growth and development. These results demonstrate that an increased metabolic cost is being incurred when developing under high hydrostatic pressure and reveal the true metabolic cost associated with hyperbaric living. The increased metabolic cost is likely associated with a pressure-induced reduction in metabolic efficiency occurring as a consequence of known physiological constraints of hydrostatic pressure (for a review see Somero 1992, Pradillon 2012, Brown & Thatje 2014). For example, the fluidity of cell membranes in shallow-water species is reduced under high pressure as a consequence of de-

Table 1 (continued)

| Species | Depth (m) | Egg volume ($mm^3$ $embryo^{-1}$) | Reference |
|---|---|---|---|
| *Munidopsis alaminos* | 776 | 0.75 | Van Dover & Williams (1991) |
| *Munidopsis barrerai* | 800 | 0.51 | Van Dover & Williams (1991) |
| *Munidopsis truculenta* | 850 | 0.90 | Macpherson & Segonzac (2005) |
| *Munidopsis sarissa* | 850 | 1.15 | Lin et al. (2007) |
| *Munidopsis abbreviata* | 887 | 3.36 | Van Dover & Williams (1991) |
| *Munidopsis hystrix* | 915 | 1.26 | Van Dover & Williams (1991) |
| *Munidopsis erinacea* | 916 | 0.85 | Kilgour & Shirley (2014) |
| *Munidopsis villosa* | 1003 | 7.25 | Van Dover & Williams (1991) |
| *Munidopsis aspera* | 1072 | 0.69 | Van Dover & Williams (1991) |
| *Munidopsis scabra* | 1083 | 1.25 | Van Dover & Williams (1991) |
| *Munidopsis alfredolaguardai* | 1097 | 0.86 | Hendrickx & Ayón-Parente (2013) |
| *Munidopsis spinoculata* | 1102 | 1.10 | Kilgour & Shirley (2014) |
| *Munidopsis sigsbei* | 1107 | 2.06 | Van Dover & Williams (1991) |
| *Munidopsis ornata* | 1212 | 0.66 | Van Dover & Williams (1991) |
| *Munidopsis armata* | 1221 | 1.35 | Van Dover & Williams (1991) |
| *Munidopsis trachynotus* | 1375 | 11.23 | Van Dover & Williams (1991) |
| *Munidopsis valdiviae* | 1378 | 5.14 | Van Dover & Williams (1991) |
| *Munidopsis curvirostra* | 1418 | 1.44 | Wenner (1982) |
| *Shinkaia crosnieri* | 1450 | 7.35 | Miyake et al. (2007) |
| *Munidopsis tridentata* | 1472 | 1.39 | Van Dover & Williams (1991) |
| *Munidopsis sinclairi* | 1525 | 1.63 | Van Dover & Williams (1991) |
| *Munidopsis curvirostra* | 1659 | 1.27 | Van Dover & Williams (1991) |
| *Munidopsis diomedeae* | 1687 | 5.41 | Van Dover & Williams (1991) |
| *Munidopsis simplex* | 1697 | 1.11 | Van Dover & Williams (1991) |
| *Munidopsis verrilli* | 1860 | 4.19 | Van Dover & Williams (1991) |
| *Munidopsis similis* | 1939 | 4.35 | Van Dover & Williams (1991) |
| *Munidopsis rostrata* | 2008 | 7.96 | Van Dover & Williams (1991) |
| *Munidopsis nitida* | 2149 | 4.4 | Van Dover & Williams (1991) |
| *Munidopsis ciliata* | 2153 | 4.04 | Van Dover & Williams (1991) |
| *Munidopsis bairdii* | 2295 | 5.01 | Van Dover & Williams (1991) |
| *Galacantha rostrata* | 2322 | 12.12 | Wenner (1982) |
| *Munidopsis latiangulata* | 2322 | 3.05 | Osawa et al. (2006) |
| *Munidopsis livida* | 2417 | 3.05 | Macpherson & Segonzac (2005) |
| *Munidopsis subsquamosa* | 2491 | 8.92 | Van Dover & Williams (1991) |
| *Munidopsis lentigo* | 2600 | 4.12 | Van Dover & Williams (1991) |
| *Munidopsis latirostris* | 2800 | 4.97 | Van Dover & Williams (1991) |
| *Munidposis hirtella* | 3149 | 12.77 | Macpherson & Segonzac (2005) |
| *Munidopsis bermudezi* | 3179 | 4.64 | Van Dover & Williams (1991) |
| *Munidopsis crassa* | 3186 | 8.45 | Van Dover & Williams (1991) |
| *Munidopsis exota* | 3255 | 9.20 | Macpherson & Segonzac (2005) |
| *Munidopsis antonii* | 3897 | 10.00 | Van Dover & Williams (1991) |
| *Munidopsis columbiana* | 4152 | 10.48 | Van Dover & Williams (1991) |
| *Munidopsis verrucosus* | 4194 | 11.26 | Van Dover & Williams (1991) |
| *Munidopsis riveroi* | 4390 | 1.18 | Van Dover & Williams (1991) |
| *Munidopsis parfaiti* | 4670 | 22.45 | Tiefenbacher (2001) |
| **Family Chirostylidae** | | | |
| *Uroptychus minutus* | 64 | 0.64 | Kilgour & Shirley (2014) |
| *Uroptychus rutua* | 173 | 0.11 | Schnabel (2009) |
| *Gastroptychus affinis* | 357 | 1.01 | Kilgour & Shirley (2014) |
| *Gastroptychus brachyterus* | 392 | 2.57 | McCallum & Poore (2013) |
| *Uroptychus worrorra* | 392 | 0.38 | McCallum & Poore (2013) |
| *Uroptychus yaldwyni* | 405 | 0.14 | Schnabel (2009) |
| *Uroptychus toka* | 420 | 0.61 | Schnabel (2009) |
| *Gastroptychus novaezelandiae* | 424 | 3.59 | Schnabel (2009) |

