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Trophic interactions between two introduced suspension-feeders, *Crepidula fornicata* and *Crassostrea gigas*, are influenced by seasonal effects and qualitative selection capacity

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Abstract

The effects of season and qualitative selection capacity on trophic relationships between two sympatric invasive suspension-feeders, *Crepidula fornicata* and *Crassostrea gigas*, were investigated in Bourgneuf Bay (France) from January 2003 to June 2004. Carbon and nitrogen stable isotopic deviations, $\delta^{13}C$ and $\delta^{15}N$, of common Atlantic slippersnails and Pacific oysters were analysed relative to isotopic composition and availability of end-members.

Slippersnail deviations were less variable over the sampling period compared with those of oysters. Significant differences between $\delta^{13}C$ and $\delta^{15}N$ of *C. fornicata* and *C. gigas* were found from winter to early summer, and linked to major isotopic changes in oysters. We identified three distinct seasonal periods: January to March when oysters were ^{15}N-enriched compared to slippersnails and to themselves at other times of the year, April to June–July when oysters showed a ^{15}N-depletion and a more marked ^{13}C-depletion compared to slippersnails and to themselves at other times of the year, and July–August to December when both species presented similar carbon and nitrogen deviations. Species-specific differences in qualitative selection capability may explain these seasonal differences in isotopic deviations. Whereas the isotopic composition of the indiscriminate suspension-feeding slippersnails reflects the composition of the seston throughout the year, the oyster is capable of qualitative selection. The oyster isotopic compositions are consistent with a facultative activation of selection mechanisms under conditions of qualitative and quantitative food limitation, notably the preferential ingestion and assimilation of the dominant organic source in the suspended pool.

We conclude that *C. fornicata* and *C. gigas* are trophic competitors only in winter and spring at this site, where detrital end-members are major POM components. These results underscore (1) the importance of long-term (annual) studies in the evaluation of potential trophic competition, and (2) the necessity to include the qualitative selection capacities of suspension-feeders in future interpretations of trophic relationships in marine coastal ecosystems.

Keywords: Competition; *Crassostrea gigas*; *Crepidula fornicata*; Diet; Introduced species

1. Introduction

Human activity has increasingly promoted dispersal and colonization of exogenous marine organisms. When

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these species become invasive, they change the structure and function of surrounding communities and ecosystems (Carlton, 1989; Grosholz, 2002; Occhipinti-Ambrogi and Savini, 2003). Invaders may also become pest species for aquaculture, as trophic competitors, predators or disease vectors (Ruesink et al., 2005).

The common Atlantic slippersnail *Crepidula fornicata* and the now-ubiquitous Pacific oyster *Crassostrea gigas* are two sympatric invaders of human-impacted European littoral habitats, where their proliferation is encouraged directly or indirectly by aquaculture activities (Blanchard, 1997; Ruesink et al., 2005). The two species have not only attained considerable biomasses from Scandinavian to Mediterranean countries (de Montaudouin et al., 2001; Thieltges et al., 2003; Ruesink et al., 2005; Cognie et al., 2006), but have also generated ecological consequences such as alterations of benthic habitats and communities, or food chain changes (e.g. Ehrhold et al., 1998; Ruesink et al., 2005; Thieltges, 2005; Wonham et al., 2005). Competitive dominance of *C. fornicata* has long been suspected (Murie, 1911; Orton, 1912a; Korringa, 1951; Cole and Hancock, 1956), generating increasing concern regarding the eventual negative effect of slippersnails on native or introduced oyster productions (Trochon, 1954; Marteil, 1963; Deslous-Paoli, 1985; Deslous-Paoli and Héral, 1986; Crepel, 1994; Blanchard, 1997; Sauriau et al., 1998; de Montaudouin et al., 1999; Riera et al., 2002).

The impact of suspension-feeders on the seston assemblage will depend not only upon their quantitative filtration ability, but also on their capacity to ingest or reject particles selectively (see review by Ward and Shumway, 2004). Selection may be based on non-nutritive criteria such as size, density and shape (hence determining the types of particles physically able to be processed by the feeding structures — Bougrier et al., 1997; Defossez and Hawkins, 1997). Selection may also be based on the biochemical characteristics of particles; being potentially related to nutritive quality, such selection is termed qualitative (Targett and Ward, 1991; MacDonald and Ward, 1994; Beninger et al., 2004). Particle selection capability will therefore be an important determinant of resource partitioning among different suspension-feeders. Although *C. fornicata* and *C. gigas* access the same pools of suspended particulate organic matter (Orton, 1912a,b; Walne, 1956; Deslous-Paoli, 1985), fundamental differences in their feeding characteristics may influence the degree of trophic competition. Indeed, *C. fornicata* presents lower clearance rates, but they retain particles over the same size range as *C. gigas*, with a marked superiority in particles <5 μm (Jørgensen et al., 1984; Méléder et al., 2001; Barillé et al., 2006; Sauriau et al., 2006). An essential difference exists between these two suspension-feeders, however, with respect to the qualitative selection of seston particles: *C. fornicata* is an indiscriminate suspension-

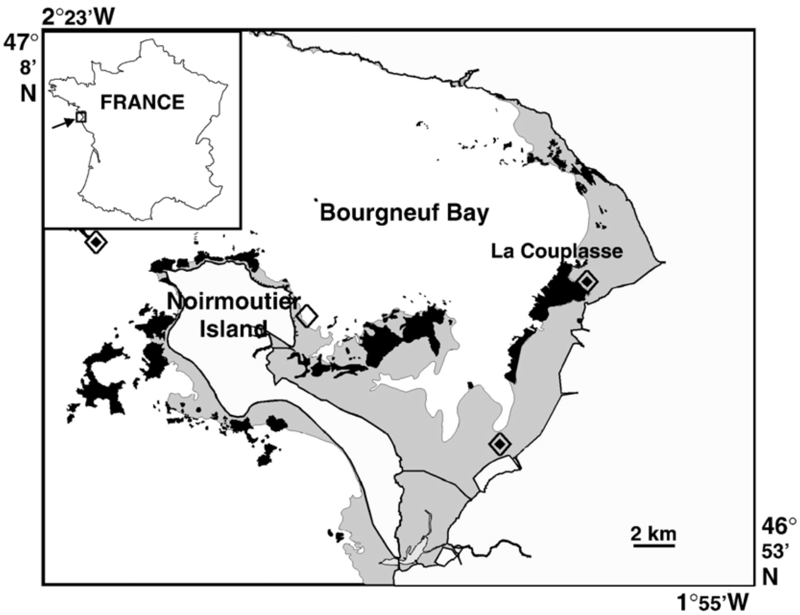

Fig. 1. Map of Bourgneuf Bay showing location of La Couplasse oyster farming site, source (◈) and REPHY (◇) sampling stations. Grey shading: intertidal area; black shading: rocky substrate.