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

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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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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

aerated for the entire duration of the experiment. After 18 days, surviving isopods were tallied and measured. Growth rates were calculated relative to the initial length (8.1 mm ± 0.05 *SE*, $n = 3$ random subsamples of 20 individuals) and means compared by PERMANOVA.

2.6. Predation risk

Risk of predation from redfin perch (*Perca fluviatilis* L.) in each seaweed habitat was tested in the laboratory. Redfin perch is a visual predator, that is common in the Baltic Sea and a known consumer of a variety of small mobile invertebrates (Järv et al., 2011). For each seaweed species, three habitat clumps identical to those used for the habitat selection experiments were placed in 5 L aquaria with 10 medium-sized isopods (~10 mm) and 2 fish (~15 cm) added. Aquaria with no seaweeds (predation only) and with no seaweeds and no predators were also included. The fish were acclimated to the aquaria for 3 days before starting the experiment, and all aquaria were aerated during the experiment. Each treatment was replicated 4 times. Surviving isopods were tallied after 36 h and their percentage survival calculated and compared among seaweed habitats by PERMANOVA.

3. Results

3.1. Abundance patterns

The seaweed biomass differed between habitat types ($MS_{habitat} = 12.1$, $F_{3,31} = 95.5$, $P = 0.001$, Fig. 1b), where *Fucus*-habitats had substantially greater standing biomass than *Furcellaria*, *Cladophora* and *Ulva*-habitats. Similarly, total cover of seafloor differed between the habitat types ($MS_{habitat} = 479$, $F_{3,46} = 5.6$, $P = 0.006$, Fig. 1c) where *Furcellaria* and *Fucus* habitats covered 4–5 times more seafloor than *Cladophora* and *Ulva* habitats. The abundance ($MS_{habitat} = 1.57$, $F_{3,31} = 3.8$, $P = 0.016$, Fig. 2a) and density ($MS_{habitat} = 7.09$, $F_{3,31} = 5.4$, $P = 0.008$, Fig. 2b) of isopods differed among the four seaweed habitats. Despite having the greatest standing biomass, *Fucus*-habitats supported significantly fewer isopods than the other seaweed habitats. The branched *Furcellaria* and *Cladophora* habitats supported most isopods per area of seafloor, but despite having the lowest standing seaweed biomass, the *Cladophora* and *Ulva*-habitats supported higher densities of isopods per seaweed biomass than the other habitats.

3.2. Grazing rates

Isopod grazing rates varied significantly among seaweed species ($MS_{species} = 0.031$, $F_{3,22} = 6.5$, $P = 0.002$). Overall, there was a 4–5 times difference in grazing rates between the most and the least grazed species, with a clear grazing hierarchy of *Ulva* > *Cladophora* > *Fucus* > *Furcellaria* (Fig. 3a). As such, the isopods grazed most on the ephemeral green seaweeds and the least on the perennial brown and red seaweeds.

3.3. Habitat selection

The distribution of isopods was significantly affected when given the choice of association with one of four seaweed species or not being associated with any seaweed habitat ($MS_{habitat} = 30.3$, $F_{4,35} = 15.5$, $P = 0.001$). The vast majority of the isopods were associated with one of the four seaweed habitats with <5% found swimming in the open between habitats (Fig. 3b). *Furcellaria* (~35% of isopods) was the most, and *Cladophora* (~20% of isopods) the least, frequently selected seaweed habitat. Although there were no statistical differences between some habitat types (*Furcellaria* = *Fucus* = *Ulva*, and *Fucus* = *Ulva* = *Cladophora*, $P < 0.05$), the pattern of successively lower proportions of habitat association was suggestive of a preference hierarchy of *Furcellaria* > *Fucus* > *Ulva* > *Cladophora* (Fig. 1b).

