**Temperature-driven inter-annual variability in reproductive investment in the common whelk *Buccinum undatum***

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**ABSTRACT**

Increasing global temperatures are changing both the biotic and abiotic environment at a rate that many organisms cannot adapt to. Species must either adapt or migrate to areas of more favorable conditions to survive these thermal challenges. Physiological plasticity in response to varying conditions is vital. We studied the effects of temperature on reproductive investment in the common whelk *Buccinum undatum*, a North Atlantic gastropod exhibiting indirect development*.* Reproductive investment was studied by calculating number of eggs per capsule volume and egg energetic status (Carbon: Nitrogen (C: N) ratio) for egg masses from a temperate population of whelks from the Solent, UK over a four-year period (2009-2013). Data were compared with egg masses from a sub-Arctic population from Iceland collected in 2011. Results were compared to local seasonal water temperatures to examine the relationship between temperature and reproductive investment. In the Solent, average autumn and winter temperatures increased by 1 and 2°C, respectively, between 2009 and 2013, the winter increase being significant (P= 0.012). Both the proportion of eggs per capsule volume and the C:N ratio of eggs increased significantly between the initial and final reproductive seasons (P= <0.05). The proportion of eggs per capsule volume was significantly lower in eggs collected in Iceland (P<0.001), but C:N ratio was significantly higher (P<0.05). The results indicate that *B. undatum* changes its reproductive investment in relation to environmental temperature. Our findings illustrate the potential for shifts in reproductive investment in marine invertebrates in response to climate change.

**Key words:** Invertebrate development; Intracapsular development; Temperature adaptation; Reproductive Investment; Neogastropoda

**Short title:** Reproductive investment in the common whelk

**1. Introduction**

Reproductive investment is described as “any parental expenditure that benefits offspring at a cost to a parent’s ability to invest in other components of fitness” (Trivers 1972, see also Oliphant and Thatje 2013). Survival rate increases with parental investment (Moran and Emlet 2001) and a bioenergetic balance can be seen between offspring size and number (Smith and Fretwell 1974). Invertebrates that exhibit direct development typically lay fewer but larger eggs resulting in a greater investment per egg (Vance 1973). Within a species, maternal investment may also vary with size; for example larger gastropods usually lay bigger egg capsules that each contain a greater number of eggs than do smaller cohorts (e.g. Valentinsson 2002, Ilano 2004, Smith and Thatje 2013a).

Contemporary life history studies indicate that ‘optimal’ offspring size and number also vary with environmental conditions (Bernardo 1996). A meta-analysis of marine invertebrate larvae shows that a larger number of smaller offspring are produced with increasing developmental temperature (Marshall and Keough 2007); at higher temperatures less energy is required for development and reproductive investment can be reduced. In nature, reproductive investment reflects the simultaneous result of all biotic and abiotic factors affecting family players (Parker et al. 2002). Higher reproductive investment is associated with abbreviated development and greater independence from external nutrition (Thorson 1936, 1950), which in turn often achieves a higher likelihood of survival per individual.

The common whelk, *Bucccinum undatum* (Linnaeus 1758),is a large, commercially exploited gastropod found across the north Atlantic. Its range extends from New Jersey, USA, to the English Channel, and north to Iceland and the White Sea. Across its distribution, *B. undatum* inhabits temperatures ranging from 0°C to 22°C. Likely due to this range in temperatures, the species has ‘sub-populations’ which have different tolerances and optimal temperatures (Smith and Thatje 2012, 2013b, Smith et al. 2013, see also Weetman et al. 2006).

