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How picky can you be? Temporal variations in trophic niches of co-occurring suspension-feeding species

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ABSTRACT

Suspension-feeders largely dominate faunal communities on rocky shores and compete for food using different feeding strategies. We used stable isotopes to assess the individual specialization within common suspension-feeder populations and to evaluate both inter-specific and intra-specific differences in food source exploitation. Trophic niches were characterized by metrics calculated in a space formed by mixing model outputs. Honeycomb worms (*Sabellaria alveolata*), blue mussels (*Mytilus edulis*) and barnacles (*Chthamalus montagui*), as well as three organic matter sources (benthic microalgae, phytoplankton and green macroalgae) were surveyed over a year using stable isotopic compositions ($\delta^{13}C$, $\delta^{15}N$). Adult specimens from each species were analyzed separately. Results showed persistent differences in $\delta^{13}C$ and $\delta^{15}N$ signatures between consumers, suggesting a possible limitation in inter-specific competition among co-occurring suspension-feeders, yet receiving the same food mixture during high tide. The width of the trophic niche was estimated for each species by transforming the isotopic space defined in a δ-space ($\delta^{13}C$ vs. $\delta^{15}N$) into a p-space defined by the proportions of food sources in a ternary plot. For each species, several metrics were calculated to estimate the diversity of individual diets of species. Species able to retain small particles and selectively sort particle based on their quality showed higher trophic diversity within the population but a smaller temporal variation in trophic niche.

1. Introduction

Suspension-feeders comprise the majority of sessile organisms in rocky intertidal marine habitats (Little et al., 2009). Large colonies of ascidians, tubiculous polychaetes or bivalves build biogenic structures adhering to rocks and create new substrata for other numerous species to settle and develop (Holt et al., 1998; Dubois et al., 2002; O'Connor and Crowe, 2007). Both intra- and inter-specific competition are important processes that have a strong influence on the structure and functioning of rocky intertidal communities (Connell, 1961; Firth et al., 2009; Firth and Crowe, 2010). Along with competition for space, grazing impacts of organisms on macroalgae canopy-forming species is one of the most studied mechanisms (e.g. Hawkins and Hartnoll, 1983; Moore et al., 2007) but far less is known about how suspension-feeders compete for food sources. It is commonly assumed that they depend primarily upon suspended particles (i.e. phytoplankton) filtered from the water column and that they ultimately all compete for the same food mixture brought by tides and wave action. However, most of the suspension-feeders exhibit different suspension-feeding mechanisms to screen, collect and transport particles from the water column (Riisgård and Larsen, 2000, 2010). Those mechanisms have been mechanistically well-studied (e.g. LaBarbera, 1984) but their consequences in food partitioning and width of the trophic niche of suspension-feeding species remain to be investigated. There is evidence to suggest that suspension-feeders select their diet based on the size of the food particles (e.g. Ward and Shumway, 2004) but nature and quality of the food are also potentially key features in particle selection mechanisms.

Dubois et al. (2007a, 2007b) used stable isotopes to detect small-scale changes within co-occurring trophic niches of suspension-feeding species. They showed significant spatial changes in $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures in four taxonomic groups of suspension-feeders (ascidians, mollusks, polychaetes and crustaceans). Similarly, Richoux et al. (2014) investigated spatial and temporal variation in isotopic compositions of common suspension-feeders in two different estuarine regions. Those studies highlighted that food source mixtures could vary at small scales (100–1000 m), and pointed out that feeding mechanisms could partly explain observed inter-specific differences, but disregarded inter-individual differences in pooling organisms into one sample. For example, Richoux et al. (2014) compared one mussel, ten barnacles and five polychaete individuals at each sampling site.

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Table 1
Diversity in feeding mechanisms involving capture, transport, sieving and sorting particles from the water column. Note that the three biological models of this study exemplify a broader range of taxonomic groups.

Biological model	Honeycom worms *Sabellaria alveolata*	Barnacles *Chthamalus montagui*	Blue mussels *Mytilus edulis*
Class	Polychaeta	Crustacea	Bivalvia
Main collecting structures	Numerous tentacular filaments	Three pairs of cirri (12 cirral branches)	Gills
Protection of feeding organs (while active)	Exposed (soft structure)	Exposed (with chitin exosqueleton)	Protected in calcareous shells
Feeding water current	Active groups of latero-frontal cilia	Passive	Complex set of active cilia
Particle transfers	Grooves and cilia	Directly from cirri to the mouth	Grooves and cilia
Mucus secretion (MPS = mucopolysaccharides)	Yes (high viscosity MPS)	None	Yes (high and low viscosity MPS)
Sorting organs	Tentacular palps	None	Palps
Selection capacity	Low	None	Strong
Retention efficiency (100%)	Ca. 6–8 μm	Ca. 20 μm	Ca. 2–3 μm
Main taxonomic groups with similar mechanisms	Feather duster Sabellidae and calcareous Serpulidae worms	Acorn barnacles and many amphipod and hermit crab species	Most bivalves and ascidians (to a large extend)
Main references	Dubois et al. (2005) and Riisgård and Larsen (2010)	Pullen and LaBarbera (1991) and Riisgård and Larsen (2000)	Jorgensen (1996) and Riisgård et al. (1996)

