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Differences in density-dependence drive dual offspring size strategies in fish

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HIGHLIGHTS

- A model of optimal offspring size in fish under juvenile density-dependent mortality is proposed.
- Two offspring size strategies emerge: as small as possible or proportional to the adult size.
- The specific strategy depends on the strength of predation mortality and reproductive efficiency.
- The strategies are consistent with fish reproduction and may apply more widely in marine animals.

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ABSTRACT

Offspring size reflects the optimal balance between female fecundity and allocation of energy to each offspring. Most fish, in particular teleost species, produce many small eggs, while others, notably elasmobranch species, have low fecundity and large offspring. No general explanation has yet been put forwards to explain these different strategies between species which occupy similar habitats. We approach the problem by (1) examining the differences between life history parameters of teleost fish and elasmobranchs and (2) an evolutionary model. We show that life history parameters characterising growth, mortality and reproductive output are almost similar between teleosts and elasmobranchs. We find that a model which accounts for density-dependence predicts dual offspring size strategies: either invariant with adult size or proportional to adult size. The model predicts that the invariant strategy is associated with an absence of density-dependence in early life whereas proportional offspring are subject to density-dependence throughout life. Parameterising the model using life history data regenerates the observed dual offspring size pattern. We conjecture that the life stage where density-dependent competition occurs is an important factor behind the observed difference in offspring size strategies.

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1. Introduction

The size of offspring is an important life history adaptation. Larger offspring typically have a competitive advantage over smaller individuals and are less exposed to predators, however, the more a parent invests per offspring the fewer offspring can be produced (Smith and Fretwell, 1974; Elgar, 1990; Berrigan, 1991; Blackburn, 1991; Baker, 2008). The evolutionarily optimal investment per offspring must therefore account for both fecundity and survival. Reviewing the patterns of offspring size across multiple marine phyla, Neuheimer et al. (2015) identified the presence of two dominant offspring size strategies which they termed `invariant' and `proportional'. The term invariant refers to offspring size being uncorrelated to adult size and should not be confused with other uses of the word, e.g. `life-history invariant'. The invariant strategy was found in *Cnidaria* (jelly fish), *Cephalopda* (ink fish) and teleost fish, where the size of the offspring is small and independent of adult size whereas proportional strategy was identified in crustaceans, *Ctenophora* (comb jellies), elasmobranchs and mammals where the adult to offspring weight ratio is approximately 100:1. Neuheimer et al. (2015) discussed possible evolutionary selection mechanisms but did not offer a causal explanation for the divergent strategies. Particularly noticeable is the discrepancy, Neuheimer et al. (2015) observed in fish, here broadly understood as teleosts (bony fish) and elasmobranchs (cartilaginous fish), which despite being of similar body plan and size and occupying similar habitats have fundamentally different offspring size strategies.

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Optimal offspring size is determined by the product of survival to maturity and lifetime adult fecundity, and thus directly related to how growth and mortality depend on body size. Generally optimisation models of offspring survival predict the ideal trade-off between offspring size and numbers to be the body size where mortality equals specific growth (Taylor and Williams, 1984; Sargent et al., 1987; Kiflawi, 2006). Therefore, if a newborn is able to grow quickly and thus escape the earliest and most vulnerable stage, small size and high fecundity may be the most advantageous option (Fenchel and Christiansen, 1979). The link between growth and mortality has been the subject of several models, often leading to dichotomous predictions such that offspring size should either be as large as possible or as small as possible. For example, different assumptions regarding the duration and mortality of larval non-feeding and feeding stages, and the cost-benefit trade-off with respect to parental care may lead to prediction of either smaller or larger offspring size (e.g. Vance, 1973a, b; Shine, 1978, 1989). Conversely, assuming that growth and mortality follow metabolic scaling rules, i.e. that growth rate is proportional to w^n where w is body weight, and mortality is proportional to w^{n-1}, Thygesen et al. (2005) predicted that the optimal offspring size in fish should be as small as possible. On the other hand, if conditions are less favourable and early growth is slower or mortality higher, small offspring may be disproportionally affected, and the optimal size increases (Jørgensen et al., 2011). Predictions from such optimisation models typically arrive at a specific optimal size, dependant on the values of other model parameters, but they are unable to explain why offspring size should depend on adult size and therefore why offspring size is proportional to adult size across so many marine phyla.

