

# Trophic interactions in *Zostera marina* beds along the Swedish coast

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**ABSTRACT:** We compared eelgrass *Zostera marina* communities in 3 regions in Sweden believed to be affected by eutrophication and overfishing, to determine whether bottom-up or top-down processes control the biomass of epiphytic macroalgae and grazers. Nitrogen and carbon isotope signatures were analyzed to explore the food webs and to identify the grazing species feeding on filamentous algae and/or eelgrass. Mixing model (IsoSource version 1.3.1) analysis of the isotope signatures indicated that the amphipods *Gammarus locusta* and *Microdeutopus gryllotalpa* fed primarily on filamentous algae and that only 2 small gastropod species consumed eelgrass. Moreover, the grass shrimp *Palaemon elegans* and *P. adspersus* were ca. 1 trophic level above amphipods and algae, but according to the mixing model played different trophic roles in the different areas. The highest biomass of filamentous algae was found in the west coast beds housing grazers with the lowest biomass and mean size (predominantly *G. locusta* and *M. gryllotalpa*, 0.5 to 3 mm). In contrast, the Baltic Sea beds had low algal biomass, but the grazers (mostly *G. locusta* and *Idotea baltica*) had higher biomass and were significantly larger (mean size ca. 10 mm). An overall negative correlation was found between grazer biomass and biomass of filamentous algae. The significantly smaller grazers and absence of isopod grazers on the west coast may be due to substantial consumption by small predatory fish. This supports the suggestions that, in Swedish eelgrass beds, grazers are top-down controlled, and overexploitation of large predators and eutrophication play an important role in the recent increases in algal biomass.

**KEY WORDS:** Seagrass · Eelgrass · *Zostera* · Stable isotopes · Mixing model · Trophic interactions

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## INTRODUCTION

The most serious and widespread anthropogenic disturbances in coastal ecosystems include eutrophication (Short & Wyllie-Echeverria 1996, Howarth et al. 2000) and overfishing (Jackson et al. 2001, Myers & Worm 2003). Eutrophication is considered to be one of the main reasons for loss of seagrass (see reviews by Hauxwell et al. 2003, Hughes et al. 2004), because an increased nutrient supply enhances phytoplankton production and turbidity and also promotes the annual rapid growth of filamentous algae and epiphytic and free-floating macroalgal mats, which in turn reduce the supply of light and nutrients to the seagrass

(Duarte 1995, Valiela et al. 1997). However, reviews by Hughes et al. (2004) and Valentine & Duffy (2005) have shown that an increased nutrient load alone often has little negative effect on seagrass growth, as long as natural populations of mesograzers (i.e. amphipods, isopods, and gastropods) are present to harvest the algae.

In addition to the effect of increased nutrient load, overfishing may indirectly influence seagrass growth via a trophic cascade (Heck et al. 2000). When top predators are removed from the system, there may be an increase in the number of smaller primary predators, mainly fish, which might reduce the abundance of small invertebrate algal grazers and thereby allow a

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rise in epiphyte biomass (Heck et al. 2000, Valentine & Heck 2001). Hence, both eutrophication and overfishing may have a pronounced impact on the growth of seagrass by affecting epiphytes through a combination of top-down and bottom-up processes. Moreover, species-specific differences in the diets of grazers can give rise to significant variation in epiphyte biomass (Duffy & Harvilicz 2001). In particular, key invertebrate grazers can consume both epiphytes and seagrass, and thus their effects on seagrass can be either positive or negative, depending on the availability of alternative food (Hughes et al. 2004, Valentine & Duffy 2005).

The aim of the present study was to assess differences in beds of eelgrass *Zostera marina* (hereafter simply *Zostera*) growing along the west, south, and southeast coasts of Sweden by studying variation in the biomasses of eelgrass, ephemeral algae, and grazers from a top-down versus a bottom-up perspective. In short, we compared 2 opposing hypotheses: (1) that eelgrass systems are generally bottom-up controlled, and therefore those with the highest production and biomass of ephemeral and epiphytic macroalgae will contain the largest mesograzer biomass and (2) that such systems are usually top-down controlled, and thus those with the lowest mesograzer biomass will have the highest algal biomass. We performed stable isotope analyses of nitrogen and carbon to investigate the trophic interactions in each of the hypothetical systems, especially to identify the diets of important mesograzers and their predators and to determine whether any of the species consume eelgrass.

*Zostera* is the most common seagrass along the coast of Sweden, and it provides a physical habitat, food, and predation refuge for a variety of organisms, including several commercial species (Baden & Pihl 1984, Orth & Van Montfrans 1984, Baden 1990, Polte et al. 2005). It has been found that *Zostera* beds off the west, south, and southeast coasts differ with regard to how they are affected by eutrophication and the abundance of predators. Since the 1980s, 58% of the eelgrass beds along the west coast have been lost (Baden et al. 2003), which can be compared with the fact that the nutrient load to Swedish coastal systems has been increasing since the 1930s (Rosenberg et al. 1990). In addition, mats of filamentous algae dominated by species of the genus *Ulva* (syn. *Enteromorpha*) have increased (Pihl et al. 1999), and abundance of the commercially important cod *Gadus morhua* has decreased dramatically (Svedäng 2003, Svedäng & Bardon 2003).