The aim of this study is hence to use individual isotopic compositions and focus on syntopic suspension-feeding species to investigate both inter- and intra-specific differences in trophic niches of species colonizing the same space and receiving the exact same food mixture from the water column. Using isotopic tools, this study aims at discussing the seasonal changes in species' and individuals' diets as well as providing tools to estimate species trophic niche width and inter-specific competition.

Barnacles and mussels are often the dominant suspension-feeders on intertidal rocky shores (Little et al., 2009). They both colonize large areas and often compete for space on exposed shore. On Atlantic coasts of Europe (Scotland to Portugal), the reef-building honeycomb-worm *Sabellaria alveolata* (Polychaeta: Sabellariidae) is a very common tubiculous gregarious species creating bioconstructions (a.k.a. veneers) adhering to rock and competing for space with barnacles and mussels (Dubois et al., 2002). We choose those three species as biological models showing evolutionary differences in their feeding organs and in their particle capture mechanisms (Riisgård and Larsen, 2000, 2010). Blue mussels *Mytilus edulis* (Bivalvia: Mytilidae) generate a current with beating latero-frontal cilia situated on the gills used to sieve and collect particles (Riisgård et al., 2000). They are capable of complex pre-ingestive selection using their labial palps (Beninger et al., 1995). Barnacles *Chthamalus montagui* (Crustacea: Chthamalidae) and honeycomb-worms *S. alveolata* use exposed appendages covered by setae or cilia, respectively, but in both cases water is not forced through a filter (gills) but through a mesh created by a complex set of filtering structures for capturing and directing particles to the mouth. Barnacles have articulated appendages (fringed with setae or cirri) to comb particles from the water column (Pullen and LaBarbera, 1991) while honeycomb worms exhibits a much more complex set of feeding organs, including numerous soft tentacular filaments with latero-frontal cilia extended in the water column (Dubois et al., 2005). In that case, particles are collected and transported to the mouth using small cilia where palps and labial organs play a role in particle selection (Dubois et al., 2005, 2006; Riisgård and Nielsen, 2006). In barnacles, the selection process is very limited as the cirral fan is composed of several pairs of cirri, with some only dedicated to cleaning activity (Anderson, 1994). These three species were used as a proxy of the variety of feeding structures and strategies to catch suspended particles from the water column and represent common biological models found in the suspension-feeding community of rocky shores (Table 1). Adaptation of suspension-feeders to fluid moving environments was approached from a physical and energetic point of view, revealing low level of energy in foraging for food and high energy transfer between pelagic and benthic compartments (Rubenstein and Koehl, 1977; Gili and Coma, 1998; Riisgård et al., 2000). An understanding of suspension-feeders' role in rocky shore communities lacks a link between the potential plasticity of suspension-feeding mechanisms (Okamura, 1990) and the possible implications in terms of trophic niche variation and exploitation of food sources in marine communities. Using stable isotopes analyses, we are investigating individual diets and population trophic niches of common suspension-feeding. We specifically tested two main hypotheses. Firstly, we expect trophic niches of suspension-feeding species to be affected by individuals' capacity to catch, sort and select particles from the water column. A higher capacity for particle selection would lead to a higher variability in individuals' diet and potentially to a broader trophic niche. Secondly, we expect seasonal changes in organic matter inputs to differentially affect suspension-feeding species diets. Species with a higher capacity to select particles would have a more consistent diet, targeting optimal food sources, irrespective of variations in proportions of food sources.

2. Materials and methods

2.1. Sampling site

An exposed rocky shore was selected in the bay of Douarnenez (Brittany, France). As in many embayments on European coastlines, this bay is influenced by both marine and terrestrial inputs: the bay opens widely toward the west, receiving direct offshore oceanic inputs. Even though freshwater inputs are limited, anthropogenic influences such as nitrogen inputs come from several streams located on the southern and eastern edges of the bay. Simulations of residual currents in this bay indicate low residual circulation, hence promoting eutrophication and seasonal development of green macroalgae (*Ulva* spp.), known as green tides (Merceron et al., 2007).