Spawning in *B. undatum* is temperature-induced (Valentinsson 2002, Smith and Thatje 2013a), and the reproductive cycle varies across the species’ distribution. In the English Channel near the southern end of its distribution, *B. undatum* spawns during the winter when the water temperatures drop below 9°C. In contrast, at the northern end of its distribution, e.g. Iceland, the species spawns in the spring when water temperatures rise to 2–3°C (Martel et al. 1986a, Kideys et al. 1993, Smith et al. 2013, Smith and Thatje 2013a). Females lay egg capsules that contain developing embryos and nurse eggs. Offspring hatch following metamorphosis to juvenile (Smith and Thatje 2013a). The capsules form egg masses which are then added to by other females, probably initiated through the release of pheromones into the water (Martel et al. 1986b).

Here, we test the hypothesis that reproductive investment in *B. undatum* will vary with temperature, and that an increase in temperature will lead to an increase in reproductive investment. The resulting reproductive investment and reproductive success is of relevance when assessing the species’ resilience toward climate warming.

**2. Materials and methods**

***2.1 Collection of egg masses***

*Buccinum undatum* egg masses were collected from the Solent, UK (50°47’ N, 001°15’ W) between December and February, from 2009 to 2013 (seawater temperature 4 to 10˚C), and from Breiðafjörður, Iceland (65°00’ N, 23°30’ W) between April and May 2011 (seawater temperature 3 to 4˚C). The differences in collection months were due to the time of spawning for each population. Egg masses were initially checked for developmental stage, and only capsules with contents still at the egg stage of development were used (see Smith and Thatje 2013a). Maternal size and condition of females was unknown.

***2.2 Capsule volume and egg number***

Female *Buccinum undatum* often group-lay, with each female laying their egg mass onto another female’s mass. Consequently larger masses often consisted of eggs from multiple females. The capsules from each female can, however, be easily distinguished because the size, shape, and colour vary between individuals. Based on these observations, egg masses were split into smaller masses representing capsules laid by a single female. If a capsule could not be allocated to a particular mass, the capsule was removed.

Three randomly selected capsules were dissected from each female’s egg mass. To calculate capsule volume, egg capsules were measured in three dimensions (length, width and depth; ±0.01 mm) using digital calipers. The following equation was used to estimate capsule volume, after Smith and Thatje (2013a):

*V* = (**π** *ab*) x (*c*)

Where *a* = length/2, *b* = width/2 and *c* = depth.

After a capsule had been measured, the contents of the capsule were washed into a Bogorov counting chamber using a pipette. The number of eggs was counted under a dissecting microscope using a hand tally counter.

In *B. undatum*, there is a direct relationship between female size, capsule size, and number of eggs per capsule (Hancock 1967, Smith 2013). Since female size could not be accounted for, the relationship between egg number and capsule volume was compared for each season, to determine inter-annual variation (see statistical analysis below for details).

***2.3 Elemental analysis (carbon, nitrogen)***

Carbon:Nitrogen (C:N) ratios were examined to compare energetic status of the eggs between seasons. C and N levels correlate to lipid and protein levels and, therefore, reflect the physiological condition of the organism. Levels of C reflect nutritional reserves, and levels of N reflect metabolic machinery and structure (Anger 2001, Anger and Harms 1990). Higher C:N ratio suggests a greater energetic input. In *B. undatum*, C:N ratio does not change with capsule volume and therefore we do not need to adjust for capsule volume in this analysis (Smith and Thatje 2013b). Approximately 200 eggs from a capsule were transferred by pipette from the Bogorov chamber into a pre-weighed, 6 mm x 4 mm tin capsule. Excess water was removed and the capsule was frozen at -80°C. Three replicate samples were collected from each capsule. Samples were freeze-dried for 24 h, and then weighed to determine the dry weight (DW) of the sample. C and N analysis was then undertaken through combustion at 1030°C in a Fison (Carlo Erba) 1108 Elemental Analyser.

***2.4 Temperature data acquisition***

Water temperature data for the Solent were collected from Bramblemet (www.bramblemet.co.uk) and occasionally Chimet ([www.chimet.co.uk](http://www.chimet.co.uk)) (used periodically when data collection at Bramblemet failed). Bramblemet and Chimet are long-term weather information systems located in the Solent, which provide real-time and historic seawater temperatures at five-minute intervals. Datasets were downloaded for every Monday of the year throughout 2009–2014. All readings for each 24h period were averaged to show temperature trends throughout the year. Seasonal temperatures were obtained by averaging the data for each seasonal period (December to February (winter), March to May (spring), June to August (summer), and September to November (autumn).

