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Research

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Does energy availability predict gastropod reproductive strategies?

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The diversity of reproductive strategies in nature is shaped by a plethora of factors including energy availability. For example, both low temperatures and limited food availability could increase larval exposure to predation by slowing development, selecting against pelagic and/or feeding larvae. The frequency of hermaphroditism could increase under low food availability as population density (and hence mate availability) decreases. We examine the relationship between reproductive/life-history traits and energy availability for 189 marine gastropod families. Only larval type was related to energy availability with the odds of having planktotrophic larvae versus direct development decreasing by 1% with every one-unit increase in the square root of carbon flux. Simultaneous hermaphroditism also potentially increases with carbon flux, but this effect disappears when accounting for evolutionary relationships among taxa. Our findings are in contrast to some theory and empirical work demonstrating that hermaphroditism should increase and planktotrophic development should decrease with decreasing productivity. Instead, they suggest that some reproductive strategies are too energetically expensive at low food availabilities, or arise only when energy is available, and others serve to capitalize on opportunities for aggregation or increased energy availability.

1. Introduction

Organisms are biological machines that require energy to perform work, maintenance, growth and reproduction [1–3]. When energy is limited, competition increases, which in turn drives adaptation to increase energetic efficiency [4]. Ultimately, individuals better adapted to secure, or use, energetic resources can convert this energy into offspring more efficiently [5]. As such, energetics is a key component of modern evolutionary theory [6], deeply rooted in the principles of Darwin and Malthus. Three distinct types of energy affect biological systems: solar radiation in the form of photons, thermal kinetic energy as indexed by temperature, and chemical potential energy stored in reduced carbon compounds [7].

Both thermal kinetic energy and chemical potential energy are posited to influence reproductive strategies [8,9]. Thorson [10] hypothesized that both poor food conditions and low temperatures should slow or postpone larval growth, thereby increasing larval life duration and ultimately predation exposure in the water column (reviewed in [11]). Lower food and temperatures would thus decrease the frequency of feeding planktonic stages (i.e. planktrophic larvae), and lower temperatures would decrease the frequency of non-feeding planktonic stages (i.e. lecithotrophic), at higher latitudes and deeper depths. This finding was supported by later modelling efforts [12]. More recent theoretical and empirical work also found that larval duration in the water column increases with decreasing temperature [13].

Alternatively, lower food availability may promote adaptations for planktotrophic larvae because these larvae tend to disperse away from areas of low food concentration [14]. Indeed, planktotrophic development may be more frequent at extreme low food availability, as populations in oligotrophic regions may represent sinks maintained only through continued recruitment requiring dispersal from distant population sources [14,15]. In contrast to these

predictions of larval type with production, others have concluded that 'the presence or absence of a feeding larval stage is only weakly and indirectly related to allocation of energy or materials to production' [16, p. 339]. Pearse *et al.* [17] concluded that in many taxonomic groups, the geographical patterns suggested by Thorson do not exist and the processes generating these patterns may be taxon specific.

These two contrasting theories alternatively predict that planktotrophic larvae should be more prevalent either at high [15] or low food availability [10]. The results in support of these two different patterns are mixed. Thorson [10] based his original hypothesis on the findings that planktotrophic larvae were under-represented among marine species near the poles, regions he equated with low temperatures and productivity. Based on the limited data available at the time, Thorson [10] also suggested that the deep sea, a low food availability environment, was dominated by non-pelagic larval strategies. Support for Thorson's hypotheses can be found in recent studies involving more direct tests by explicitly quantifying both temperature and productivity. Fernandez *et al.* [18] tested for variation in species richness of planktotrophic and direct developers, i.e. pelagic feeding versus non-pelagic, in crustaceans and molluscs from the Chilean shelf as a function of both sea surface temperature and minimum chlorophyll concentration. Increases in temperature lead to significant decreases in direct development but increases in planktotrophic development in both molluscs and crustaceans. Increases in chlorophyll *a* (chl-*a*) concentration lead only to increases in direct development crustaceans and planktotrophic molluscs but both relationships were weak. In a subsequent study on crustacean and mollusc species on the southeastern Pacific and southwestern Atlantic coasts, planktotrophic species richness were found to decrease polewards while direct developers increased, reflecting variation in temperature and not chl-*a* [19]. Similarly, Calyptraied gastropods exhibit decreases in planktotrophic and increases in direct development with increasing latitude [20]. Recently, Marshall *et al.* [21] compiled information for 1500 species across five phyla, finding that planktonic larvae and smaller egg sizes were more common where both temperature and/or productivity were high.

