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Trophic ecology in a Northern Brittany (Batz Island, France) kelp (*Laminaria digitata*) forest, as investigated through stable isotopes and chemical assays

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ABSTRACT

This study aimed at characterizing the relationships between the food web's structure and the nutritive value of basal food sources in a Northern Brittany (France) *Laminaria digitata* bed. Stable isotopes were used to identify the food sources consumed by benthic invertebrates, and the nutritive value of primary producers was assessed according to four descriptors (total organic matter, C/N ratio, proteins content, lipids content). Although the food web appeared to be based on a wide diversity of food sources, only Rhodophyta (red algae) and biofilms (epilithic and epiphytic) were heavily consumed by grazers. In contrast, Phaeophyta (brown algae), which are dominant in this habitat, have no specialized grazer (with the exception of *Helcion pellucidum*, specialized grazer of *Laminaria digitata*). This selective consumption may be related to the higher protein content and lower C/N ratio of Rhodophyta and biofilms, in comparison with Phaeophyta. Fresh brown algae are thus of poor nutritive value, but processes associated with their degradation are likely to improve this nutritive value, leading in the assimilation of detritus by filter-feeders, revealed by high $\delta^{13}C$ in these consumers. Our results thus suggest that the nutritive value of basal food sources may be an important factor involved in the structuration of kelp-associated food webs.

1. Introduction

Kelps form extensive beds around temperate and polar coasts in all the oceans of the world. Their importance for global biogeochemical cycles is recognised, since this kind of environment is considered to be one of the most productive of the world (Mann 1973). In European coastal areas, kelp beds are dominated by the genus *Laminaria*. In Brittany, kelp forests occur along rocky coasts from the mean low waters at spring tides to a depth of about 30 m (Arzel, 1998). The three-dimensional structure created by these algae forms in a large variety of microhabitats, resulting in a high algal and animal diversity characterizing these environments (Christie et al., 2003).

In spite of their ecological importance, few are known about the functioning of the food web associated to these habitats (but see Fredriksen, 2003). Particularly, the major trophic resources of consumers inhabiting kelp beds remain unclear yet. Indeed, although kelps represent an important potential food supply for consumers inhabiting these environments, most of kelp species are characterized by low nitrogen content and the presence in their tissues of herbivore-deterrent secondary metabolites (Duggins and Eckman, 1997; Norderhaug et al., 2003). These characteristics result in a low nutritive value of kelps, which prevents them to be intensively grazed, as previously observed for various grazers fed *Laminaria hyperborea* (Norderhaug et al., 2003). However, coevolution processes may result in an adaptation of these grazers to a low nutritive value food (Steinberg et al., 1995). In this way, there are several evidences of kelp consumption by various consumers such as sea urchins (Lawrence, 1975) or gastropods (Fredriksen, 2003; Norderhaug et al., 2003). Moreover, some studies have shown that kelps could be consumed through the detrital pathway by various consumers, such as amphipods (Norderhaug et al., 2003) or bivalves (Duggins and Eckman, 1997). Microbial processes occurring during the degradation of kelp-derived organic matter are responsible of an enrichment in nitrogen of the detritus (Norderhaug et al., 2003), which makes these detrital complexes readily available for several consumers. The role of kelps as a food supply for consumers inhabiting kelp forests is thus still not clear. In addition, these habitats host a large diversity of understory algae. In *L. digitata* beds, the dominant algae under the canopy-forming kelps are *Fucus serratus* and *Himanthalia elongata* for Phaeophyta, *Mastocarpus stellatus*, *Chondrus crispus* and *Corallina elongata* for Rhodophyta, as described by Castric-Fey et al. (1997). Other species, such as the Rhodophyta *Palmaria palmata*, may be seasonally important (G. Schaal, pers. obs.). These understory algae are also likely to be exploited by grazers inhabiting kelp forests, as reported by Fredriksen (2003). The relative importance of kelps and understory algae as a basis for the food web is unclear yet.

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Factors affecting the consumption of food sources in benthic invertebrates remain to date unclear. Several studies have investigated this issue through food choice laboratory experiments (Pavia et al., 1999; Cruz-Rivera and Hay, 2000; Karez et al., 2000). Although providing precious data on factors susceptible to affect herbivores' food choice, the conclusions of these studies appear sometime contradictory and difficult to extrapolate to natural conditions. For example, Pavia et al. (1999) found that the amphipod *Gammarus locusta* preferred to feed on *Ascophyllum nodosum* macroepiphytes rather than on the host, while Karez et al. (2000) found the contrary. Some studies suggested that herbivores consume preferentially the more nutritive food source (Cruz-Rivera and Hay, 2000), while others found that herbivores prefer to consume a temporally perennial food source rather than a more nutritive, but seasonal one (Paine and Vadas, 1969). Several mesograzers have been observed to choose low nutritive value seaweeds to avoid predation by omnivorous fishes (Hay et al., 1987). Finally, food choice experiment studies have contributed to a strong background in the knowledge of factors which affect herbivore's consumption of food sources. However, generalising results from laboratory experiments to processes occurring in the wild is not straightforward, and a more thorough understanding of the relative importance of these factors in the consumption of coexisting sources requires necessarily field approaches. In European kelp forests, the important diversity of potential food sources (macroalgae, epiphytic and epilithic biofilms, suspended particulate organic matter) associated to the diversity of consumers makes these issues challenging and relevant.