*Zostera* beds in the Baltic Sea of the south and southeast coasts of Sweden have also been affected by the growing nutrient load over the last century, and the winter concentrations of  $\text{PO}_4$  in that area are similar to those seen off the west coast, whereas the levels of  $\text{NO}_3$  are about 3 times lower (Rosenberg et al. 1990,

Lundgren 2004, Andersson & Andersson 2006). However, in contrast to the west coast, there is no indication that the distribution of the Baltic eelgrass beds has decreased in recent years. On the south coast, monitoring results show that there has been an increase in *Zostera* shoot density and biomass over the last 10 yr (Lundgren et al. 2006). Filamentous algae have not been observed in large amounts in *Zostera* beds in the Baltic, whereas they are frequently abundant in shallower areas (Norkko & Bonsdorff 1996, Lundgren et al. 2006). The overfishing of the Baltic stock of cod is alarming, but there is a stable population of that species in Öresund close to our south coast sampling site, where individuals >30 cm in length are common (Lagenfelt & Svedäng 1999). In addition, there are reports indicating several years of recruitment failure for both small and large predatory fish (e.g. perch *Perca fluviatilis*, pike *Esox lucius*, and roach *Rutilus rutilus*) in the area of our southeast location, which indicates extremely low abundances (Andersson et al. 2000, Nilsson et al. 2004). Thus it seems that the abundance of fish differs between *Zostera* beds in the west, south, and southeast coastal waters of Sweden, although at present there are no quantitative data available that can show the occurrence of large individual fish in the separate beds. Nevertheless, the indications of disparities between the areas with regard to the abundance of different fish species and epiphytic algae can allow interesting comparisons of potential top-down and bottom-up effects in Swedish eelgrass beds. Little is currently known about the biomass and composition of ephemeral algae and grazers in the *Zostera* beds of the Swedish south and southeast coasts, and indeed there are no data that have identified the species that graze on *Zostera* in Swedish waters.

## MATERIALS AND METHODS

The investigation was carried out in 5 *Zostera* beds in 3 different regions: the west coast (2 sites in Gullmar Fjord), the south coast (1 site at Fredshög), and the southeast coast (2 sites in Kalmar Sound in the Baltic Sea) (Fig. 1). The sampling at all 5 sites was carried out between 26 August and 7 September 2004 during the period of peak *Zostera* biomass on the west coast (Baden & Pihl 1984). The 2 west coast *Zostera* beds are located in sheltered bays with soft sediment (mainly clay) on the eastern side of Gåsö Island (Site 1) and on the western side of Lindholmen Island (Site 2). The south coast site (Site 3) is in a more exposed location with sandy sediment, and there is one continuous *Zostera* bed along the shore. In the southeast coastal region, we studied an eelgrass bed growing on sandy

sediment in an exposed location near Saxnäs (Site 4) and another bed at Beijershamn that was in a more sheltered area with a clay sediment (Site 5). Salinity varied from 6‰ on the southeast coast to ca. 20‰ on the west coast (see Table 1 for details of the study sites).

**Field sampling and analysis.** *Zostera* was sampled by a SCUBA diver using a trap designed as a bag (mesh size 0.2 mm, height 1.0 m) with a quadratic steel frame measuring 0.12 m<sup>2</sup> (0.35 × 0.35 m) in the opening. The trap was carefully lowered over the *Zostera*, and the shoots were cut at the bottom. Six samples were taken randomly in each bed, and they were immediately put on ice and later frozen before analysis in the laboratory. For analysis of *Zostera* biomass, leaf length, and shoot density, 5 to 6 additional samples were taken using steel rings with an area of 0.1 m<sup>2</sup> that were placed randomly in the bed, and the shoots were cut at the bottom. Temperature and salinity were noted. To obtain an estimate of the organic content of the sediment, 3 to 5 samples of the upper 5 cm of sediment were randomly collected within the *Zostera* beds at each site by use of a corer (diameter 4.5 cm). The organic content was measured as loss on ignition (LOI) by calculating the difference in weight before and after heating at 450°C for 3 h. LOI was measured to allow comparison of our data with the findings of Baden & Pihl (1984) in the 1980s.