Yet, other studies do not support Thorson's hypothesis, instead finding that planktotrophic larvae are more frequent in habitats inferred to be energy limited. In a transect from the northwest Atlantic Ocean, from depths of 478–4970 m, planktotrophic development in gastropods increased with increasing depth, and a presumed reduction in food availability [14]. Likewise, in both the eastern and western North Atlantic, planktotrophic development becomes the predominant strategy in gastropods inhabiting the abyssal plains, an environment associated with extremely low food availability [15]. Bradbury *et al.* [22] also found that planktonic larval duration increased with both increasing depth (up to 1000 m) and increasing latitude—opposite of those patterns predicted by Thorson [10]. Antarctic taxa also exhibit equivalent levels of pelagic development as more temperate regions [8,17].

Hypotheses have also been put forth to predict shifts in other reproductive strategies over gradients of energy availability. The frequency of hermaphroditism may also increase under low food availability as population density, and hence mate availability, decreases [23,24]. Yet, to our knowledge, this hypothesis has never been quantitatively tested in marine organisms. Here, we assemble and analyse a database of reproductive traits, life-history attributes and energy availability, measured as particulate organic carbon (POC) flux and bottom temperature, for marine gastropod families of the western Atlantic Ocean. We include in our database all 189 families present in the western North Atlantic for which we have life-history data available. We specifically test whether food availability and temperature increases or decreases the presence of specific reproductive strategies with regard to gametes, embryos, larvae and hermaphrodistism. We build upon prior work by including an additional suite of reproductive strategies, using an evolutionary framework and explicitly quantifying energy availability. Additionally, we include multiple families that have been excluded in prior analyses that comprise geographical ranges that predominately occur in deep oceans and are characterized by low productivity levels. The inclusion of these groups allows us to explore clines over a much greater range of energy availability.

2. Material and methods

For each gastropod family, as defined by Bouchet & Rocroi [25], we collected data about the dispersal of male and female gametes, the dispersal of fertilized embryos, the mode of larval development and the prevalence of hermaphroditism. Our level of analysis was chosen because family-wide information was readily available and because reproductive strategies are fairly conserved at this taxonomic level, i.e. most variation in the reproductive strategies we examine occurs between families [26]. Information was collected from a literature review.

For each family, character states were merged into the following binary categories: gametes (dispersing versus non-dispersing), embryos (dispersing versus non-dispersing), and hermaphroditism (present versus absent). Gametes were considered dispersing if either the female or male gametes are expelled (e.g. broadcast, spermatophore). As such, the absence of dispersing gametes infers that copulation is required. For embryos, we combined retained (e.g. brooded by the mother) and attached (i.e. deposited in an egg mass on the substrate), into a non-dispersing category; dispersed (embryos released into the water and dispersed into the pelagic zone) and mixed (multiple strategies were exhibited among species within a family) were likewise combined into a dispersing category. Hermaphroditism was combined into present (100% and mixed (multiple strategies were exhibited among species within a family)) and absent (0%).

We classified gastropod families in four different larval categories: direct (young develop directly into the adult form without a larval phase and typically have limited dispersal potential), planktotrophic (young feed in the plankton during their larval stage and are considered to have longer dispersal potential), lecithotrophic (larvae derive nourishment from yolk and are non-feeding and are considered to have longer dispersal potential) and a mixed category including families that exhibited a combination of the three above states.