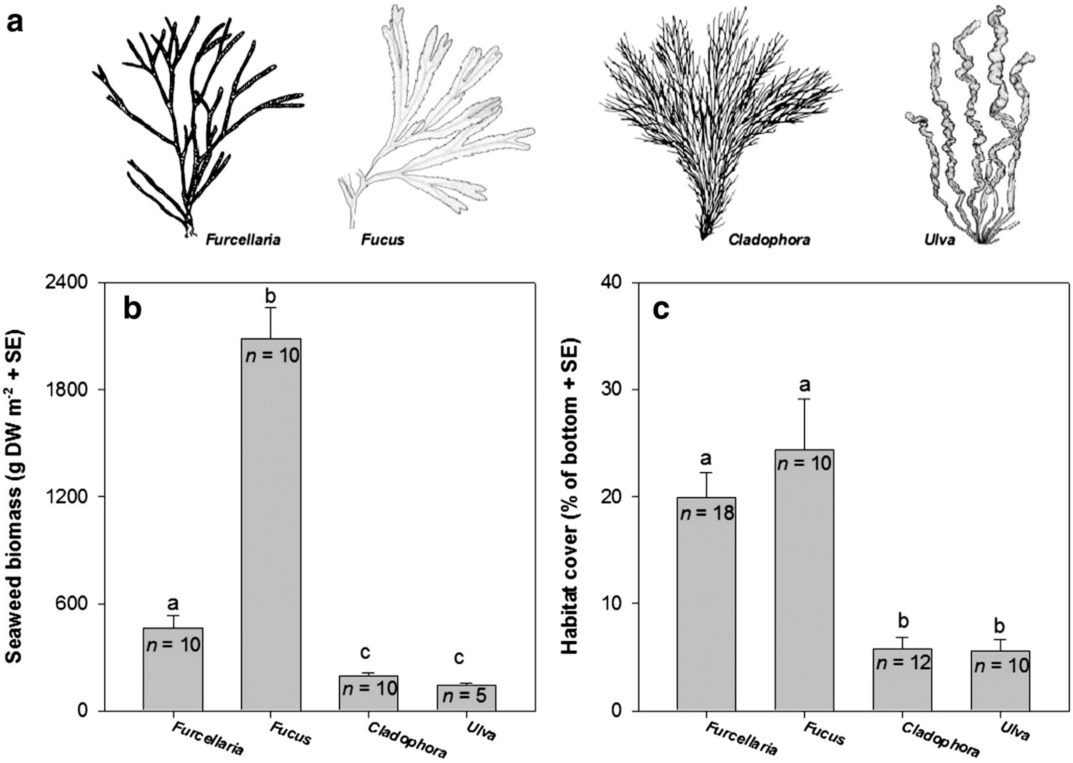

Fig. 1. (a) Seaweed species considered in this study, ordered from left to right in descending order of anatomical, structural and functional complexity (cf. Table 1): *Furcellaria lumbricalis*, *Fucus serratus*, *Cladophora rupestris* and *Ulva intestinalis*. (b) Standing biomass of each seaweed habitat type. (c) Cover of each seaweed habitat type (0–6 m depth) across sites around the island of Bornholm. Letters above bars indicate significant ($P < 0.05$) differences among treatments. Seaweeds are not drawn to scale.