To determine the biomass of algae in the *Zostera* beds, loose parts of filamentous free-floating macroalgae were selected, and the epiphytes were scraped from the top 20 cm of the leaves from 20 randomly chosen *Zostera* shoots (minimal fouling is found below that point). Epiphytic and free-floating macroalgae were separately dried at 60°C for 24 h to estimate dry weight (DW). In the samples from the west coast sites, the leaves were coated with a mixture of short epiphyte filaments, amphipod tubes, and detritus. The biomass of the epiphytic algae was calculated by estimating the volume percentage of algal species in the mixture and weighing to determine the total amount of fouling (excluding epifauna). In the samples from the sites in the other 2 regions, the *Zostera* leaves bore mainly epiphytic microalgae, which were collected by scraping the leaves in a bowl of seawater and subsequently pouring the water through a GF/F glass fiber filter (0.4 mm mesh), after which the filter was weighed to estimate the DW of the algae. Dominant algal species were identified by examination in a light microscope at 100× magnification. Since the dominant filamentous brown algae *Ectocarpus* sp. and green algae *Ulva* sp. grow both as epiphytes and as free-floating mats, and because filaments easily break when frozen, a clear distinction between epiphytes and free-floating macroalgae could not be made. Therefore, the data on

algae were pooled to represent total algal biomass in the analyses. All animals associated with each *Zostera* sample were collected using a sieve (0.2 mm mesh). The crustaceans and gastropods were identified to species or family using a stereomicroscope and then counted and dried (60°C, species separated) for at least 24 h, and total ash-free dry weight (AFDW) was estimated after combustion in a muffle furnace at 450°C for at least 3 h. We used AFDW instead of DW to measure grazer biomass because different invertebrate species contain different amounts of organic tissue in relation to their total body weight.

To investigate differences between the *Zostera* beds in the 3 regions, we performed 1-way ANOVA followed by planned post hoc comparisons (Sokal & Rohlf 1995). The ANOVA was carried out using the sites (5 levels) as the independent variable and *Zostera* biomass (g DW), *Zostera* shoot density, the biomass of filamentous algae (g DW), and the biomass of all potential grazers on filamentous algae (g AFDW) as dependent variables. As the literature is not clear regarding the feeding preferences of the invertebrates that inhabit eelgrass beds, we performed a second assessment of the biomass of algal grazers based on the results of the isotope analyses (see below). The planned post hoc analyses were then carried out to



Fig. 1. Study locations along the west (Sites 1 and 2), south (Site 3), and southeast (Sites 4 and 5) coasts of Sweden

compare the samples from the west coast (Sites 1 and 2) with those from the south coast (Site 3) and the southeast coast (Sites 4 and 5) and to compare the south coast samples with those from the southeast coast. Correction for multiple comparisons was achieved using the Dunn-Sidak method. Data on shoot density, filamentous algae, and grazer biomass were square root transformed to make them homogeneous and normally distributed (determined by Levene's test and Kolmogorov-Smirnov test, respectively). To assess the relationship between the different estimates of grazer biomass and filamentous algae, and between the biomass of algae and *Zostera* biomass and shoot density in each *Zostera* bed, mean values were calculated for each variable at each of the 5 sites, and the relationships were tested using Pearson's correlation analysis and SPSS 14.0.

**Stable-isotope analyses.** To explore the trophic structure in Swedish eelgrass communities and to test whether grazer species consumed both algae and *Zostera* leaves, stable-isotope analyses of nitrogen and carbon on plant and animals in eelgrass beds from each region were analyzed. Stable-isotope studies have been carried out to investigate trophic interactions in seagrass communities (Davenport & Bax 2002, Smit et al. 2006, Tomas et al. 2006), but there appear to be few of this type of study in temperate eelgrass beds (Kharlamenko et al. 2001, Fredriksen et al. 2004). The technique is straightforward and comparatively simple (Peterson & Fry 1987, Post 2002). Organisms often exhibit characteristic isotopic signatures. The isotope distributions of  $\delta^{15}\text{N}$  have been successfully used to define an organism's trophic position since  $\delta^{15}\text{N}$  values typically increase during each trophic transfer (Peterson & Fry 1987, France 1994). The enrichment of 3.4‰ (1‰ SD; Post 2002) as a mean increase between trophic levels has been globally accepted and used recently (Sherwood & Rose 2005, Moens et al. 2005, Nyström et al. 2006), but considerable variations in the enrichment in  $\delta^{15}\text{N}$  between diet and consumer have been reported for marine invertebrates (McCutchan et al. 2003, Vanderklift & Ponsard 2003, Svensson et al. 2007).

In contrast, the carbon isotope value changes little as carbon moves through the food web and is therefore used to evaluate the sources of carbon for an organism. Organisms usually have  $\delta^{13}\text{C}$  signatures of  $\pm 0.4$  (1.3‰ SD; Post 2002) or up to 1‰ higher values than their food (DeNiro & Epstein 1978, Peterson & Fry 1987).

The nitrogen and carbon isotope signatures were studied and analyzed within 3 *Zostera* beds (1 from each region) on the west coast (Site 2), south coast (Site 3), and the southeast coast (Site 4). *Zostera* leaves and the dominating species of filamentous algae and fauna were collected using the trap design described

above. Detritus was picked out from sediment samples. Due to low abundance of algae in the south and southeast coast beds, the algae species were not separated before analysis. Additional fish specimens for stable-isotope analysis of dominant smaller fish species on the west coast that were not efficiently sampled with the trap method were kindly donated from simultaneously occurring fish investigations in the *Zostera* bed at Site 2 (Pihl et al. 2006). Despite extra fishing efforts on the southeast coast, no predatory fish such as perch or sticklebacks were caught or seen (SCUBA diving) at the study sites.