(Table continued on next page)

Table 1 (continued)

| Species | Depth (m) | Egg volume ($mm^3$ $embryo^{-1}$) | Reference |
|---|---|---|---|
| *Uroptychus maori* | 442 | 4.51 | Schnabel (2009) |
| *Uroptychus sibogae* | 455 | 0.90 | Baba (1981) |
| *Uroptychus glaber* | 470 | 0.70 | Baba (1981) |
| *Uroptychus nanophyes* | 485 | 0.52 | Baba (1981) |
| *Uroptychus webberi* | 625 | 1.77 | Schnabel (2009) |
| *Uroptychus magnispinatus* | 750 | 1.44 | Baba (1977) |
| *Uroptychus setosidigitalis* | 750 | 0.58 | Baba (1977) |
| *Uroptychus similis* | 750 | 1.77 | Baba (1977) |
| *Uroptychus setosipes* | 785 | 0.76 | Baba (1981) |
| *Uroptychus parilis* | 800 | 0.90 | Cabezas et al. (2012) |
| *Uroptychus nitidus* | 847 | 1.80 | Kilgour & Shirley (2014) |
| *Uroptychus soyomaruae* | 865 | 2.88 | Baba (1981) |
| *Gastroptychus salvadori* | 874 | 3.32 | Rice & Miller (1991) |
| *Uroptychus pilosus* | 1125 | 1.44 | Baba (1981) |
| *Gastroptychus spinifer* | 1312 | 1.68 | Kilgour & Shirley (2014) |
| *Uroptychus cartesi* | 1410 | 1.31 | Baba & Macpherson (2012) |
| *Uroptychus scambus* | 1475 | 2.00 | Baba (1981) |