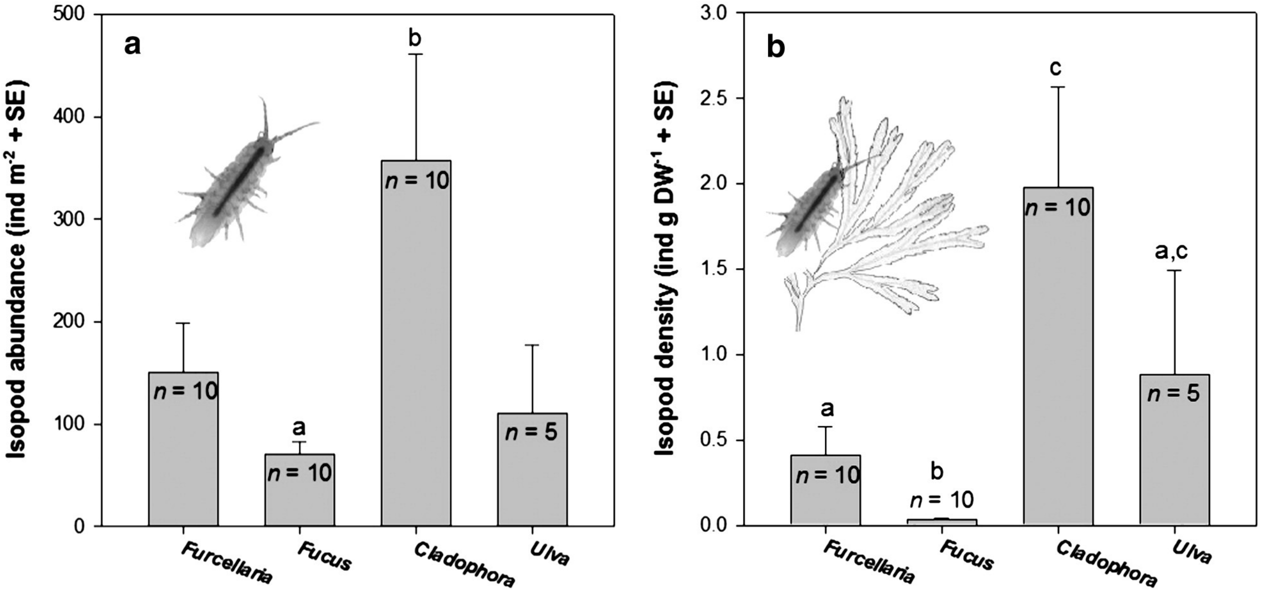

Fig. 2. Prevalence of isopods (*Idotea baltica*) in different seaweed habitats when (a) calculated per area of sea floor and (b) per biomass of seaweed. Letters above bars indicate significant ($P < 0.05$) differences among treatments. Bars with no letters are not different from other treatments. Animals and seaweeds are not drawn to scale.

3.4. Growth and survival rates

There were no differences in survival ($MS_{diet} = 7.22$, $F_{3,8} = 0.77$, $P = 0.587$) or growth ($MS_{diet} = 0.166$, $F_{3,8} = 1.51$, $P = 0.307$) rates of isopods when fed different types of seaweeds. Still, there was a trend suggesting that most isopods survived on a diet of *Ulva* (50% ± 5, *SE*, $n = 3$) and least on a diet of *Cladophora* (32% ± 3). When the data were re-analysed only comparing these treatments, survival rates were indeed significantly different (pairwise test, $t = 3.05$, $P(MC) = 0.037$). A similar trend was observed for growth rates; although not statistically significant in the PERMANOVA test, mean growth rates were nevertheless >2 times higher on a diet of *Ulva* compared to on a diet of *Furcellaria* (Fig. 3c).

3.5. Predation risk

There was a significant difference in isopod survival among the different predation treatments ($MS_{predation} = 2764$, $F_{5,18} = 3.96$, $P = 0.013$). Almost all (>90%) isopods survived when fish were absent (Fig. 3d). In contrast, survival was severely reduced (to ~10%) by predation when no habitat was present. The presence of seaweed refugia increased survival rates 6-fold (to ~60%), there were no differences between individual habitat types where mortality was around 40% in all treatments (Fig. 3d).

4. Discussion

Interactions between meso-grazers and their seaweed habitats are expected to be complex and may include structural, biochemical and trophic aspects. Understanding these complexities is crucial to understanding how this trophic guild affects habitat structure and various ecosystem functions, particularly in ecosystems lacking macro-grazers such as the Baltic Sea. We showed that the distribution and abundance of *Idotea* isopods are disconnected from small-scale habitat availability; the slow-growing perennial seaweeds (*Furcellaria*, *Fucus*) with high standing biomass and cover were sparsely populated by isopods compared to the fast-growing more ephemeral seaweeds (*Cladophora, Ulva*) with low standing biomass and cover. Controlled laboratory experiments suggested that this disconnect could be partially explained by differential seaweed palatability (grazing rates), and nutritional value (translated into isopod growth), but not short-term performance and behavioural responses (selectivity and survival with and without predators).

Grazing rates were highest on the simple seaweeds, and because growth rates were generally also high on these species, this is unlikely to reflect compensatory feeding on a low-quality diet (Cruz-Rivera and Hay, 2000). Rather, this result is consistent with previous studies which have documented how ephemeral seaweeds (especially *Ulva*) are more rewarding food for marine invertebrates, being more nutritious, more palatable and generally support higher growth rates (Orav-Kotta and Kotta, 2004; Wernberg et al., 2008). On the other hand, tough thalli of perennial species resist grazing (Jormalainen et al., 2001; Kotta et al., 2006; Wernberg et al., 2008).