Isotope signatures were analyzed in all dominant macroinvertebrates and fish encountered in the present study. Average-sized individuals of the amphipods, isopods, and gastropods from each *Zostera* bed were used for the analyses. Muscle tissues from the fishes and the shrimp were dissected and then homogenized to a fine powder before analyses (Peterson & Fry 1987, Post 2002). Entire individuals of large amphipods and isopods were homogenized before analysis. For invertebrates <3 mm in body length, several individuals were pooled within species, and not homogenized, to obtain enough biomass to carry out the analysis. For the smallest gastropods (e.g. *Hydrobia* spp.) enough tissue could not be gained to carry out the analysis. Body sizes of the analyzed individuals are described as total length (TL), or in carapace length (CL), or width (CW).

The isotope analysis was carried out using a continuous flow isotope ratio mass spectrometer PDZ Europa 20-20 isotope analyser. All isotope values are reported in the  $\delta$  notation where  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$ . R is the ratio of  $^{15}\text{N}:^{14}\text{N}$  or  $^{13}\text{C}:^{12}\text{C}$ , and as standard, Pee Dee Belemnite is used for carbon, and atmospheric nitrogen is used for nitrogen. Glycine was used as the internal standard. The precision of the measurement was 0.1‰ for carbon and 0.2‰ for nitrogen. The isotope signatures in the present study are given as mean delta notations in per mille (‰).

One of the main difficulties in using stable isotopes to assess trophic transfers within coastal food webs is the large number of potential food sources. Recently, mixing models based on stable isotopes have been proposed to derive the relative contributions of each food source. To estimate proportions of food sources using the isotopic signatures of the grazing herbivore species we used linear mixing model IsoSource, Version 1.3.1 (available at [www.epa.gov/wed/pages/models.htm](http://www.epa.gov/wed/pages/models.htm)) designed by Phillips & Gregg (2001, 2003). For the crustacean grazers (*Gammarus locusta*, *Idotea baltica*, and *Microdeutopus gryllotalpa*) and the gastropod grazers (*Rissoia* spp., *Littorina* spp., *Radix baltica*, and *Theodoxus fluviatilis*) we used  $\delta^{13}\text{C}$  signatures to estimate the relative contribution (%) of *Zostera*, filamen-

tous algae, and detritus. As the trophic fraction of  $\delta^{13}\text{C}$  is relatively small (about  $\pm 1\%$  of values of their food; DeNiro & Epstein 1978, Peterson & Fry 1987) and because we lack information about the number of trophic levels between basal resources and consumers, we did not correct consumer  $\delta^{13}\text{C}$  values for trophic fractionation. The nitrogen isotope signatures of the crustacean and gastropod grazers did not reveal clear enrichment compared to any of the predictable food sources. Due to the lack of knowledge of true nitrogen enrichment of the species, we only included the carbon isotope signatures in the model. We carried out independent *t*-tests to test for significant differences in isotope signature between species where  $\delta^{15}\text{N}$  signatures were overlapping. Source increment was set at 1% in the model, and tolerance was initially set at 0.1% (Phillips & Gregg 2003).

In addition, we estimated the relative contribution (%) of food sources (e.g. crustaceans, gastropods, and filamentous algae) for the omnivore grass shrimp *Palaemon adspersus* and *P. elegans*, since their functional roles in the different beds are unclear and since the results revealed high abundance of the shrimp in the south coast bed. The nitrogen isotopic signature was enriched in *P. adspersus* and *P. elegans* compared to the food sources.

The  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  signatures were studied combined in the model. For  $\delta^{15}\text{N}$  we employed the enrichment of 3.4‰ with each trophic level (Post 2002). Source increment was set at 1%. Tolerance was initially set at 0.1‰ (Phillips & Gregg 2003). If mixture isotope values were out of bounds (i.e. outside the polygon delineated by the food web end members; Phillips & Gregg 2001), we incrementally increased the tolerance value to a maximum of 0.5‰. Descriptive

statistics are provided as a way to describe the entire distribution of feasible solutions. To avoid misrepresenting the results, mean and the distribution of feasible solutions (1st to 99th percentile) are reported (Phillips & Gregg 2003). The  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of higher trophic levels (e.g. fish) were only analysed graphically.

## RESULTS

### *Zostera* community characteristics

The characteristics of the sediment and *Zostera* differed between the 2 west coast sites and the sites in the Baltic (south and southeast coast). Compared to the sediment samples from the Baltic, those from the west coast had higher LOI values (Table 1), which indicates low exposure but not necessarily high anthropogenic enrichment. In addition, we found a maximum value of 25% for LOI at west coast Site 2, which means that the level today is about the same as the value of 20% measured in the same area in 1980 to 1982 (Baden & Pihl 1984).

