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Seasonal dependence on seagrass detritus and trophic niche partitioning in four copepod eco-morphotypes

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ABSTRACT

Benthic copepods dominate meiofaunal communities from marine phytodetritus, both in terms of numerical abundance and species diversity. Nevertheless, ecological factors driving copepod co-existence and population dynamics are still largely unknown. Here, we aimed to explore feeding habits of four copepod species commonly found in Mediterranean seagrass detritus accumulations, representing distinct eco-morphotypes (planktonic, phytal, epibenthic and mesopsammic). Joint use of fatty acid and stable isotope trophic markers showed that co-occurring harpacticoid copepods have diversified diets. Contrary to what was expected, microphytobenthos does not serve as their main food source. Instead, we found evidence from both techniques that major food items include heterotrophic biomass, macro-epiphytes and, depending on eco-morphology and season, of seagrass detritus-derived organic matter. Isotopic niches suggested that eco-morphotypes showed resource segregation. This segregation varies temporally, and partial overlap occurs between niches of phytal and epibenthic eco-morphotypes in some seasons. Our results highlight that, contrary to what is often assumed for meiofaunal consumers, considerable trophic diversity exists among copepod assemblages. They also indicate that, through multiple non-exclusive possible mechanisms, copepods could constitute a major link between seagrass detritus and associated biomass and higher trophic levels (namely macroinvertebrates and juvenile fish).

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1. Introduction

Seagrass meadows are net autotrophic ecosystems and key components of carbon cycle in marine coastal areas (Champenois and Borges, 2012). An important proportion of seagrass and macroalgae productivity is exported as shed biomass, accumulating on the sea bottom to form habitats called 'exported macrophytodebris accumulations' (hereafter EMAs) (e.g. Vetter, 1995; Hyndes and Lavery, 2005; Lepoint et al., 2006; Boudouresque et al., 2016) and fuelling the detrital pool (Cebrian, 2002). The endemic and highly productive Neptune grass, *Posidonia oceanica* (L.) Delile, covers from 25 to 45.10³ km² and the meadows it forms represent one of the dominant ecosystems found in the coastal Mediterranean (Pasqualini et al., 1998). EMAs formed by *P. oceanica* dead leaves are ubiquitous features of shallow areas of the Mediterranean Sea (Boudouresque et al., 2016). These patches of necromass accumulation are heterogeneous in their composition, being variable in thickness, size, and persistence in the environment (i.e. from very ephemeral to year-along presence) (Boudouresque et al., 2016). Their

occurrence and persistence in the environment are determined by the local *P. oceanica* biomass cycle, by the local hydrodynamics and by the sea bottom morphology (Ricart et al., 2015).

Marine macrophytodebris is considered an important trophic subsidies for food webs in many marine, estuarine, salt marsh, or terrestrial systems, both in temperate and tropical areas (Bouillon and Connolly, 2009; Heck Jr et al., 2008), providing habitats for many organisms (Como et al., 2008; Duggins et al., 2016; Mancinelli and Rossi, 2002; Vetter, 1995). Nevertheless, most literature focuses on macro- and megafauna, and smaller animals (i.e. meiofauna, animals with a body size between 38 µm and 1 mm) have received comparatively little attention. Small crustaceans (i.e. harpacticoid copepods) are the dominant taxa of meiofauna colonizing EMAs and represent up to 10⁵ individuals per square meter (Mascart et al., 2015b). The copepod assemblages found in *P. oceanica* EMAs are diverse, and different morphotypes (sensu Noodt (1969)) can be found among the necromass. These morphotypes have different biological traits, behavioural patterns, and occupy different micro-habitats. Phytal (i.e. often flattened copepods, mobile but strongly associated to macrophyte substrate, often grasping dead or living plant) and epibenthic eco-morphotypes (i.e. free-living benthic copepods, less associated to a substrate, able to live on and often in sediment) are dominant, but truly planktonic (i.e. copepods living in the water column) and

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mesopsammic (i.e. copepods living inside sediment but sometimes able to live as epibenthic copepods) species are also encountered (Mascart et al., 2015b). Given those differences, it is likely that feeding habits, and therefore the role of these copepods in EMAs' food web functioning differs. In other environments, trophic niches of copepod species belonging to the same eco-morphotype can be different (Arroyo et al., 2006; Azovsky et al., 2005; Carman and Fry, 2002; Carman and Thistle, 1985; De Troch et al., 2006b; Pace and Carman, 1996; Steinarsdóttir et al., 2010). How resource partitioning determines co-existence of dominant eco-morphotypes in EMAs remains unknown.

Because of their short life cycle and high turnover rates, harpacticoid copepod communities respond rapidly to organic matter inputs, and their life cycles are closely coupled to these inputs (Danovaro et al., 2002). In addition, EMAs are seasonally pulse-sourced by dead seagrass leaves and the epiphytic community covering them (Mascart et al., 2015b; Remy et al., 2017). Therefore, food item availability fluctuates over time, and this could have consequences for copepod trophic ecology and food partitioning between the different copepod eco-morphotypes (Mascart et al., 2015b).