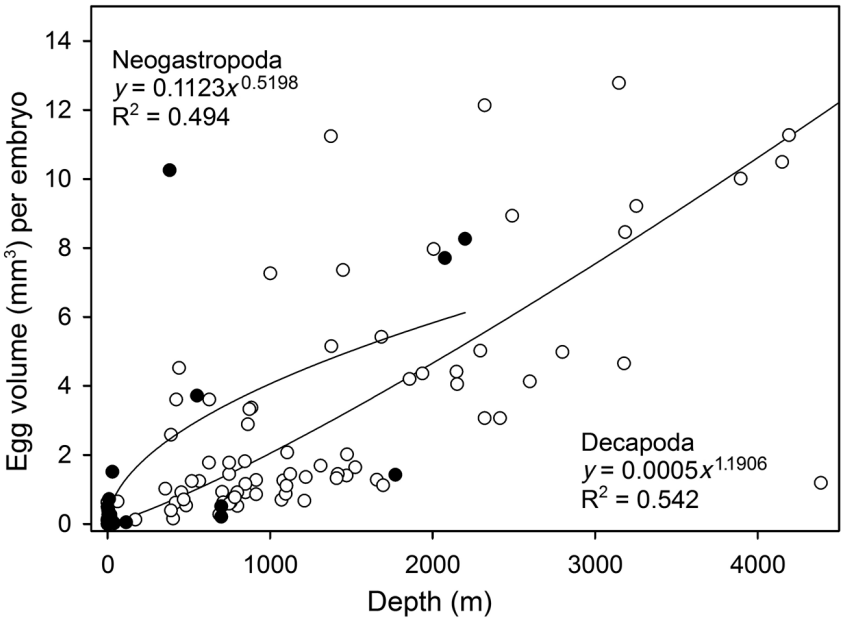


Fig. 1. Trends of increasing egg volume per embryo with depth for Neogastropoda (closed circles) and Decapoda (open circles). All examples included show lecithotrophic development. Data from studies included in Table 1

creased flexibility in lipids, nucleic acids and carbohydrates (Balny et al. 2002). Simultaneously, enzyme function is reduced as high pressure causes dissociation of protein subunits leading to denaturing of enzymes (for a review see Boonyaratanakornkit et al. 2002). Metabolism is dependent on cellular and enzyme function and, therefore, reduction in functionality will reduce metabolic efficiency and growth. This will consequently increase the energetic cost of development, including an increased use of N, as the relationship between use of resources and metabolic output shifts. Similar effects on cell membranes and enzymes are observed below optimal temperatures, resulting in reduced growth efficiency (Hazel 1995, Peck et al. 2004, Pörtner 2004), which indicates a higher energy requirement for completion of development. We suggest that an increase in the development of metabolic machinery to compensate for reduced metabolic efficiency, and higher energy requirements, as a direct result of reduced metabolic efficiency occur during development. These factors collectively explain the increased use of energetic reserves, and thus metabolic cost, observed under high pressure.

A rise in energy use during development has also been reported in gastropods and crustaceans in response to above-optimal temperatures. Responses include increased energy expenditure with decreased developmental efficiency (García-Guerrero et al. 2003), increased metabolic rate (Cancino et al. 2011) and a reduction in embryo size (Fernández et al. 2006). These effects were evident throughout development and resulted in reduced offspring survival. Consequently, in *Buccinum undatum* we infer that the increase in metabolic expenditure evident at 200 atm will be maintained during sustained exposure to high pressure, leading to rapid depletion of available reserves. Additionally, we hypothesise that the observed slowdown of development will persist with continued exposure to high pressure and that the delay in development will therefore escalate over time (see also Mestre et al. 2009). The simultaneous increase in developmental time and use of energetic reserves will ultimately result in a mismatch of energy supply and demand at a critical threshold as the amount of energy necessary for development exceeds the avail-

able reserves. Over evolutionary time scales, this mismatch may have selected for an increase in energy allocation to eggs in taxa colonising the deep sea.

