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# Complex offspring size effects: variations across life stages and between species

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## Abstract

Classical optimality models of offspring size and number assume a monotonically increasing relationship between offspring size and performance. In aquatic organisms with complex life cycles, the size–performance function is particularly hard to grasp because measures of performance are varied and their relationships with size may not be consistent throughout early ontogeny. Here, we examine size effects in premetamorphic (larval) and postmetamorphic (juvenile) stages of brooding marine animals and show that they vary contextually in strength and direction during ontogeny and among species. Larger offspring of the sea anemone *Urticina felina* generally outperformed small siblings at the larval stage (i.e., greater settlement and survival rates under suboptimal conditions). However, results differed when analyses were conducted at the intrabrood versus across-brood levels, suggesting that the relationship between larval size and performance is mediated by parentage. At the juvenile stage (15 months), small offspring were less susceptible than large ones to predation by subadult nudibranchs and both sizes performed similarly when facing adult nudibranchs. In a sympatric species with a different life history (*Aulactinia stella*), all juveniles suffered similar predation rates by subadult nudibranchs, but smaller juveniles performed better (lower mortalities) when facing adult nudibranchs. Size differences in premetamorphic performance of *U. felina* were linked to total lipid contents of larvae, whereas size-specific predation of juvenile stages followed the general predictions of the optimal foraging strategy. These findings emphasize the challenge in gathering empirical support for a positive monotonic size–performance function in taxa that exhibit complex life cycles, which are dominant in the sea.

## Introduction

A key principle of life-history theory is the occurrence of a trade-off between the number and size of offspring produced (Smith and Fretwell 1974; Stearns 1992). This trade-off is driven by the balance between energy spent on individual offspring and parental fitness (Smith and Fretwell 1974), with two important underlying assumptions: (1) a negative relationship between offspring number and energy invested per offspring and (2) a positive relationship between investment per offspring and offspring performance (quality). Both assumptions have been explored from numerous angles, in countless taxa and environments, with variable outcomes. In aquatic systems, some studies have determined that offspring (egg) size reflects parental investment (Quattro and Weeks 1991; Jaeckle 1995) and the amount of reserves available for early growth, while others have shown that energetic content and egg size are not always directly related (Moran et al. 2013). Contrary to terrestrial models such as insects and birds (Fox and Czesak 2000; Krist 2011), support for the assumption that larger offspring perform better has been inconsistent in aquatic models (Sogard 1997; Moran 1999; Marshall et al. 2003; Dziminski and Roberts 2006; Dibattista et al. 2007). It has been proposed that the relationship between offspring size and performance may not always be monotonic (Hendry et al. 2001).