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Feeding strategies of co-occurring suspension feeders in an oligotrophic environment

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ABSTRACT

Suspension-feeders predominate in the vast majority of the coastal marine benthic ecosystems, with several species co-occurring at low spatial scale. Understanding how these species cope with competition for trophic resources has been the core of numerous studies, mostly in coastal shallow systems where food supplies are diverse and abundant. Oligotrophic systems have received less attention. The aim of the present study was thus to investigate the trophic relationships established between 9 suspension feeders collected in an oligotrophic zone (Bay of Marseille, French Mediterranean). Species displayed similar isotopic ratios, consistently with the use of one main source, identified as nanophytoplankton and diazotrophic bacteria as the $\delta^{15}N$ values were low, in contrast to interspecific differences generally observed. The seasonal variations of the isotopic ratios and isotopic niche indices were explained by differential sorting abilities, higher for bivalves than for ascidians and the polychaete *Chaetopterus variopedatus*. The present results demonstrate that resource availability in oligotrophic systems is a major driver of trophic competition. It precludes a general conclusion about suspension feeders trophic patterns drawn exclusively from highly productive systems, and stresses the need for an extensive assessment of those patterns in a vast range of ecosystems.

1. Introduction

Interspecific competition is one of the major mechanisms driving biological functioning, at both individual and community level (Connell, 1961; Schoener, 1974). In marine benthic communities, space has long being considered as the dominant limiting resource but food resource limitation by co-occurring species is also recognized as a predominant driver of individual and community functioning (Buss and Jackson, 1981; Côté et al., 1994; Dubois and Colombo, 2014; Svensson and Marshall, 2014). Resource partitioning and trophic plasticity are commonly considered as strategies established by co-occurring organisms to limit the adverse effects of trophic competition (Gutt, 2006; Riera, 2008; Kang et al., 2009; Lefebvre et al., 2009). Suspension-feeders predominate in most benthic ecosystems, where they are considered as engineer species, since they create new biogenic habitats and alter the tridimensional structure of the community (Gili and Coma, 1998; Ribes and Coma, 2005). They also drive bentho-pelagic coupling, as their strong filtering abilities alter the organic matter (hereafter OM) fluxes and provide trophic subsidies for other benthic consumers, directly or through OM pools (Gili and Coma, 1998; Dubois et al., 2007b; Cheung et al., 2010; Bracken et al., 2012).

Most benthic suspension-feeder communities are composed of several co-occurring species which have to cope with competition at a small spatial scale (Kang et al., 2009; Yakovis et al., 2012; Richoux and Ndhlovu, 2014; Dubois and Colombo, 2014). Understanding how trophic competition drives interspecific relationships and OM fluxes provided case studies to document interspecific trophic competition and resource sharing mechanisms.

Suspension-feeders are of major commercial interest and are cultivated worldwide. Documenting how the biomass production of cultivated species might be affected by trophic competition with wild or invasive species has thus been widely investigated (Lesser et al., 1992; De Montaudoin et al., 1999; Riera et al., 2002; Decottignies et al., 2007; Dubois et al., 2007b, 2007c; Riera, 2007; Xu and Yang, 2007; Kang et al., 2009; Lefebvre et al., 2009; Lacoste et al., in press). Patterns in natural uncultivated systems received less attention until recently (Bode et al., 2006; Schaal et al., 2010; Colombo et al., 2013; Dubois and Colombo, 2014; Richoux et al., 2014). In both cases, studies have been conducted in coastal shallow eutrophic ecosystems, where trophic subsidies available to suspension feeders are diverse and abundant. Stable isotope analyses were powerful tools to discriminate the relative contribution of these sources. The premise of this technique is that the isotopic ratios of a consumer are dependent upon the ratios of its diet with a trophic enrichment factor (hereafter TEF) between consumer and diet. Since C and N isotopic ratios differ between OM sources, measuring isotopic ratios of suspension-feeders enables identification

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of the major contributing source. These studies demonstrated that, although receiving the same mixture of suspended matter, co-occurring suspension feeders are able to be largely plastic in their diet and to partition the food resources to limit competition (Coma et al., 2001; Riera et al., 2002; Riera, 2008; Marín Leal et al., 2008; Lefebvre et al., 2009; Dubois and Colombo, 2014; Richoux and Ndhlovu, 2014; Richoux et al., 2014). Size and nutritional quality of the particles appeared to be the main factors explaining the difference in resource use, since species differ in their filtration and retention mechanisms and in their ability to sort and select particles before ingestion and then to digest them. In bivalve species, laterofrontal cirri are key organs located in the gills. They beat alternatively to generate a current and to collect particles, with 100% retention efficiency for particles up to 4 μm. In addition, labial palps can sort and select particles, and reject particles of low nutritional interest in pseudo feces. Some species, such as *Mimachlamys varia*, lack such cirri, and possess only prolaterofrontal cirri, causing a less efficient retention of particles (Dubois and Colombo, 2014; Riisgård and Larsen, 2010; Ward and Shumway, 2004). The annelid *Chaetopterus variopedatus* and the ascidians use a similar system, based on the active pumping of water by muscular pistons in *C. variopedatus* or through the inhalant siphon in ascidians, and the retention of particles on a mucous net, constantly ingested and renewed. This system is efficient to retain 100% of particles down to 0.5 to 1 μm for *C. variopedatus* and to 1–3 μm for ascidians (Flood and Fiala-Médioni, 1982; Jumars et al., 2015; Petersen, 2007; Riisgård and Larsen, 2010). Seasonal variation of the available food sources was also demonstrated to be a crucial factor, as suspension-feeders use the predominant component of the suspended OM (Coma et al., 2001; Lefebvre et al., 2009; Richoux and Ndhlovu, 2014). Nevertheless, since patterns in deep and oligotrophic environments are poorly documented (Ribes et al., 2003; Elias-Piera et al., 2013; Lesser and Slattery, 2015), it is rather difficult to provide generalized trends regarding the suspension-feeders' trophic mechanisms. The deployment in the bay of Marseille of the largest Mediterranean artificial reef system in 2007–2008 provided a major opportunity to assess the effect of oligotrophy on suspension-feeders trophic mechanisms. Artificial reefs are efficient scientific tools to question ecological hypotheses concerning suspension-feeders, since they provide a man-made ecosystem where there are few technical and ethical issues related to the sampling of natural communities (Miller, 2002) and they are mainly colonized by suspension-feeders (Rouanet et al., 2015). Thus, the aims of the present study were to assess the trophic relationships between co-occurring suspension-feeders and to answer the following questions. How does food scarcity in an oligotrophic system affect resource sharing? Are food-sorting mechanisms still applicable in this context? How do suspension-feeders cope with the seasonal variation of food resources?