There is consensus that the extant deep-sea fauna originated primarily from shallow-water ancestry (for a review see Brown & Thatje 2014). Today, bathymetric patterns in species diversity typically demonstrate a unimodal trend, the peak of which coincides with an area of high species turnover. The main area of high faunal change, reported globally at depths ranging from 1000 to 1700 m (Carney 2005), indicates a general limit in the distribution of shallow-water and upper-slope biota. Synthesising evidence for the absence of a significant decrease in the respiration rate of *B. undatum* veliger with pressure (Smith & Thatje 2012) and evidence for slowed, and energetically more expensive, development at high pressure, as observed in the present investigation, suggests that the efficiency of metabolism of shallow-water fauna may be reduced with increasing hydrostatic pressure. A pressure-induced shift in the metabolic cost of living will contribute to bathymetric bottlenecks, and only species which are adapted physiologically to tolerate the conditions of the deeper environment may be capable of further depth penetration (Brown & Thatje 2011). Bathymetric trends already recognised within the oceans, such as decreased metabolic rates with depth (Ikeda 2013) or shifts in enzyme function and membrane structure (Gibbs & Somero 1989, Somero 1992), may, therefore, reflect evolutionary selection for physiological adaptations to tolerate the conditions typical of the deep sea, including high pressure (e.g. Somero 2003). Several of these recognised adaptations, such as adjustments for enzyme and membrane function, are, however, understood to be incomplete or occur at a greater metabolic cost in deep-sea species (Somero 1992). Consequently, increased egg size or energy investment per egg with increasing depth (e.g. King & Butler 1985, Van Dover & Williams 1991) may be one adaptation that evolved to compensate for the increased metabolic cost associated with developing under high pressure.

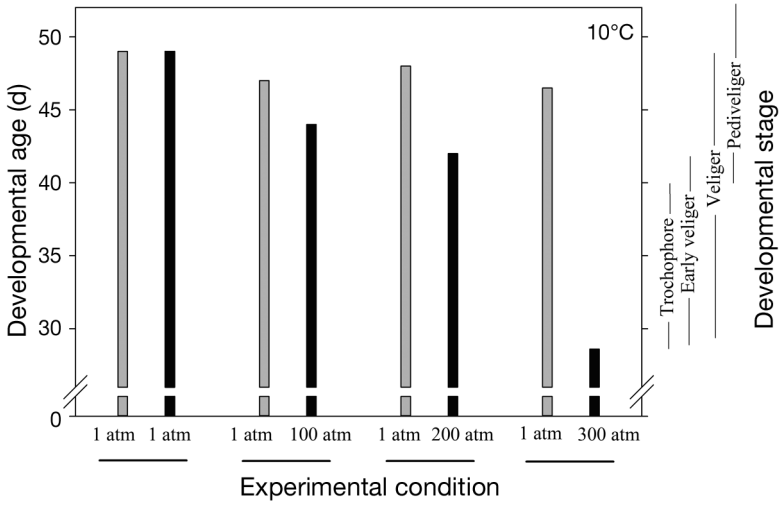


Fig. 2. Developmental age of developing *Buccinum undatum* determined relative to animals developed at 10°C, 1 atm (after Smith et al. 2013). All egg masses developed at 10°C but under different pressure treatments (grey bars, control; black bars, experimental). Only results from treatments linked on the *x*-axis by bars are directly comparable, as these estimates are taken from halves of the same egg masses. The age during which each developmental stage was expected is indicated on the *y*-axis to the right

Table 2. Percentage of *Buccinum undatum* embryos which developed to or beyond each independent developmental stage at 10°C under different pressure treatments. Under each experimental condition the 2 pressures recorded are directly comparable, representing halves of egg masses. Each estimate is based on 3 egg masses developed in parallel

| Experimental condition | Pressure (atm) | Percentage of embryos reaching developmental stage | | | |
|---|---|---|---|---|---|
| | | Trochophore | Early veliger | Veliger | Pediveliger |
| 1 atm | 1 | 100 | 100 | 96.7 | 61.7 |
| | 1 | 100 | 100 | 86.7 | 56.7 |
| 100 atm | 1 | 100 | 100 | 71.9 | 25.4 |
| | 100 | 100 | 100 | 56.7 | 11.7 |
| 200 atm | 1 | 100 | 100 | 98.3 | 56.4 |
| | 200 | 100 | 100 | 79.6 | 5.0 |
| 300 atm | 1 | 100 | 100 | 71.7 | 48.2 |
| | 300 | 1.7 | 0.0 | 0.0 | 0.0 |