The biomass of *Zostera* differed significantly among the 5 sites, but the difference was too small to be detected by the planned post hoc test among regions (Table 2, Fig. 2). The *Zostera* plants in the west coast beds had longer and wider leaves, but lower shoot density, compared to those at the Baltic sites, and thus the biomass was similar for the regions (Table 1). The shoot density was significantly higher in the south coast than in southeast coast beds, and in turn was significantly higher in the southeast beds than in those off the west coast (Table 2, Fig. 2).

Table 1. Geographical position, salinity, sampling depth, sediment organic content (loss on ignition), and *Zostera* leaf length for the different study sites

Site	Position	Depth (m)	Salinity (psu)	Organic content (%)			Leaf length (cm)		
				Mean	SD	N	Mean	SD	N
<b>West coast</b>									
1	58° 14' 32.7" N, 11° 24' 43.0" E	1.5–2	18.2	10.4	3.0	3	69.3	5.1	18
2	58° 15' 48.9" N, 11° 29' 45.6" E	1.5–3.5	20.1	25.2	4.8	5	89.8	29.3	18
<b>South coast</b>									
3	55° 23' 16.3" N, 13° 00' 37.1" E	1.3–3.2	7.9	0.7	0.3	4	35.5	7.5	18
<b>Southeast coast</b>									
4	56° 42' 09.6" N, 16° 28' 36.1" E	2.5–3	5.8	0.7	0.2	4	44.3	8.2	18
5	56° 36' 31.8" N, 16° 24' 51.9" E	2.0–4.0	5.9	3.0	0.7	5	63.6	7.0	18

Table 2. One-way ANOVA using the sites (5 levels) as the independent variable and the following as dependent variables: *Zostera* shoot density and biomass (g DW), filamentous algae (g DW), all potential grazers (g AFDW) of filamentous algae (Grazer 1), and specific grazer species (g AFDW) selected based on the results of isotope analysis (Grazer 2). Planned post hoc tests were subsequently carried out to compare the west coast *Zostera* beds (Sites 1 and 2) with the south coast (Site 3) and southeast coast (Sites 4 and 5) beds, and to compare the south coast bed with the southeast coast beds. Correction for multiple comparisons was done using the Dunn-Sidak method. Significant ( $p < 0.05$ ) and non-significant ( $p > 0.05$ ) results are indicated by \* and NS, respectively

Source of variation	SS	df	MS	$F_s$	
<b>Zostera biomass</b>					
Sites	56330.11	4	13506.62	3.64	*
West vs. south	20981.04	1	20981.04	5.89	NS
West vs. southeast	22679.84	1	22679.84	6.37	NS
South vs. southeast	194.41	1	194.41	0.05	NS
Within	74798.43	21	3561.83		
<b>Zostera shoot density</b>					
Sites	982.34	4	245.58	11.79	*
West vs. south	738.85	1	738.85	35.48	*
West vs. southeast	274.07	1	274.07	13.16	*
South vs. southeast	186.72	1	186.72	8.97	*
Within	416.47	20	20.82		
<b>Filamentous macroalgae</b>					
Sites	20.80	4	5.20	21.43	*
West vs. south	17.10	1	17.10	70.38	*
West vs. southeast	11.36	1	11.36	46.73	*
South vs. southeast	1.62	1	1.62	6.66	NS
Within	4.61	19	0.24		
<b>Grazer 1 biomass</b>					
Sites	3.58	4	0.89	1.75	NS
West vs. south	2.54	1	2.54	4.97	NS
West vs. southeast	0.04	1	0.04	4.97	NS
South vs. southeast	2.54	1	2.54	0.09	NS
Within	12.76	25	0.51		
<b>Grazer 2 biomass</b>					
Sites	7.89	4	1.97	6.00	*
West vs. south	6.89	1	6.89	20.96	*
West vs. southeast	3.22	1	3.22	9.80	*
South vs. southeast	1.35	1	1.35	4.09	NS
Within	7.34	25	0.33		

The total biomass of filamentous algae was significantly greater in the 2 west coast beds than in the beds in the other regions (Table 2, Fig. 2). At the west coast sites, there was a predominance of filamentous brown algae (*Ectocarpus* spp. 40%), filamentous green algae (*Ulva* spp. 28% and *Cladophora* sp. 6%), and filamentous red algae (*Ceramium* sp. 21% and *Polysiphonia* spp. 6%), and the fouling also included sediment tubes from the amphipods *Erichtonius difformis* and *Corophium insidiosum*. The algae noted in both the south and the southeast beds were *Ceramium* sp., *Polysiphonia* spp., *Cladophora* sp., *Ectocarpus* spp., and *Brogniartella* sp. The red algae dominated, but it was not possible to estimate the relative dominance of different taxa due to the overall low abundance of algae.