***2.5 Statistical analysis***

Statistical analyses were coded in R (R Core Development Team 2008). Prior to analysis, data were checked for homoscedasticity. The relationship between number of eggs per capsule and capsule volume was compared using an Analysis of Covariance (ANCOVA). Post-hoc analysis (Tukey’s test) was carried out using the R package ‘multcomp’. Seasonal temperatures were compared using a one-way Analysis of Variance (ANOVA). Seasonal temperatures were compared from December 2009 to February 2013, to reflect the period over which egg masses were analysed. Homoscedasticity criteria were not met for elemental composition data (C:N ratio). These data were compared using the non-parametric Kruskal-Wallis test. Wilcoxon rank sum test was used for post-hoc analysis. Bonferroni corrections were applied where necessary.

**3. Results**

***3.1 Capsule volume and egg number***

The relationship between number of eggs per capsule and capsule volume was compared across egg masses collected over three seasons from the Solent, UK (26 in 2009-2010, 42 in 2010-2011, and 10 in 2012-2013), and one season (10 egg masses) from Iceland (Fig. 1). The number of eggs within a given capsule volume changed significantly with season and location (ANCOVA, F3, 272=49.57, P<0.001). Post hoc analysis using Tukey’s test revealed the number of eggs per volume to increase significantly between the 2009-2010 season and the 2012-2013 season (Padj=0.003). Number of eggs per volume was greater in the UK egg masses from every season than in the egg masses collected from Iceland (Padj<0.001). There was no difference in the relationship between egg number and capsule volume between the 2009-2010 season and the 2010-2011 season (Padj=0.515).

***3.2 C:N ratio***

Elemental composition of eggs was compared for 9, 13, 13, and 10 egg masses collected in the 2009-2010 through 2012-2013 seasons respectively, and for 4 egg masses collected in Iceland (Fig. 2). C:N ratio differed significantly across seasons and locations (Kruskal-Wallis test, H4=18.667, P<0.001). Post-hoc analysis (Wilcoxon rank sum test) revealed C:N ratio to be significantly lower in 2009-2010 than in 2012-2013 (Padj=0.030) for egg masses from the Solent, UK. C:N ratio did not differ significantly between any other seasons at this location (Padj>0.05 for all four comparisons), although a trend of increasing C:N ratio was visible (Fig. 2). The C:N ratio in the Iceland egg masses was, however, significantly greater than the C:N ratio recorded in UK egg masses in 2009-2010 (Padj=0.028), 2010-2011 (Padj=0.008), 2011-2012 (Padj=0.008), and 2012-2013 (Padj=0.020).

***3.3 Seawater temperature***

Autumn and winter seawater temperatures increased by 1°C and 2°C respectively between 2009-2010 and 2012-2013, although the change was only significant during winter (One-Way ANOVA, winter: F1,50=6.733, P=0.012; autumn: F1,50=0.384, P=0.538). Data presented for one year before and after the duration of this study indicate the trend of increasing temperatures for both seasons to continue (Fig. 3a,b). Average temperatures for spring and summer remained constant across the 2009-2013 time period (One-Way ANOVA, F1,51=2.399, P=0.128; F1,50=1.065, P=0.307 for spring and summer, respectively).

**4. Discussion**

***4.1 Study rationale***

The present study aimed to investigate the interannual relationship between reproductive investment and temperature in the Solent population of the common whelk *Buccinum undatum*, and compare the results to data gathered on a colder-water population from Iceland. We hypothesised that within the Solent population, reproductive investment would increase with increasing temperature due to the greater energy requirement needed at higher temperatures. Factors other than temperature may also influence the differences in reproductive investment observed here; however, they have not been studied in this work. Overall, significant increases in egg number per capsule volume and C: N ratio were observed between the initial and final seasons studied for the UK population, along with increases in average winter sea temperatures.

