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Upwelling affects food availability, impacting the morphological and molecular conditions of the herviborous limpet *Fissurella crassa* (Mollusca: Archeogastropoda)

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Oceanographical processes, such as upwelling, induce variations in nutrient availability in marine ecosystems, and evidence indicates that nutrient input can strongly influence the physiological activities, structure, and dynamics of marine communities. Intertidal organisms have long been considered ideal study units in which to quantify the relationship of physical variations and differential energy allocations in specimens that undergo environmental variations, such as observed with nutrient availability. In habitats with differential nutrient input (upwelling versus non-upwelling), both food availability (algae abundance) and seasonal gonadal and foot weight variations were determined in the keyhole limpet Fissurella crassa. *Gonadal weight is used as a measure of reproduction allocation whereas foot weight is an indirect indicator of energy allocation towards survival. RNA:DNA ratio in limpets was used as an indicator of biosynthetic capability. Our results indicate that, in general, algae abundance, muscular foot weight, and gonadal weight were higher in upwelling sites during all seasons studied. The same result was found for RNA:DNA ratios. Energetic allocation in animals that inhabit intertidal upwelling habitats supported a constant allocation towards reproduction and soft tissues. In contrast, animals that inhabit non-upwelling habitats showed important energetic restrictions associated with higher water temperature and lower food availability. Our results clearly show that in the keyhole limpet* F. crassa *food availability is a more important determinant of an individual's condition than a physical variation such as environment temperature.*

Keywords: RNA:DNA ratio, life histories, food availability, keyhole limpet, upwelling

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INTRODUCTION

Oceanographical processes such as upwelling induce variability in nutrient availability in marine ecosystems, and evidence indicates that nutrient input can strongly influence the structure and dynamics of marine communities (Menge *et al.*, 2003).

At a local scale, biological interactions, such as competition and predation, are determinants of the intertidal communities' functioning (Paine, 1966; Dayton, 1971; Menge, 1976; Lubchenco, 1978). However, scarce evidence exists about how the physiological condition and performance of consumers is affected by environmental variations (e.g. upwelling versus non-upwelling) and the assemblage of prey. Understanding the variability in the physiological performance of consumers in nature is of great interest, given the important role that consumers play in the structure of intertidal communities (Paine, 1966; Dayton, 1971; Menge, 1976; Lubchenco, 1978; Menge *et al.,* 2002).

The upwelling phenomenon affects many physiological activities at different trophic levels (Menge *et al.,* 2004; Nielsen & Navarrete, 2004; Wieters, 2005; Thiel *et al.,* 2007). Evidence of the ecological impact of upwelling indicates that invertebrates and algae grow faster and cover far more of the rocky intertidal surface in upwelling than in non-upwelling habitats (Menge *et al.,* 2003; Palumbi, 2003). Moreover, biological interactions are modulated by upwelling, and these responses are associated with modifications on all biological levels, from molecular (i.e. biosynthetic capability) to population and community processes (i.e. growth rate and reproductive aggregations) (Menge *et al.,* 2003; Palumbi, 2003; Wieters, 2005; Pulgar *et al.,* 2011). All

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