The invertebrate communities associated with the *Zostera* beds differed between the study areas. At the west coast sites, the predominant crustaceans were the amphipods *Erichtonius difformis*, *Corophium insidiosum*, *Microdeutopus gryllotalpa*, and *Gammarus locusta* (TL 0.5 to 3 mm), and the omnivorous grass shrimp *Palaemon elegans* and *P. adspersus* (TL 26 to 48 mm), and the most numerous gastropods were *Rissoa* spp. and *Hydrobia* spp. In the south coast beds, *Palaemon* spp. predominated together with *G. locusta* and the isopod *Idotea baltica*, which were larger there than at the west coast sites (avg. TL  $6.6 \pm 3.9$  and  $9.2 \pm 5.1$  mm  $\pm$  SD, respectively). The gastropods were primarily *Theodoxus fluviatilis*, *Radix baltica*, and *Hydrobia ventrosa*. The invertebrate community in the southeast beds was dominated by very large *G. locusta* and *I. baltica* (avg. TL  $10.5 \pm 5.8$  and  $10.7 \pm 4.1$  mm, respectively), and there were also large numbers of the gastropods *T. fluviatilis* and *H. ventrosa*. A complete list of the composition, abundance, and biomasses of the invertebrate species is presented in Table 3.

Based on information in the literature, we included *Microdeutopus gryllotalpa*, *Gammarus locusta*, *Idotea*

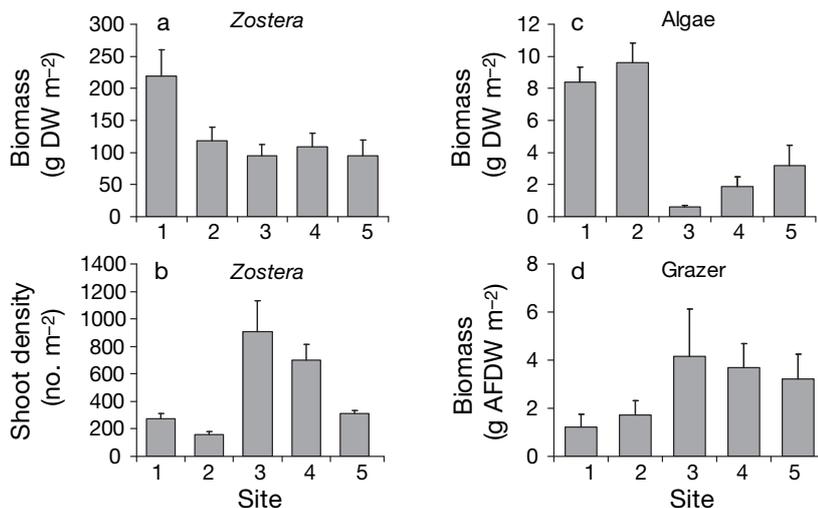


Fig. 2. Mean  $\pm$  SE (a) *Zostera* biomass, (b) *Zostera* shoot density, (c) biomass of filamentous algae, and (d) biomass of all potential grazers ( $\pm$ SE) in the 5 *Zostera* beds off the Swedish west coast (Sites 1 and 2), south coast (Site 3), and southeast coast (Sites 4 and 5)

Table 3. Mean  $\pm$  SE biomass (g AFWD) and density (ind.  $m^{-2}$  bottom) of crustaceans and gastropods in *Zostera* beds off the west (Sites 1 and 2), south (Site 3), and southeast (Sites 4 and 5) coasts of Sweden