In this context, stable isotopes provide promising insights. This method provides a time-integrated measure of really ingested food, and is thus complementary with food choice experiments. Due to the low carbon isotope fractionation occurring from a food source to its consumer, $\delta^{13}C$ is often used to assess basal sources in food webs, while $\delta^{15}N$ is an indicator of trophic level and food webs length, due to the higher trophic fractionation occurring at each trophic transfer (Peterson, 1999). Numerous examples have highlighted that rocky shore's macroalgae were efficiently discriminated by their $\delta^{13}C$ and $\delta^{15}N$ (Fredriksen, 2003; Bode et al., 2006; Kang et al., 2008). Due to the possibility to clearly identify macroalgal food sources with stable isotopes, this method appears to be a powerful tool for the study of rocky shores' food webs.

The present study aimed thus at (1) describing the general features of the food web in a *L. digitata* forest (2) identifying the main herbivores and their food sources (3) assessing the nutritive value of the food sources potentially available for the consumers inhabiting this habitat and (4) linking the biochemical characteristics of primary producers to their utilisation in the food web.

2. Material and methods

2.1. Study site

Sampling was carried out in a granite boulder field of Western Batz Island (Brittany, France) (Fig. 1). Although the intertidal shore is mainly unvegetated, a dense *L. digitata* forest occurs from the mean low water spring tides. This site is characterized by a high hydrodynamism exposure, due to water motion and the intensity of tide currents along the northern coast of Brittany (Castel et al., 1997). The English Channel, where our sampling site is located, is a megatidal sea. The maximal tidal amplitude at Roscoff is higher than 9 m. Due to the absence of city close to this study site and the high hydrodynamic exposure, this site can be considered as totally preserved from anthropogenic perturbations.

2.2. Samples processing

Sampling was carried out during spring tides in October 2006 and May 2007. At each sampling date, the most representative food sources (i.e. algae, epiphytic and epilithic biofilms, suspended particulate organic matter (SPOM)) and the most abundant consumers were sampled by hand. In May 2007, detrital drifted macroalgae were also opportunistically sampled floating on the surface of the water at the study site. The water sample was carried

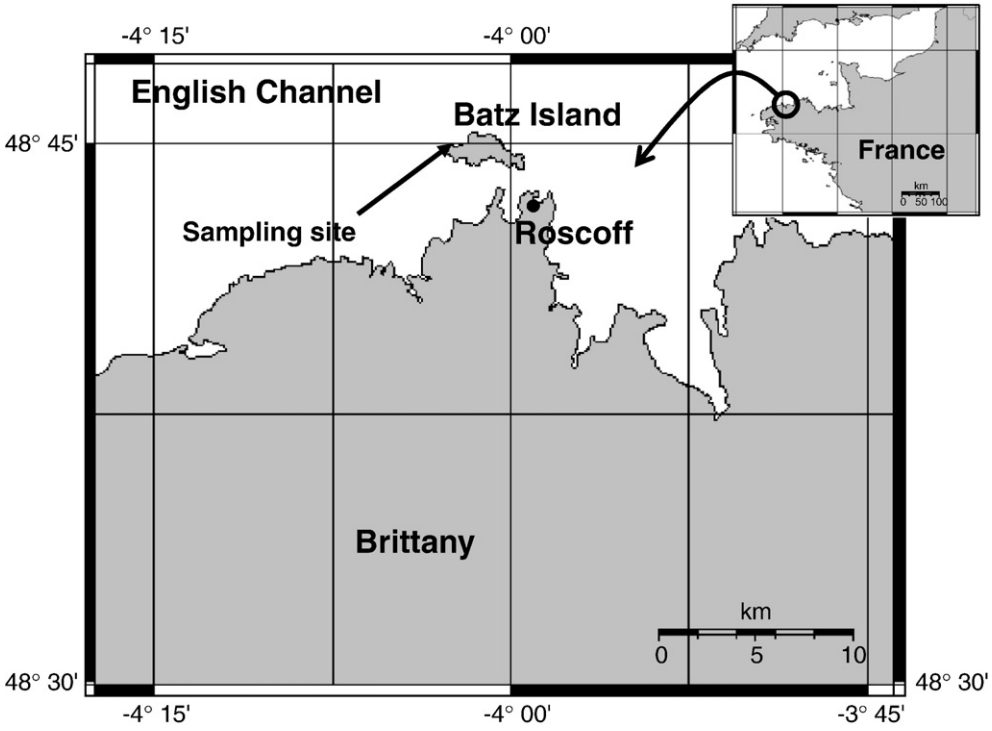

Fig. 1. Localization of the sampling site in the Eastern English Channel.