Although the pattern was weak, the perennial, complex seaweeds *Furcellaria* and *Fucus* were selected over the ephemeral and simpler *Cladophora* and *Ulva* as habitat. This short-term behavioural response contrasts both the field distribution data and laboratory based grazing rates (and to some extent growth rates). We have no obvious explanation for this seemingly counter-intuitive result. It cannot be ruled out that temporal (both ontogentetic and phenotypic) shifts in habitat preferences or interactions with other meso-invertebrates could have influenced the distribution patterns of *Idotea*, although neither seem likely given all surveys and experiments were undertaken around the same time in summer, focussing on similar-sized individuals, and few other species were observed in the samples. It is possible that habitat selection is disconnected from trophic drivers because perennial seaweeds in the field often host a diverse ephemeral epiphyte assemblage (Kotta et al., 2000). We speculate that the weak preference for complex seaweeds could relate to their spatio-temporal 'stability' (found year-round with little inter-annual fluctuation) and/or their total abundance. As demonstrated, *Fucus* and *Furcellaria* are much more abundant than *Ulva* and *Cladophora* around Bornholm and it is possible that the isopods 'recognize' these habitats through previous adaptive or phenotypic interactions.

Weak habitat selectivity suggests a lack of strong adaptive or phenotypic affinities to specific seaweeds and associated traits. This is consistent with the lack of significant differences in fish predation among seaweed habitats (shown in our experiments and in Kotta et al., 2010). Also, studies on gastropods (Foster et al., 1999) and isopods (Jormalainen et al., 2001) have shown that feeding exclusively on a single seaweed species may result in reduced growth and fecundity. A need to pursue diverse dietary sources would reduce the strengths of trophically mediated associations (Cruz-Rivera and Hay, 2000). Still,