Migration of a sensitive life stage to a tolerable shallow-water environment may be an alternative adaptation in deep-water species. Patterns of ontogenetic vertical migration (OVM), whereby deep-water species transport eggs or larvae to shallow water to complete development, have been reported in a range of invertebrates and fishes (Moser 1974, Bouchet & Warén 1979, Kobari & Ikeda 2001, Yoshiki et al. 2011, Arellano et al. 2014). These patterns are typically attributed to higher tempera-

Table 3. Results of analysis by paired *t*-tests for *Buccinum undatum* egg masses developed at 10°C under different pressure treatments. Each analysis was a direct comparison between control (developed at 1 atm) and experimental (developed under pressure) halves of egg masses. No statistical analysis was conducted for 300 atm samples because no development occurred in the experimental treatment at this pressure. Analysis of dry weight, carbon biomass, nitrogen biomass (µg), and C:N ratio were carried out on individuals sampled at the veliger stage only. For each comparison, number of samples (n) is indicated, and p-values are shown. * $p \leq 0.01$; ** $p \leq 0.001$.

| Variable | 1 atm | | 100 atm | | 200 atm | |
|---|---|---|---|---|---|---|
| | n | p | n | p | n | p |
| Number of embryos | 30 | 0.227 | 30 | 0.977 | 30 | 0.573 |
| Dry weight (µg) | 60 | 0.912 | 60 | 0.356 | 60 | ≤0.001** |
| Carbon (µg) | 10 | 0.713 | 10 | 0.451 | 10 | 0.007* |
| Nitrogen (µg) | 10 | 0.721 | 10 | 0.455 | 10 | 0.006* |
| C:N ratio | 10 | 0.562 | 10 | 0.857 | 10 | 0.069 |

ture and greater food availability in shallow water. We suggest that hydrostatic pressure is an additional factor explaining these migrations; shallow-water development of a deep-water species avoids the energetic cost of development under high pressure. In this scenario, OVM reduces both the metabolic demand and the duration of development that would otherwise be expected under deep-sea conditions. Such adaptation may allow deep-sea species to maintain the fecundity typical of shallow-water taxa. Evolutionary adaptations observed in a species, can give important clues to ancestral