Optimisation models often assume that growth and mortality rates are fixed. However, field observations have suggested that juvenile survival is affected by population density (Myers and Cadigan, 1993; Johnson, 2006). For teleost fish, density-dependence appears to be influenced by age (Hixon and Jones, 2005), and to be strongest post-settlement (Ford and Swearer, 2013), suggesting that older juveniles are more affected than younger. Specifically, density-dependent mortality may arise as a consequence of competition over food (Herczeg et al., 2009) or availability of refuges (Ford and Swearer, 2013). Models which incorporate density-dependence as a dynamic effect arising from juvenile abundance and emphasise the importance of competitive ability have successfully been used to predict variable progeny size among plants (Rees and Westoby, 1997; Rees and Venable, 2007) and mammals (Falster et al., 2008). In particular, it has been shown that density-dependent competition among non-siblings can increase the optimal offspring size (Kindsvater et al., 2014), to the point where offspring size may scale with adult size (Falster et al., 2008).

We focus on teleost and elasmobranch fish as characteristic examples of the two different offspring size strategies identified by Neuheimer et al. (2015). Our objective with this paper is two-fold: first, we try to discover if the identified strategies are associated with any other life history patterns and second, we build a model to explore to what extent incorporating density-dependence into the model can explain the observed patterns. As in Neuheimer et al. (2015), we focus on marine and brackish-water species, even though we recognise the diversity of species, especially viviparous teleosts, that are found in freshwater. We also exclude species with parental care (e.g. Syngnathids, gobies, sticklebacks, etc.) to avoid complicating the model. We begin by looking for systematic differences in the life history parameters of each group, as well as how the reproductive strategies in terms of oviparity and viviparity link to offspring size strategies. We then build a model which combines the assumption of density-dependent mortality from Falster et al. (2008) with the life history models of fish based on size-dependent growth and mortality (Beyer, 1989; Andersen and Beyer, 2006; Jørgensen et al., 2011), and analyse the predictions of optimal offspring size.

2. Life history data

2.1. Data collection

Data on length at birth or hatch (L_0), length at maturation (L_m), asymptotic length (L_∞), von Bertalanffy growth parameter (K), adult natural mortality (M) and predicted fecundity at maturation, as well as species-specific length-weight conversion parameters ($w = \alpha L^\beta$) were collected for a large set of fish species (for length at hatch/birth analysis, $n=136$, for life history analysis $n=33$; data tabulated in Olsson). To calculate annual reproductive output at maturation (R_m), L_0 was converted to weight (w_0) and multiplied by fecundity at maturation. The species were classified according to the two offspring strategies identified by Neuheimer et al. (2015) ("invariant" and "proportional") by plotting L_0 against L_m, and the strategies were analysed by phylogeny (elasmobranch and teleost) and reproductive mode (oviparous and viviparous). We used analysis of covariance to test for differences in the slopes and intercepts for the relative size at maturation (L_m vs. L_∞), the mortality-growth ratio (M vs. K) and the annual reproductive output (R_m vs. w_m). We applied ordinary least square regressions to estimate the degree to which predictor variable explained the dependent variable. When the logarithm of a data point was used, base 10 was chosen for ease of interpretation and in accordance with the convention established in earlier studies.

2.2. Results

Plotting length at birth/hatch against length at maturity demonstrates the existence of two distinct strategies: offspring size that is either proportional to or invariant of the adult size (Fig. 1). The proportional strategy covers all elasmobranch species, both oviparous and viviparous, but also some viviparous teleosts, predominantly brackish-water species such as blennioids (Clinidae). The offspring length in viviparous species was slightly longer than oviparous species, though the actual offspring weight may be similar. Length at maturation explained 90% of the variance. The invariant strategy is only followed by teleosts, both oviparous and viviparous (represented by rockfish, genus *Sebastes*). The difference in strategy is therefore neither explained by phylogeny nor by ovi-/viviparity.

Life history data from species with either proportional or invariant strategy was compared (Fig. 2). Because no life history data was available for any of the proportional viviparous teleosts, only the difference between elasmobranchs and invariant teleosts could be examined. The relative length at maturity (L_m vs. L_∞) did not differ between proportional and invariant species, either with respect to slope ($p=0.19$) or intercept ($p=0.89$). As expected the fit was good ($r^2=0.95$). The $\log_{10}(M)/\log_{10}(K)$ ratio was slightly lower for proportional species though this was barely significant ($p=0.049$) and the regression fit was relatively poor ($r^2=0.36$). There was also no difference in annual reproductive output (R_m vs. w_m), either with respect to slope ($p=0.79$) or intercept ($p=0.18$). Weight at maturity explained 80% of the variance in reproductive output. Apart from a slightly higher mortality or lower growth rate of invariant compared to proportional species, there is no systematic difference in life history parameters.

3. Evolutionary model

We build an evolutionary model to examine how optimal offspring size can differ for species with similar adult size. Inspired by the model by Falster et al. (2008) we divide life into three distinct stages. In the first early life stage, hatchlings are exposed to density-independent predation. The second, juvenile stage commences when the hatchlings have reached a transition size w_s. At this point,

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