Chemical energy available to the gastropods was estimated as POC flux (g of C m^{-2} yr^{-1}) based on the Lutz *et al.*'s [27] model. Specifics of the model can be found in [28]. Temperature data was gathered from the National Oceanographic Data Center (NODC) database [29]. For each family, we quantified the median and standard deviation of carbon flux and temperature over their known latitudinal and depth ranges. To obtain the energy values, each family's biogeographic range was overlaid upon the Lutz *et al.*'s [27] model or NODC data. Depth and latitudinal range were pulled from Malacolog for the western Atlantic Ocean to estimate the biogeographic range of family. Data from each family were manipulated using ArcGIS Workstation 10 (Environmental Systems Research Institute, Redlands, CA, USA). We created a

geographic information system (GIS) layer for each family's north–south range extent. This was overlaid upon bathymetry data (General Bathymetric Chart of the Oceans 08, 30 arcsecond grid, September 2010 release, www.gebco.org) to limit each family's distribution to their recorded depth range.

Binary and binomial regression models were implemented in R using the package MCMCglmm, with uninformative priors and uniformly low levels of belief [30]. Model chains were run for 500 000 iterations with a burn-in of 200 000 iterations and thinning intervals of 100 iterations. To evaluate convergence, we assessed the mixing of Markov chain Monte Carlo (MCMC) chains visually [30] and computed formal diagnostics from Geweke [31] and Heidelberger & Welch [32] via the R-package 'coda' [33]. For each parameter in our models, we report mean estimates from the posterior distribution along with the 95% credible interval (CI) and the corresponding MCMC p-value [30]. Median energy flux values were square root-transformed prior to analysis to minimize skew and bimodality in the data. Taxonomic Order—from the most current taxonomy for Gastropoda [25]—was included as a random effect to account for the possible effects of shared phylogenetic history in our model. A more explicit estimation of phylogenetic covariance was not possible owing to the current lack of a comprehensive molecular phylogeny for this clade.

Some species may exhibit values for POC or temperature that differ from their representative family, i.e. the environmental values encountered over the entire range of a taxonomic family may not be representative of the environment experienced by a particular species within it. To evaluate the extent to which our results depend on taxonomic sampling level, we explored the distribution of carbon flux values taken for individual species within a family. Values of chemical energy availability (temperature data were not available) were taken from previous work on the same geographical region of our family-level samples [28]. In this exploration, the carbon flux value for every GIS cell was taken for every individual species within a family. For all the families explored, median values for the family were near the median values based on individual species. A high correlation (0.67, Spearman's ρ: $p < 0.0001$) exists between the median for the family and the median value based on individual species.
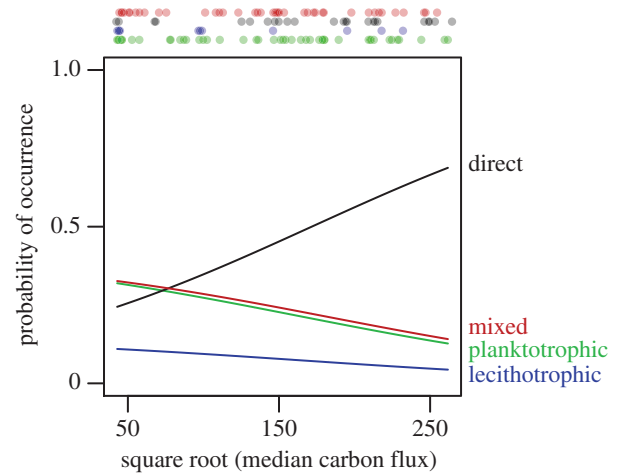
3. Results

Pairwise χ^2 tests indicated that the probability distributions of gamete retention, egg dispersal and hermaphroditism are not independent from each other. Larval dispersal type is significantly associated with gamete retention ($p = 0.03$) and egg dispersal ($p < 0.001$) but not with presence of hermaphroditism ($p = 0.12$). Thus, below we analyse only the presence of hermaphroditism and the larval category, as it was strongly correlated with gamete and egg type.