***4.2 Capsule volume and egg number***

Number of nurse eggs and veligers are significantly related to capsule volume in *Buccinum undatum* (Smith and Thatje 2013a). Our data indicate that this relationship remains evident across seasons, but with higher seasonal temperatures, the number of eggs per given capsule volume increases. Development at higher temperatures can result in a smaller number of veligers successfully developing per capsule, meaning a larger number of nurse eggs (and therefore nutrition) are available for each veliger (Smith et al. 2013, Smith and Thatje 2013b). However, the aforementioned studies involved experimental manipulation of temperatures using egg masses from a single season and did not consider the important effects of temperature on gametogenesis. Number of veligers per capsule was not recorded in this study and further investigation is necessary to determine whether the ratio of veligers and nurse eggs per capsule varies seasonally.

Rate of nurse egg consumption increases with temperature in *B. undatum* (Smith and Thatje 2013b, Smith et al. 2013). This, combined with the increased energetic content of nurse eggs, may be a maternal response to the need for greater energy levels at higher temperatures. However, under experimental conditions, higher temperatures lead to a decrease in the number of developing embryos per capsule, and an increase of embryo size at the same time (Smith and Thatje 2013b). The common whelk has a predominantly cold-water distribution, and therefore any variation found in southern populations will likely be evolutionary consequences of adaptations to warmer conditions. In some species of crab, changes in egg size have also been observed across timescales as narrow as a single reproductive season, with differences following distinct thermal regimes (Diez et al. 2012). A similar trend has been found to occur in gastropods as environmental conditions vary through changes in biotic and abiotic conditions (Collin and Salazar 2010, Zelaya et al. 2012).

***4.3 Elemental composition of eggs***

The observed increase in C:N ratio in the 2012/13 season may be a maternal response to the increases in average winter seawater temperatures in the Solent, UK. Gametogenesis occurs in autumn/winter in the southernmost populations of *Buccinum undatum* (Staiger 1951). Average winter temperature increased significantly from 6°C to 8°C throughout the duration of this study. The highest recorded winter water temperature was in 2013, with an average of 8.3°C. In the Solent (UK), *B. undatum* lay egg masses during the winter, when the local water temperature drops below approximately 8-9°C (Hancock 1967, Kideys et al. 1993). If the mother experiences gradual increases in temperature during gametogenesis and laying over a series of seasons, an adaptive maternal effect may be seen whereby the nutritional value of nurse eggs is increased in response. Nurse eggs with higher nutritional value will provide veligers with a greater amount of energy, as is necessary for development at higher temperatures (Garcia-Guerrero et al 2003, Smith et al. 2013). In *B. undatum*, development at higher temperatures leads to an initial increase in proportions of C and N in early veligers. By hatching, however, the energetic disposition of individuals is comparable across all temperatures. The greater use of energetic reserves at higher temperatures is likely due to the related increased energetic demand, and thus a greater metabolic loss is the result (Smith et al. 2013).

***4.4 Comparison to Icelandic population***

Although a lower number of eggs per capsule volume was observed in the colder water, Icelandic population of *Buccinum undatum*, following the thermal trend observed in the UK population, the C:N ratio of eggs was significantly higher, which is the opposite of what was observed in the UK population. Presumably, these contrasting patterns are the result of an evolutionary adaptation to particularly low temperatures; veligers moves slower at low temperatures and consume nurse eggs at a much lower rate (Smith and Thatje 2013b, Smith et al. 2013. By increasing the energetic content of each egg, the veliger can obtain enough energy to develop with a lower number of nurse eggs. It is possible that the opposing strategies for reproductive investment are related to the temperature at which gametogenesis occurs in each population; in the UK, gametogenesis takes place at warmer temperatures than does development, whereas in Iceland, gametogenesis takes place at colder temperatures than development (Martel et al. 1986a, Kideys et al. 1993, Smith et al. 2013, Smith and Thatje 2013a). Further studies are necessary to understand inter-annual changes in reproductive investment in the Iceland population of *B. undatum*.