	Site 1 (W)		Site 2 (W)		Site 3 (S)		Site 4 (SE)		Site 5 (SE)	
	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density
<b>Crustacea</b>										
<i>Erichthonius difformis</i>	0.620 $\pm$ 0.1328	22233 $\pm$ 4803	0.120 $\pm$ 0.043	4046 $\pm$ 1117	0	0	0	0	0	0
<i>Corophium insidiosum</i>	0.1968 $\pm$ 0.0627	2684 $\pm$ 923	0.076 $\pm$ 0.022	1925 $\pm$ 530	0	0	0	0	0	0
<i>Corophium volutator</i>	0.038 $\pm$ 0.038	356 $\pm$ 356	0	0	0	0	0	0	0	0
<i>Microdeutopus gryllotalpa</i>	0.167 $\pm$ 0.142	418 $\pm$ 356	0.072 $\pm$ 0.047	391 $\pm$ 272	0	0	0	0	0	0
<i>Gammarus locusta</i>	0.064 $\pm$ 0.059	144 $\pm$ 118	0.099 $\pm$ 0.057	240 $\pm$ 121	0.0194 $\pm$ 0.015	24 $\pm$ 12	0.854 $\pm$ 159	226 $\pm$ 50	0.501 $\pm$ 0.201	95 $\pm$ 31
<b>Amphipoda</b>										
(Unknown < 3 mm)	0.020 $\pm$ 0.009	711 $\pm$ 474	0.043 $\pm$ 0.017	370 $\pm$ 144	0.0034 $\pm$ 0.0032	10 $\pm$ 6	0.004 $\pm$ 0.002	49 $\pm$ 35	0.010 $\pm$ 0.010	30 $\pm$ 38
<i>Jaera albifrons</i>	0	0	0	0	0.010 $\pm$ 0.01	16 $\pm$ 8	0.004 $\pm$ 0.002	5 $\pm$ 3	0.0003 $\pm$ 0.0003	1 $\pm$ 1
<i>Idotea baltica</i>	0	0	0	0	0.093 $\pm$ 0.043	35 $\pm$ 12	0.583 $\pm$ 0.1408	128 $\pm$ 26	0.174 $\pm$ 0.091	41 $\pm$ 14
<i>Idotea chelipes</i>	0	0	0	0	0.012 $\pm$ 0.010	12 $\pm$ 11	0.002 $\pm$ 0.002	5 $\pm$ 5	0.0004 $\pm$ 0.002	3 $\pm$ 2
<i>Idotea granulosa</i>	0	0	0	0	0.002 $\pm$ 0.002	1 $\pm$ 1	0	0	0.006 $\pm$ 0.006	3 $\pm$ 3
<b>Decapoda</b>										
<i>Palaemon adspersus</i>	0.489 $\pm$ 0.326	8 $\pm$ 7	0.714 $\pm$ 0.467	3 $\pm$ 3	1.087 $\pm$ 0.803	7 $\pm$ 4	0.835 $\pm$ 0.327	7 $\pm$ 3	0.344 $\pm$ 0.219	3 $\pm$ 2
<i>Palaemon elegans</i>	0.0126 $\pm$ 0.008	5 $\pm$ 4	0.158 $\pm$ 0.158	3 $\pm$ 3	2.635 $\pm$ 1.126	35 $\pm$ 11	0.701 $\pm$ 0.318	7 $\pm$ 3	0	0
<i>Crangon crangon</i>	0.097 $\pm$ 0.0065	5 $\pm$ 3	0	0	0	0	0	0	0	0
<i>Macropodia rostrata</i>	0	0	0.163 $\pm$ 0.100	5 $\pm$ 3	0	0	0	0	0	0
<i>Carcinus maenas</i>	0	0	5.933 $\pm$ 3.221	13 $\pm$ 3	0	0	0	0	0	0
<b>Gastropoda</b>										
<i>Rissoa</i> sp.	0.374 $\pm$ 0.105	403 $\pm$ 77	0.331 $\pm$ 0.104	1336 $\pm$ 458	0	0	0.067 $\pm$ 0.02	240 $\pm$ 71	0.045 $\pm$ 0.019	155 $\pm$ 53
<i>Lacuna vincta</i>	0.008 $\pm$ 0.008	1 $\pm$ 1	0	0	0	0	0	0	0	0
<i>Littorina littorea</i>	0.083 $\pm$ 0.055	72 $\pm$ 59	2.890 $\pm$ 1.913	5.44 $\pm$ 3.44	0	0	0	0	0	0
<i>Potamopyrgus</i> sp.	0	0	0	0	0.005 $\pm$ 0.005	1 $\pm$ 1	0.0003 $\pm$ 0.0003	3 $\pm$ 3	0.002 $\pm$ 0.002	11 $\pm$ 5
<i>Hydrobia</i> sp.	0	0	0.269 $\pm$ 0.128	372 $\pm$ 184	0.007 $\pm$ 0.003	45 $\pm$ 29	0	0	0	0
<i>Hydrobia ulvae</i>	0	0	0	0	0	0	0	0	0.391 $\pm$ 0.367	207 $\pm$ 133
<i>Hydrobia ventrosa</i>	0	0	0	0	0	0	0.171 $\pm$ 0.133	23 $\pm$ 7	0.311 $\pm$ 0.166	491 $\pm$ 270
<i>Littorina saxatilis</i>	0	0	0	0	0.096 $\pm$ 0.050	35 $\pm$ 10	0	0	0.001 $\pm$ 0.001	1 $\pm$ 1
<i>Theodoxus fluviatilis</i>	0	0	0	0	0.213 $\pm$ 0.064	106 $\pm$ 43	0.615 $\pm$ 0.335	166 $\pm$ 74	1.098 $\pm$ 0.323	431 $\pm$ 88
<i>Radix baltica</i>	0	0	0	0	0	0	0.143 $\pm$ 0.056	19 $\pm$ 5	0.395 $\pm$ 0.147	120 $\pm$ 35
Gastropoda (unknown)	0.0005 $\pm$ 0.0005	16 $\pm$ 16	0.020 $\pm$ 0.014	114 $\pm$ 59	0.012 $\pm$ 0.01	1 $\pm$ 1	0.001 $\pm$ 0.001	5 $\pm$ 5	0.002 $\pm$ 0.002	15 $\pm$ 15