Stable isotope (SI) analyses of carbon and nitrogen allow identification and quantification of food sources that are assimilated into the tissues of consumers over time. Fatty acid (FA) profiling complements stable isotope analysis as a second biomarker, providing additional information on the feeding ecology of meiofauna (Cnudde et al., 2015; De Troch et al., 2012; Leduc et al., 2009), as several FAs can be used as markers for specific food sources (Dalsgaard et al., 2003; El-Sabaawi et al., 2009).

By combining stable isotope ratios and fatty acid profiles, we aimed to study the trophic ecology of four co-occurring species of copepods, representing four dominant eco-morphotypes of *Posidonia* litter meiofauna (Noodt, 1969): *Diosaccus tenuicornis* (phytal type, harpacticoid), *Tisbe furcata* (epibenthic type, harpacticoid), *Ectinosoma dentatum* (mesopsammic type, harpacticoid) and *Calanus arcuicornis* (water column type, calanoid) (Fig. 1). Specifically, we addressed 4 questions and put forward the following hypotheses.

1) What are the food sources sustaining copepod consumers in seagrass detritus accumulations? While copepods are typically regarding as depending mostly on microphytobenthos, we

hypothesized that their food items in EMAs are diverse because available food sources are diverse.

- 2) Do different copepod eco-morphotypes exhibit resource segregation? Despite the “black box” approach generally applied to meiofaunal consumers in ecological literature (i.e. meiofaunal consumers are considered ecologically redundant and feeding on the same items regardless of consumer species) (Danovaro et al., 2002), we hypothesized that the 4 species studied here can have different diets and occupy different niches, and that this could facilitate co-existence of these abundant consumers.
- 3) Does copepod trophic ecology vary seasonally? Given the high turnover of copepod populations, we expect their feeding habits in EMAs to change temporally as food availability and composition varies seasonally.
- 4) Do copepods feed on dead seagrass tissue? In saltmarsh ecosystems, copepods assimilate detritus-derived organic matter and, like macrofauna, depend on dead plant material not only as a shelter but also as a food source (Couch, 1989). Therefore, we expect that it is also the case in seagrass detritus accumulation. Using trophic markers, we aim to explicitly test that, and to propose mechanisms through which copepods could feed on and assimilate seagrass detritus.

2. Materials and methods

2.1. Study site and field sampling

A sandy patch close to a continuous *P. oceanica* seagrass meadow was located near the STARESO marine research station (University of Liège) in the Revellata Bay (Calvi Bay, Corsica, France, NW Mediterranean; 42°35'N, 8°43'E). Sampling of consumers and their potential food sources (macrophytodebris, epiphytes, drifted macroalgae and particulate organic matter) was carried out at a depth of 10 m on a seasonal basis. Four sampling events were conducted, each representing a season, namely winter (February 2012), spring (May 2012), summer (August 2011) and autumn (October 2011). 30 L plastic bags were used to hand-collect copepod consumers and food sources, as well as the seagrass detritus, with which they are associated. Subsequently, the collected material was kept alive in a 0.75 m³ aquarium with 38

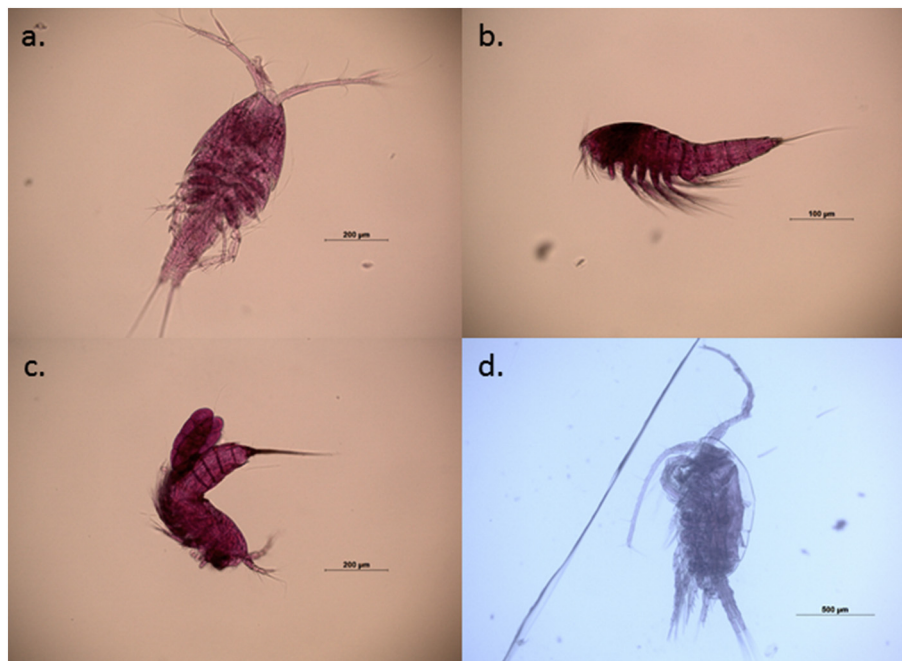


Fig. 1. Pictures of focal copepods: a. *Tisbe furcata*; b. *Ectinosoma dentatum*; c. *Diosaccus tenuicornis*; d. *Clausocalanus arcuicornis*.

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