***4.5 Implications for biogeography and fisheries***

Full development has previously been achieved by the Solent population of *Buccinum undatum* from 6-18°C (Smith et al. 2013). At higher temperatures, however, development is halted due to energetic supplies being used up before development is complete (Smith and Thatje 2013a). Development can also be so rapid that embryos do not successfully consume all of the nurse eggs within a capsule at the stage that they are able to do so, leaving some nutritional reserves unused (Smith and Thatje 2013b). Despite some adjustment in reproductive investment to increases in temperature, if water temperatures continue to rise at current rates, recruitment may fail and whelk stocks may fall in southern populations of the common whelk (Solent, UK).

Molecular studies suggest that populations of *B. undatum* around the coasts of the UK are moving offshore into deeper water (Weetman et al. 2006). The Solent population in particular is reported to be the product of a genetic bottleneck, and thus shows large differences from more northern populations. This bottleneck was likely caused by anthropogenic input of tribuytl tin (TBT), which can cause imposex in gastropods (Gibbs 1996, Strand and Jacobsen 2002). Weetman et al. (2006) suggest such separated populations may provide genetic diversity, but are also susceptible to exploitation due to a lack of gene flow to and from other populations (Colson and Hughes 2004). Reproduction is slow, and dispersal is limited; consequently, recovery from decimation is likely a slow process. Swedish populations of the common whelk show the same level off differentiation between populations 2 km apart, as those 200 km apart (Valentinsson 2002b), highlighting the lack of gene flow between even nearby populations. In general, populations may need close management due to genetic isolation and low levels of population connectivity.

Despite these limitations to dispersal, *B. undatum* has colonised thousands of kilometres of sub-tidal coastline spanning large latitudes. Their large range may be related to bathymetric movements through isothermal water columns. Experimental hydrostatic pressure treatments have identified that *B. undatum* are able to survive hydrostatic pressures experienced in the deep-sea, although at an increased metabolic cost (Smith and Thatje 2012, Smith et al. 2015). If water temperatures continue to rise, this species may utilise their tolerance of high hydrostatic pressure and migrate to deeper, cooler water over the continental slope (see also Weetman et al. 2006).

The future of *B. undatum* fisheries around the English Channel largely relies on the species’ ability to reproduce successfully in rising sea temperatures. Understanding whether or not this is possible requires further insight into the effects of temperature on recruitment, and on the phenotypic transfer of experience and reproductive investment from parents to offspring.

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**Ethical approval**

All applicable international, national, and/or institutional guidelines for the use of animals were followed.

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**Legends to figures**

**Fig. 1** Variation in average number of eggs per capsule in relation to capsule volume obtained for a population of *Buccinum undatum* from the Solent (UK) for three reproductive seasons (December to February, 2009 to 2013) and a population from Icelandic waters for one season (2011). Lowercase letters to the right of each trendline indicate significant differences in the relationship between egg number and capsule volume across seasons (ANCOVA followed by Tukey’s test post-hoc).

**Fig. 2** Average C:N ratios of eggs for a population of *Buccinum undatum* sampled from the Solent, UK, between 2009 and 2013, and from Iceland in 2011. Significant differences indicated by lowercase letters (Kruskal-Wallis followed by Wilcoxon rank sum test post-hoc). Error bars indicate standard error.

**Fig. 3** Average seasonal seawater temperatures for Solent waters, UK, from 2009 to 2014. a) Average daily temperature for every Monday of the year throughout 2009–2014. b) Average seasonal temperatures. Winter temperatures are averaged from December the previous year through to February of the current year, with the exception of 2009 which consists of January and February data only.