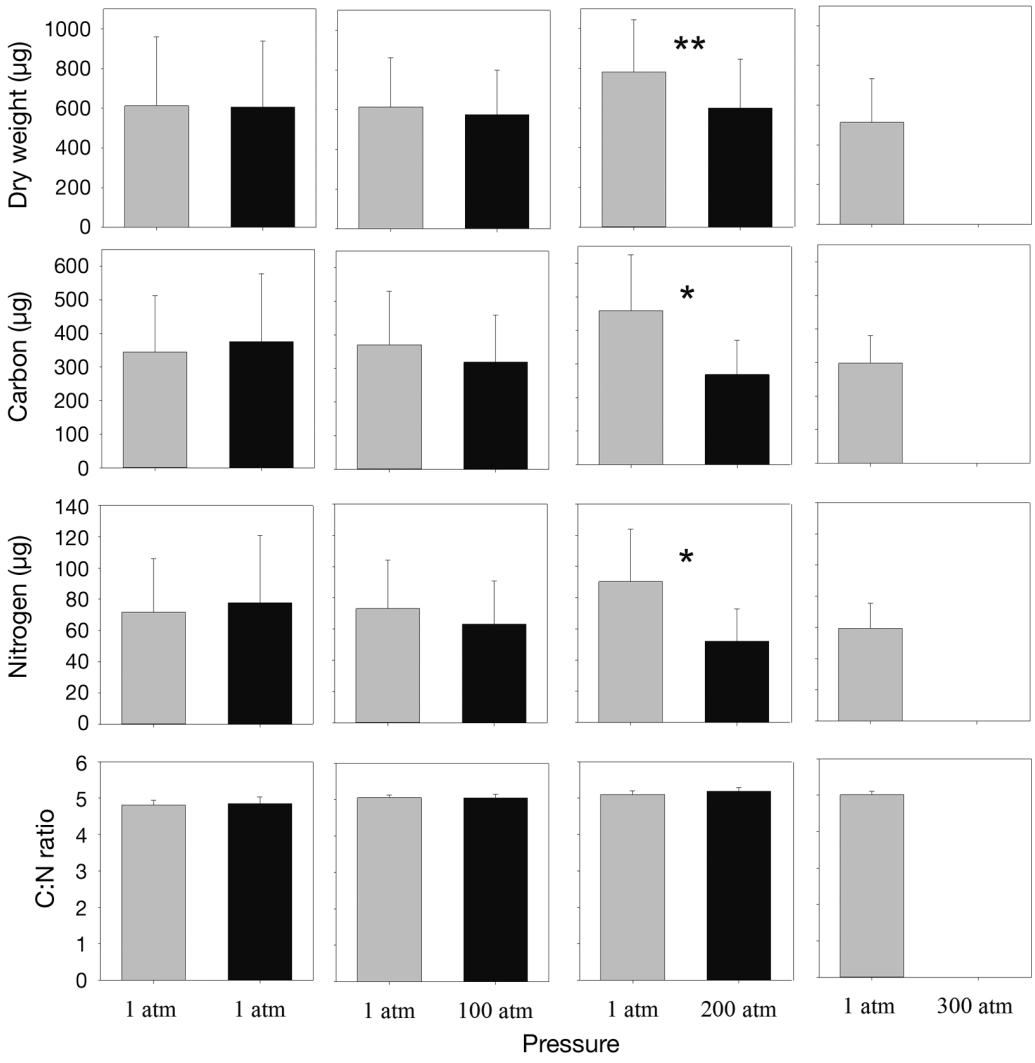


Fig. 3. Differences in dry weight, carbon, and nitrogen biomass, and C:N ratio of *Buccinum undatum* veligers developed at 10°C under different pressure treatments (grey bars, control; black bars, experimental). Veligers developed at 1, 100 and 200 atm but not 300 atm. Only results from treatments displayed within each plot are directly comparable as these are taken from halves of the same egg masses. For each bar, n = 60 for dry weight and n = 10 for all other variables. Error bars indicate 1 SD significant differences between samples (paired *t*-tests), are indicated in each plot by asterisks; *$p \leq 0.01$; **$p \leq 0.001$

origin. Patterns of OVM point to a shallow-water origin for the species employing this life history trait, supporting previous proposals of deep-water invasions by shallow-water species (Brown & Thatje 2014). The proposal that OVM is an adaptation to high pressure may explain why migration patterns are not always synchronised to favourable surface conditions such as periods of increased food availability (Kobari & Ikeda 2001). It may also explain the lower pressure tolerance observed in the eggs of some species following this life-history trait (Yoshiki et al. 2011). The implication that certain developmental stages may have a historical intolerance of high pressure also supports hypotheses of a shallow-water ancestry for many deep-sea species. Although high pressure has never been used before as an explanation for OVM, the idea of an ontogenetic decrease in pressure tolerance has previously been proposed to explain patterns of reverse OVM noted in Antarctic krill, in which eggs sink and develop at depth (George 1984).

Our study clearly demonstrates that hyperbaric conditions increase the metabolic cost of development in a shallow-water marine invertebrate. These findings show that hydrostatic pressure directly affects the energetic requirements necessary to sustain life. We hypothesise that the metabolic cost of any physiological processes are increased under pressure. Consequently, it is likely that adaptations to bathyal life over an evolutionary period of time may, to some extent, have offset energetic demands as exemplified in shallow-water species. Hydrostatic pressure is an important and previously underestimated factor in metabolic theory and its consideration offers new perspectives on ecological and physiological adaptations observed with depth.

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