(a) Larvae

Compared with direct development, all planktotrophic, lecithotrophic and mixed categories were less frequent at high levels of carbon flux (figure 1). In all models, mean temperature was excluded from the MCMC models ($p > 0.05$ and CI's include zero, table 1). In a non-taxonomic model, intercepts between larval categories were not significantly different (table 1). A significant change occurred in lecithotrophic versus direct development ($p = 0.0433$), with lecithotrophic being less represented at lower levels of median POC flux (table 1 and figure 1).

Models including the taxonomic relationships provided better fits than non-taxonomic models (deviance information criterion (DIC) = 274.43 versus 313.38). In the MCMC models that

Figure 1. Relationships between the square root of median POC flux and probability of a gastropod family possessing a particular larval type. Lines represent logistics fits of the data for each larval type compared to direct development (table 1). Coloured dots represent the median POC flux values for individual families.

included taxonomic structure intercepts were not significantly different (table 1). Lecithotrophic development was more frequent at higher productivities than direct development but not significant ($p = 0.075$). However, planktotrophic development was less frequent at higher productivities than direct development ($p = 0.05$). In this model, the probability of a given family having planktrophic larvae versus direct development *decreases* 1% for every one-unit increase in square root median of POC flux.
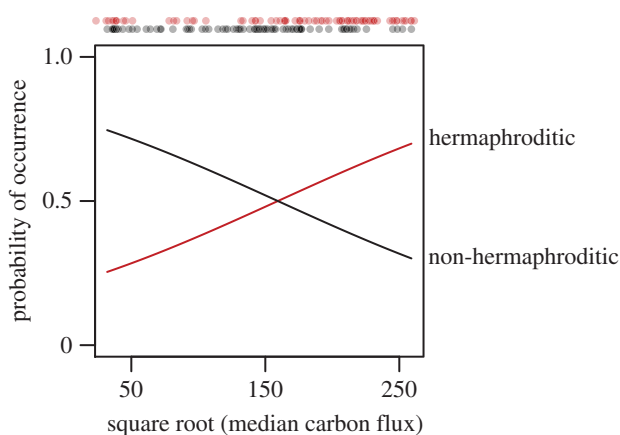
(b) Hermaphroditism

In the non-taxonomic model, the presence of hermaphroditism increases with increasing median POC flux ($p = 0.001$) The non-taxonomic model suggests that the probability of exhibiting hermaphroditism within a family *increases* by 1% for each one-unit increment in the square root of median POC flux (figure 2 and table 1). However, this model is poorly supported in comparison to a model that incorporates taxonomic relatedness (DIC 215.94 versus 69.75). In the latter case, POC flux is no longer significant.

4. Discussion

After accounting for taxonomic relatedness, energy availability appears to influence only one of the life-history variables considered in our analyses. Specifically, with every one-unit increment in the square root of median POC flux, the probability of having planktotrophic larvae over direct development in gastropods decreases by 1%. Likewise, although marginally non-significant, our results suggest lecithotrophic development may also decrease with increasing productivity. Our findings for larval dispersal contrast with some previous hypotheses and findings. Thorson [10] posited that cold temperatures and limited food would increase larval duration and consequently larval mortality owing to predation, thereby selecting against planktotrophic phases. Our findings of planktotrophic development in colder and more limited food regions, like the deep sea, do not support this. Similarly, our study is also in contrast to recent findings that planktotrophic development increases with increasing productivity [18,21] but matches those studies

4

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Table 1. Summary of results for linear models that either account or not for potential taxonomic effects (modelled as a random effect from Order). (For each parameter estimate, we report the mean of the posterior distribution, the 95% credible interval (CI) and the MCMC *p*-value. Parameters reported as 'non-significant' (n.s.) were excluded from the final model because their CIs included zero and MCMC *p*-value > 0.05.)

