Journal of Experimental Marine Biology and Ecology 449 (2013) 51–56

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Complex plant–herbivore–predator interactions in a brackish water seaweed habitat

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ARTICLE INFO

Article history:
Received 7 June 2012
Received in revised form 17 August 2013
Accepted 19 August 2013
Available online 13 September 2013

Keywords:
Grazing
Growth
Habitat selection
Herbivory
Isopods
Macroalgae

ABSTRACT

Seaweeds are inhabited by small mobile invertebrates that use their hosts as habitat, food and protection against predators. Patterns of distribution and abundance may therefore reflect complex trade-offs between suitable space, nutritional requirements and refuge. We tested differences in abundance and density of isopods (*Idotea baltica*) in four different seaweed habitats (*Furcellaria*, *Fucus*, *Cladophora*, *Ulva*; Island of Bornholm, Baltic Sea) and experimentally assessed different ecological interactions between isopods and seaweeds. We found marked differences in abundance of isopods among seaweed habitats in the field, with a prevalence for form-functionally simple seaweeds. Patterns of isopod densities on seaweeds in the field resembled patterns of grazing and growth rates, but were opposite to habitat selection in laboratory experiments. Habitat selection resembled patterns of standing seaweed biomass and cover in the field. Laboratory experiments also showed that all seaweed habitats dramatically reduced fish predation on isopods regardless of seaweed identity. The strong affinity of isopods to seaweeds likely reflects predator avoidance whereas their selectivity between seaweeds could be due to grazing interactions and habitat availability. We therefore conclude that *in situ* patterns of isopod distribution and abundance, at least in part, reflect complex interactions between bottom-up (food type and availability) and top-down (predator refugia) forces.

1. Introduction

Small mobile invertebrates that live within and among the fronds of seaweeds (macroalgae) (e.g., Christie et al., 2009; Kotta et al., 2006; Taylor, 1997; Wernberg et al., 2004) are important constituents of near-shore ecosystems because of their phyletic and functional diversity (Hayward, 1988), because they are prey to many larger animals including commercially and recreationally important birds and fish (e.g., Järv et al., 2011), and because of their potentially large influence on community structure as habitat-modifying herbivores (Kangas et al., 1982; Poore et al., 2012; Sala and Graham, 2002).

The relationship between seaweed-associated invertebrates and their habitat is multi-facetted because many use the seaweeds for both food and shelter (e.g., Christie et al., 2009; Duffy and Hay, 1991). Several properties of the seaweeds can determine the strength and direction of their interactions with their associated fauna. Grazing rates, for example, can depend on thallus chemistry (e.g., concentration of phenolic compounds, Haavisto et al., 2001) and thallus structure (toughnes, size, shape and arrangement of algal tissue, Orav-Kotta and Kotta, 2004). The palatability and nutritional value of different seaweed species may in turn affect the survival and growth of herbivores feeding on them (Hemmi and Jormalainen, 2002; Kraufvelin et al., 2006). Similarly, properties such as seaweed density, colour, texture and branch morphology can influence the quality of shelter, e.g., in providing protection against predators, and thereby also influence habitat selection (Hacker and Madin, 1991; Orav-Kotta and Kotta, 2004; Thomsen et al., 2010). Importantly, seaweed properties associated with high quality food or shelter and low predation risk might not coincide in nature. Thus, in a dynamic and spatially variable environment, patterns of herbivore distribution and abundance are therefore likely to reflect complex interactions between the need for protection against environmental fluctuations and predators, the need for proximity to conspecifics for reproduction as well as nutritional requirements and availability of preferred seaweeds (Hacker and Madin, 1991; Hillebrand et al., 2009; Kotta et al., 2010). An understanding of the ecological role of meso-grazers (~0.2–2 cm, usually small crustaceans and gastropods) in seaweed dominated ecosystems is now emerging (e.g., Korpinen et al., 2007). More research that integrates interactions across multiple trophic levels are therefore required in order to reveal the mechanisms that drive the dynamics of marine communities and ultimately increase our ability to predict impacts of pressures such as eutrophication, invasive species and climate change (Korpinen et al., 2007; Kotta et al., 2009; Thomsen et al., 2010; Wernberg et al., 2012).

Meso-grazers are particularly important in systems where macrograzers such as herbivorous fishes and sea urchins are absent. Thus,

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http://dx.doi.org/10.1016/j.jembe.2013.08.014

mesograzers are crucial in most estuaries as well as hyposaline seas such as the Baltic Sea (e.g., Lotze et al., 1999). Due to the low salinity and short geological history of the Baltic Sea, the aquatic flora and fauna is species-poor, and the predominant herbivores are small gastropods and crustaceans such as the isopod *Idotea baltica* (Pallas) (Voipio, 1981). However, although prominent macro-grazers are absent and meso-grazers are few in species numbers, mesograzers are highly abundant throughout the Baltic Sea (Bonsdorff and Pearson, 1999; Lotze et al., 1999). In order to understand the range of factors that influence animal–seaweed relationships in these habitats requires knowledge about distribution among available habitats and consideration of multiple ecological processes. Here, we investigate experimentally, the relationship between habitat occupancy in the field and ecological interactions between a dominant meso-grazer (*I. baltica*) and seaweeds representing different form-functional groups, in its subtidal habitat in the Baltic Sea. *Idotea baltica* is a medium-sized isopod (up to 3 cm), which is widely distributed throughout Europe (Poore and Schotte, 2013). It can be omnivorous (Poore and Schotte, 2013) but is mostly known as a voracious herbivore that can occur in large numbers (e.g., Kangas et al., 1982). We test (1) if *I. baltica* have different abundances in seaweed habitats with different qualities, and if these abundance patterns match (2) habitat selection, (3) grazing rates, (4) growth and survival rates, and (5) predation risk.