2. Material and methods

In the bay of Marseille, artificial reefs were deployed in 6 triangular-shaped groups named “villages”. Sampling was carried out on two “metal basket” artificial reefs in the north (village V3, 30 m depth) and the south (village V6, 25 m depth) of the deployment zone, with V6 reef located close to the shore and to the mouth of the Huveaune River (Fig. 1). Metal basket reefs were large, high structures (6 m high, 187 m^3) of which the architectural complexity was increased by the addition of devices such as concrete cubes or oyster bags (i.e. bags filled with dead oyster shells deployed inside artificial reefs), creating shelter for small cryptic organisms. More details on the architectural structure of the bay of Marseille's artificial reefs can be found in previously published works (Charbonnel et al., 2011; Rouanet et al., 2015). The bay of Marseille is considered oligotrophic, with chlorophyll-*a* concentrations always lower than 0.5 μg L^{-1} during sampling periods (SOMLIT data, http://somlit-db.epoc.u-bordeaux1.fr/bdd.php?serie=ST&sm=6, P. Raimbault, pers. Comm.; Cresson et al., 2012). In summer and winter 2012, all suspension-feeding species were collected by scuba diving, manually scraping organisms settled on artificial reef structures or sampling the oyster bag fauna. Back in the laboratory, all organisms were

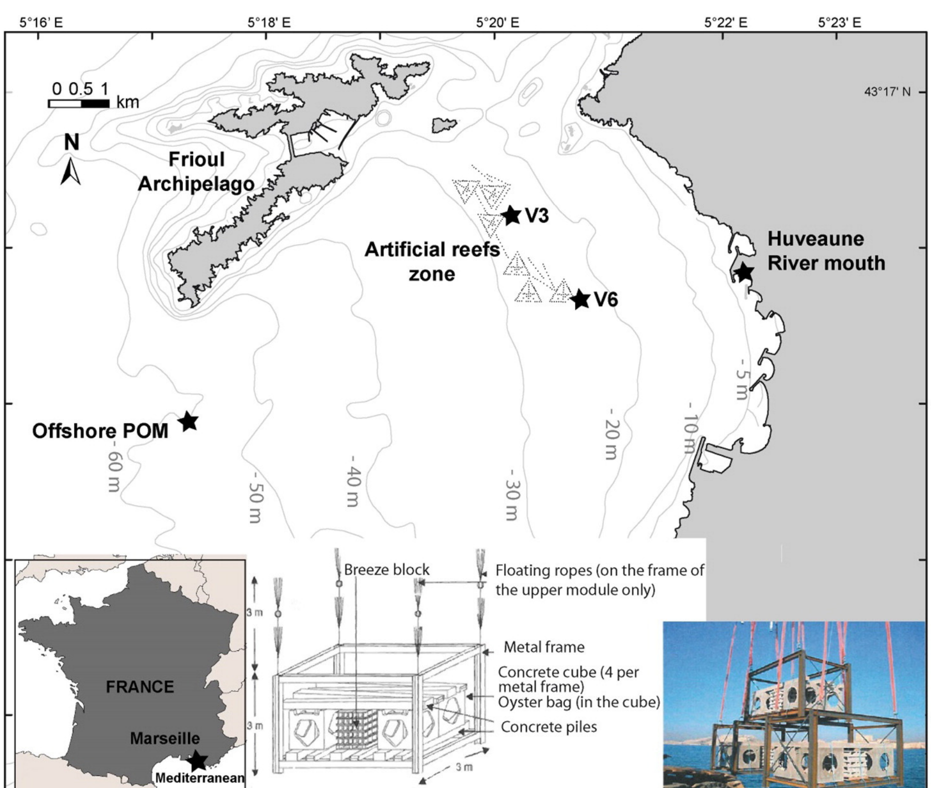

Fig. 1. Map of the sampling zone, with sampling sites identified with black stars. Bottom pictures represent a schematic view of the unitary cubic module and a picture of the whole “metal basket” artificial reef before its deployment (modified from Charbonnel et al., 2011).