	posterior mean	lower 95% CI	upper 95% CI	MCMC *p*-value
larvae/reference = 'direct' (DIC: 313.38)				
intercept (mixed)	0.916	−0.061	1.945	0.074
intercept (lecithotrophic)	0.322	−0.867	1.561	0.599
intercept (planktotrophic)	0.920	−0.088	1.905	0.077
median temperature (mixed)	n.s.	n.s.	n.s.	n.s.
median temperature (lecithotrophic)	n.s.	n.s.	n.s.	n.s.
median temperature (planktotrophic)	n.s.	n.s.	n.s.	n.s.
square root median POC flux (mixed)	−0.003	−0.009	0.004	0.355
square root median POC flux (lecithotrophic)	−0.010	−0.019	−0.001	0.043
square root median POC flux (planktotrophic)	−0.002	−0.009	0.004	0.462
larvae/reference = 'direct'; with Order as random effect (DIC: 274.43)				
intercept (mixed)	0.657	−0.840	2.017	0.369
intercept (lecithotrophic)	−0.417	−2.215	1.354	0.677
intercept (planktotrophic)	0.652	−0.932	2.127	0.410
median temperature (mixed)	n.s.	n.s.	n.s.	n.s.
median temperature (lecithotrophic)	n.s.	n.s.	n.s.	n.s.
median temperature (planktotrophic)	n.s.	n.s.	n.s.	n.s.
square root median POC flux (mixed)	−0.009	−0.018	0.001	0.075
square root median POC flux (lecithotrophic)	−0.009	−0.023	0.005	0.205
square root median POC flux (planktotrophic)	−0.009	−0.018	0.000	0.050
hermaphroditism/reference = 'absent' (DIC: 215.94)				
intercept	−1.347	−2.221	−0.453	0.003
median temperature	n.s.	n.s.	n.s.	n.s.
square root median POC flux	0.008	0.003	0.014	0.001
hermaphrodite/reference = 'absent'; with Order as random effect (DIC: 69.15)				
intercept	0.023	−1.856	1.710	0.972
median temperature	n.s.	n.s.	n.s.	n.s.
square root median POC flux	−0.002	−0.015	0.010	0.752

Figure 2. Relationships between the square root of median POC flux and probability of a gastropod family being hermaphroditic. Lines represent logistics fits of the data (table 1). Coloured dots represent the median POC flux values for individual families.

where depth was considered a proxy variable for productivity [14,15,22]. One potential reason for this discrepancy is that our study includes a greater range of productivity values owing to the inclusion of gastropod families with deep-sea ranges. Indeed, the greatest rates of change in the presence of dispersing strategies occur across the lowest median POC flux values. Another reason for the discrepancies in these findings may be that larval duration differs as function of geography itself even when taxonomy and larval type are constant [34]. Our study focuses on the northwest Atlantic, similar to Rex & Waren [14] and Rex *et al.* [15], whereas Fernandez *et al.* [18] examine relationships in the southeast Pacific and Marshall *et al.*'s [21] study is a global meta-analysis.

Worth noting is that Thorson [10] based his hypothesis on the findings of decreased presence of planktotrophic development in both the Arctic and Antarctic Oceans, areas he equated with low productivity. He suggested that despite high productivity at the poles in surface waters little of production arrived at the seafloor to be consumed by benthic invertebrates

([10], p. 25). However, more recent studies of carbon flux to the seafloor suggest that the pattern is complex and does not follow systematic latitudinal patterns [27]. Nonetheless, regions of high latitudes often experience elevated carbon fluxes to the seafloor [27,35,36]. This suggests that Thorson's own work may indicate that planktotrophic development may occur with greater frequency in higher productivity regions. Similarly, Thorson [10] indicated that the presence of planktotrophic larvae decreased into the deep sea, a finding that has not been supported in either fishes or gastropods [14,22].