2. Methods

2.1. Study area

Samples were collected from rocky coasts in the Baltic Sea proper (the Island of Bornholm, Denmark, 55°8.440 N 15°8.410E) where the salinity is ~8 psu and annual variation in water temperature ranges from ~4 to 22 °C. The Baltic Sea is micro-tidal and all major algal habitats are therefore subtidal. In the ~2–5 m depth range, habitats are dominated by boulders covered by a canopy of *Fucus serratus* L. punctuated by patches of *Furcellaria lumbricalis* (Hudson) J.V. Lamour. and *Cladophora rupestris* (L.) Kütz (Thomsen and Wernberg, 1995; Wernberg, 2006). *Ulva intestinalis* L. is found sporadically in locally disturbed areas and near the water's edge. For brevity, we refer to these species by genus name. These seaweeds represent four different form-functional groups, i.e. have different anatomy, morphology and phenology (Table 1, hereafter referred to as 'complexity' or 'complex vs. simple'; see also Fig. 1a), and these traits likely affect their ecological qualities (Littler and Littler, 1980). All specimens of algae and isopods were collected from these subtidal *Fucus* beds. Our studies took place in late summer (August–September, 2004–08) when the water temperature was ~18–20 °C. Laboratory experiments were conducted under matching constant temperature (~18 °C) at a 12:12 light–dark cycle.

2.2. Abundance patterns

Field densities of *Idotea baltica* (Pallas) were determined by collecting frame samples from *Furcellaria*, *Fucus*, *Cladophora* and *Ulva* dominated habitats (the respective seaweed cover close to 100%). Scuba divers carefully hand-picked all seaweeds within 20 × 20 cm (0.04 m^2) quadrats, placing everything within 1 mm mesh bags (Tuya et al., 2008). Each sample was sieved (1 × 1 mm mesh) and the residuals preserved in a deep freezer at −20 °C. The fauna was dominated by isopods, but most samples also contained small (<5 mm) mussels (*Mytilus trossulus*) and amphipods (*Gammarus* sp.). In the laboratory, isopods >7 mm were counted under a dissecting microscope, in order to order to match sizes used in the experiments. Seaweed biomass was measured wet and converted to dry weight using species-specific conversion factors (J. Kotta, unpublished data). Data on seaweed habitat cover were obtained from a Danish monitoring program. Scuba divers visually estimated seaweed cover of the seafloor at sites throughout Bornholm every year from 1989 to 2005 (a detailed description of sampling methods, and further references, can be found in Stæhr et al., 2000). We pooled all cover estimates between 0 and 6 m depth and across all years and calculated habitat cover as the average across all sites where each species was found. Analysis of variance by permutation (PERMANOVA, Anderson et al., 2008), followed by pairwise comparisons, tested for differences in habitat biomass, cover and isopod densities among seaweed habitat types (fixed factor).

2.3. Habitat selection

Potential preference of *Idotea* for occupancy in particular habitat types was tested in a laboratory colonisation experiment. Similarly-sized (~5 × 5 × 5 cm ≈ 125 cm^3) clumps of each of the four seaweed species were placed in the corners of 5 L aquaria ($n = 8$). 12 medium sized (~10 mm, Wernberg unpublished data) isopods were released in the centre of each aquarium and left undisturbed for 2 h, after which habitat occupancy was assessed by counting the number of isopods in each seaweed habitat. Differences in habitat occupancy were tested with PERMANOVA on square-root transformed data on percent isopods associated with each habitat type. In this analysis treatment levels are not independent (because all the four habitats are placed in the same aquaria) and results should be interpreted cautiously.

2.4. Grazing rates

The ability of isopods to graze on different algae was tested in a no-choice laboratory grazing experiment. Pre-weighed pieces of each seaweed species (0.2–0.8 g FW) were added to 0.25 L containers with 10 medium-sized *Idotea* (~10 mm) that had been starved for 24 h. The isopods were left undisturbed to feed for 2 days at which time the remaining seaweed tissue was re-weighed. Control samples without grazers demonstrated that autogenic changes to the seaweed biomass were negligible (<5%) so these were ignored. Grazing rates were expressed as biomass consumed per individual per 24-h and compared among diet species by PERMANOVA.

2.5. Growth and survival rates

We tested if growth and survival rates of isopods depended on seaweed species in a no-choice laboratory feeding experiment. 300 small evenly-sized *Idotea* individuals were picked haphazardly from a stock population and placed randomly into small jars in batches of 20 which were then randomly distributed among twelve 5 L aquaria (3 replicates of each diet) and 3 sacrificed samples (60 individuals) to measure the size at the start of the experiment. Fresh seaweeds were added at the beginning of the experiment and again after 9 days. All aquaria were

Table 1
Characteristics of the four seaweed habitat types considered in this study (see Fig. 1a), in decreasing order of form-functional complexity (complex to simple), considering tough > delicate, branched > flat, perennial > ephemeral and slow growth > rapid growth. Data compiled from Wallentinus (1984), Bird et al. (1991) and Pedersen et al. (2005).

Species	Tissue structure	Morphology	Life cycle	Growth rate (d^{-1})
Furcellaria lumbricalis (red alga)	Tough (pseudoparenchymatous)	Coarse complex branches	Perennial	0.001 – 0.023
Fucus serratus (brown alga)	Tough (parenchymatous)	Simple, very coarse flat branches	Perennial	0.019 – 0.066
Cladophora rupestris (green alga)	Delicate (filamentous)	Fine complex branches	Ephemeral/perennial	0.251 - 0.300
Ulva intestinalis (green alga)	Delicate (sheet)	Simple hollow tube	Ephemeral	0.144 – 0.260