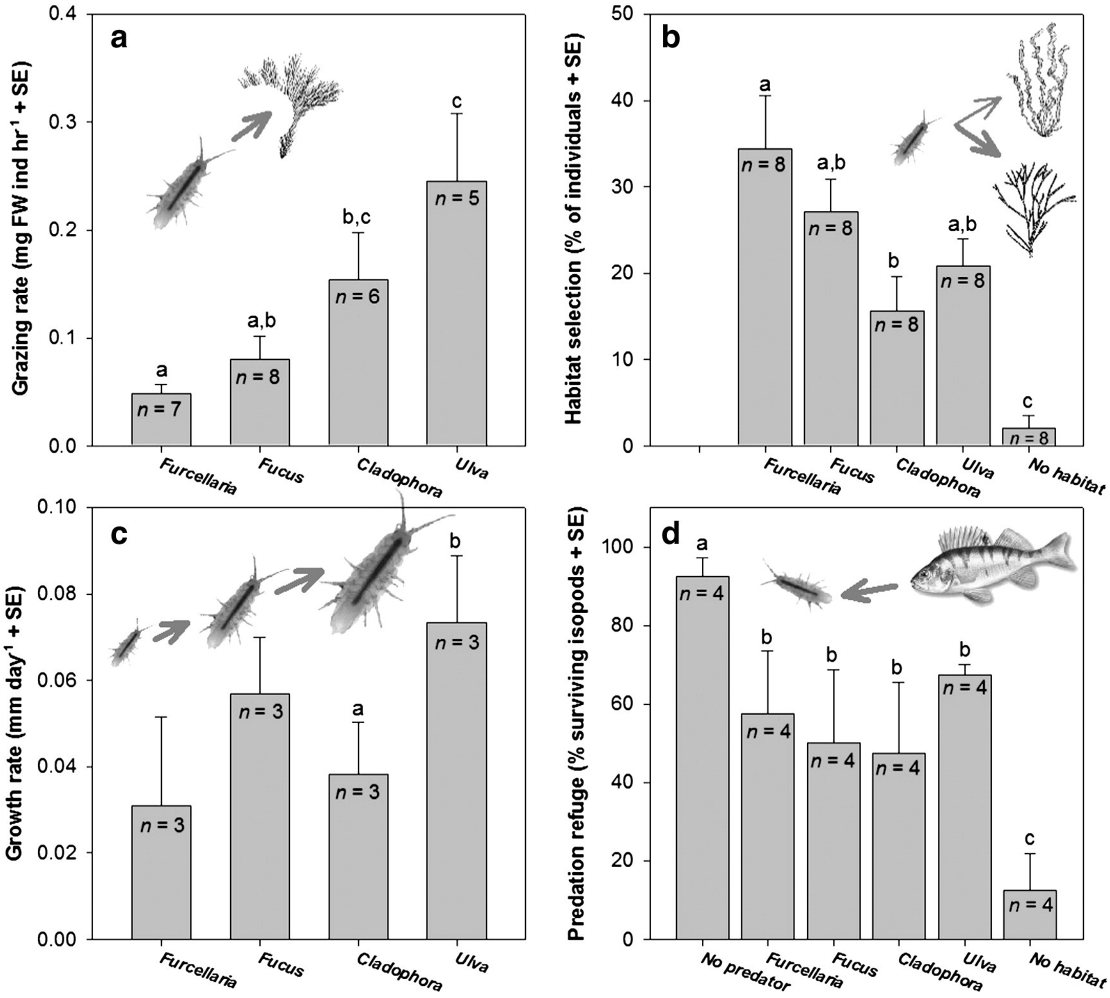

Fig. 3. Interactions between medium-sized (~10 mm) *Idotea baltica* (inserts a–d) and different seaweed habitat types (see Table 1). (a) Grazing rates on different species of seaweeds. (b) Selection of occupancy in different habitats. (c) Growth rates on a diet of different seaweeds (d). Survival of *I. baltica* in different seaweed habitats under predation from *Perca fluviatilis* (e, insert). Letters above bars indicate significant ($P < 0.05$) differences among treatments. Bars with no letters are not different from other treatments. Animals and seaweeds are not drawn to scale.

there was a strong affinity of isopods to (any) structural habitat as is commonly observed for invertebrates under fish predation (Walls et al., 1990). This likely reflects strong adapted predator avoidance behaviour (Merilaita and Jormalainen, 1997) (shown in our experiments and in Kotta et al., 2010). Also, studies on gastropods (Foster et al., 1999) and isopods (Jormalainen et al., 2001) have shown that feeding exclusively on a single seaweed species may result in reduced growth and fecundity. A need to pursue diverse dietary sources would reduce the strengths of trophically mediated associations (Cruz-Rivera and Hay, 2000). Still, there was a strong affinity of isopods to (any) structural habitat as is commonly observed for invertebrates under fish predation (Walls et al., 1990). This likely reflects strong adapted predator avoidance behaviour (Merilaita and Jormalainen, 1997). Thus, predation risk potentially explains why mesograzers are typically found in seaweeds, and rarely in the water column (e.g., this study), but did not provide insights into why some seaweeds were more densely populated than others.

High densities of isopods in the simple habitats, despite their relatively low standing biomass, could therefore, at least partially, reflect isopod feeding behaviours. In contrast, active habitat selection could not help explain the strong field-based distribution patterns we observed. We did not test performance on a diet of mixed species; it is possible that, in order to increase their overall performance, the isopods have to actively move between seaweed habitats, while still avoiding predators. Thus, it is plausible that the distribution of isopods in the field reflects a balance between feeding within *Ulva* and *Cladophora* habitats and movements among other seaweed habitats in the search for a mix of seaweed species rich in insoluble sugars, low in total carbon content and physical toughness of the thallus (Hemmi and Jormalainen, 2002).

In conclusion, our study confirmed that the patterns of distribution of the isopod *Idotea* are not driven by a single forcing factor but are likely caused by a combination of interactions across three trophic levels, including habitat properties, isopod grazing and fish predation. Our interpretation is that, the strong affinity of isopods to seaweeds is likely to be driven by a need to reduce the risk from predation. Within the seaweed habitats, however, the isopods get the greatest benefit from grazing primarily on *Ulva* while occasionally occupying other habitats to acquire multiple food sources in order to maximize their performance.

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