Our results may indicate that low energy availability favours planktotrophic larvae, and possibly lecithotrophic larvae, versus direct development potentially indicating selection for greater dispersal ability. Dispersing larvae may serve as a bet-hedging strategy which insures that at least some juveniles will find and settle in highly productive patches. Previous work by Rex & Waren [14] demonstrated that in prosobranch gastropods, planktotrophic development increases with depth and the associated decline in food availability. Our expanded analyses with a broader taxonomic scope support this finding. Indeed, the increase of dispersing larvae in the most food poor (i.e. oligotrophic) regions may reflect source/sink dynamics. Many mollusc populations in the abyssal plains, which are some of the most oligotrophic areas of the oceans, are probably maintained through the continued recruitment of larvae from source populations in more productive ocean regions [15].

Alternatively, planktotrophic development may be an energetically less expensive strategy [12]. Planktotrophic larvae require less parental investment as the larvae vertically migrate into surface waters to feed. The ability of larvae to feed themselves allows lower energetic investments from parents during offspring production, and the larval tendency to exploit resources outside of the adult habitat decreases competition between life-stages. By contrast, direct development requires species in low food environments to convert limited energy into non-feeding offspring. This may translate into the caloric requirement of offspring development not being met.

Increased energy availability also appears to favour the occurrence of hermaphroditism, in conjunction with gamete retention and egg dispersal, in one of our models. This finding is also counter to earlier suggestions that simultaneous hermaphroditism may allow any two individuals to engage in successful mating and could therefore increase the chances of reproduction when population densities are low, as expected for low energy environments [23,24]. Nevertheless, the possible effect of energy availability on hermaphroditism is poorly supported by the data and appears to be driven by phylogeny. In particular, this pattern mirrors the distribution of nudibranch and opisthobranch gastropods, two predominately hermaphroditic clades whose density and richness decrease with depth and reduced food availability [37]. In addition, hermaphrodites might be competitively excluded from the deep sea because the production of both sexes is energetically expensive and therefore possibly untenable when resource abundance is low. The increased representation of the nudibranch and opistobranch orders in higher energy regions is not totally unexpected given their higher standard metabolic requirements compared with other gastropods [38].

Our findings may also be consistent with the view that reproduction in low energy environments is opportunistic at aggregations and that selection in those habitats favours traits that improve an individual's ability to locate and colonize the highly localized but spatio-temporally unpredictable resource patches where they occur. Highly localized food falls tend to attract large numbers of mollusc individuals [39,40] with highly specific energy requirements [41,42]. Under these conditions, selection for dealing with mate availability, i.e. hermaphroditism, is likely to be minimal because opposite-sex partners may be readily available wherever individuals congregate.

Alternatively, hermaphroditism is associated with the brooding of young found predominately in small marine invertebrates [43]. Hermaphroditism thus may show reverse predictions if either reduced dispersal or reduced body size are being selected for at higher productivities. Given that size in gastropods increases considerably in areas with greater productivity [28], it is likely that selection would favour limited dispersal as opposed to reduced size.

Overall, our results do not support two hypotheses that predict variance in reproductive strategies with gradients in energy availability. Gastropods may reflect a unique case among invertebrates as they exhibit certain reproductive strategies more frequently, e.g. simultaneous hermaphroditism and encapsulated brood protection, not typical in other molluscs or invertebrate phyla. Future studies are needed to test for the generality of the patterns we report here for gastropods. Our results indicate that for gastropods, with decreasing productivity, hermaphroditism decreases or shows no pattern when accounting for shared evolutionary history, and the frequency of planktotrophic larvae increases. Future studies should benefit from a more nuanced phylogenetic hypothesis that allows a better estimate of the effects of differential levels of relatedness within and among Orders and from sampling at a lower taxonomic level (e.g. at the level of species) as more data become available.

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6

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