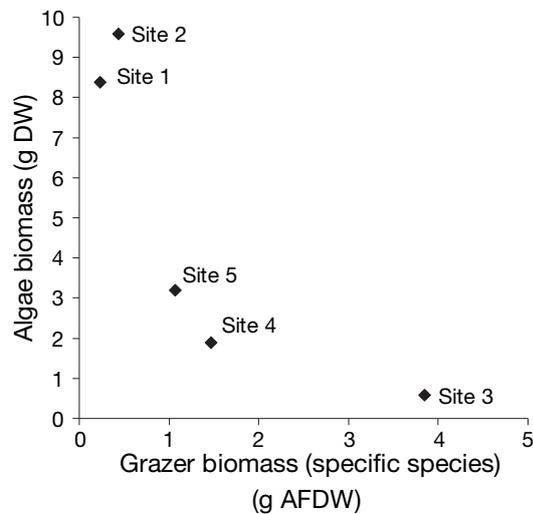


Fig. 3. Correlation between filamentous algae and biomass of grazers (g AFDW) selected based on the results of isotope analysis

spp., *Palaemon* spp., *Rissoa* spp., *Littorina* spp., *Hydrobia* spp., *Radix baltica*, *Theodoxus fluviatilis*, and *Potamopyrgus* sp. in the analysis of potential algal mesograzers. The small, tube-building amphipods *Erichthonius difformis* and *Corophium insidiosum* were not included, since these species are suspension- or deposit-feeders (Rasmussen 1973, Nair & Anger 1979) and hence have no negative impact on macroalgal growth (Moksnes et al. 2008). The biomass of potential algal grazers did not differ significantly between the 5 *Zostera* beds (Table 2, Fig. 2). However, according to the results of the isotope and mixing function analyses (see below), the omnivorous grass shrimp *Palaemon* spp. fed mainly on filamentous algae in the south coast bed, whereas algae constituted a less important part of their diet at the west and southeast coast sites. Therefore, in the second analysis of mesograzers biomass,

*Palaemon* spp. were not included as algal grazers in the analyses of samples from the west and southeast regions. For the same reason, the gastropods from the west coast, and *T. fluviatilis* from the south and southeast coasts, were excluded from the analysis. The biomass values for the selected algal grazers differed markedly between the *Zostera* beds, with significantly lower biomasses of mesograzers at the west coast sites compared to the south and southeast coast sites, which did not differ from each other (Table 2).

Testing for relationships between the mean biomasses of filamentous algae and mesograzers at the 5 study sites, we found a significant negative correlation between algae and all potential mesograzers (Pearson's correlation  $p < 0.05$ ,  $n = 5$ ,  $r^2 = 0.94$ ). A similar trend was detected between algae and selected grazers when we tested biomass values derived from the isotope analyses, but the correlation was not significant ( $p = 0.10$ ,  $n = 5$ ,  $r^2 = 0.65$ ; Fig. 3). However, that correlation showed a non-random distribution of residuals, indicating a log-linear relationship, and thus a log transformation of the algal biomass data improved the random distribution of residuals, giving a significant negative correlation ( $p = 0.01$ ,  $r^2 = 0.93$ ).

#### Fauna community and stable isotope analysis

The stable isotope analyses revealed complex trophic interactions in which filamentous algae appeared to constitute the most important food base in the *Zostera* communities in all 3 study regions. Few species seemed to utilize detritus as food, and only 2 of the gastropod species appeared to assimilate *Zostera*. The results also implied that large amphipods and isopods were the most important grazers on filamentous algae, and those crustaceans were in turn consumed by both shrimp and fish. However, the trophic

Table 4. Proportional contribution of  $\delta^{13}\text{C}$  in food sources of the most predominant crustacean and gastropod grazers in each study region, as given by the IsoSource linear mixing model (Phillips & Gregg 2003). Values (%) are means and distribution of feasible solutions (1st to 99th percentile)

Study region	Consumer	Food source		
		<i>Zostera marina</i>	filamentous algae	Detritus
West coast	<i>Gammarus locusta</i>	8 (0 to 16)	83 (81 to 86)	9 (0 to 19)
	<i>Microdeutopus gryllotalpa</i>	5 (0 to 11)	89 (87 to 90)	6 (0 to 13)
	<i>Rissoa</i> sp.	80 (63 to 94)	3 (0 to 6)	17 (0 to 36)
	<i>Littorina littorea</i>	35 (0 to 69)	23 (14 to 31)	43 (0 to 85)
South coast	<i>Gammarus locusta</i>	3 (0 to 7)	92 (90 to 94)	5 (0 to 10)
	<i>Idotea baltica</i>	23 (0 to 45)	46 (36 to 55)	32 (0 to 63)
Southeast coast	<i>Gammarus locusta</i>	0 (0 to 2)	98 (95 to 100)	2 (0 to 5)
	<i>Idotea baltica</i>	30 (13 to 47)	27 (0 to 53)	43 (0 to 86)
	<i>Theodoxus fluviatilis</i>	98 (96 to 99)	1 (0 to 2)	2 (0 to 4)
	<i>Radix baltica</i>	9 (0 to 18)	68 (51 to 83)	24 (0 to 48)

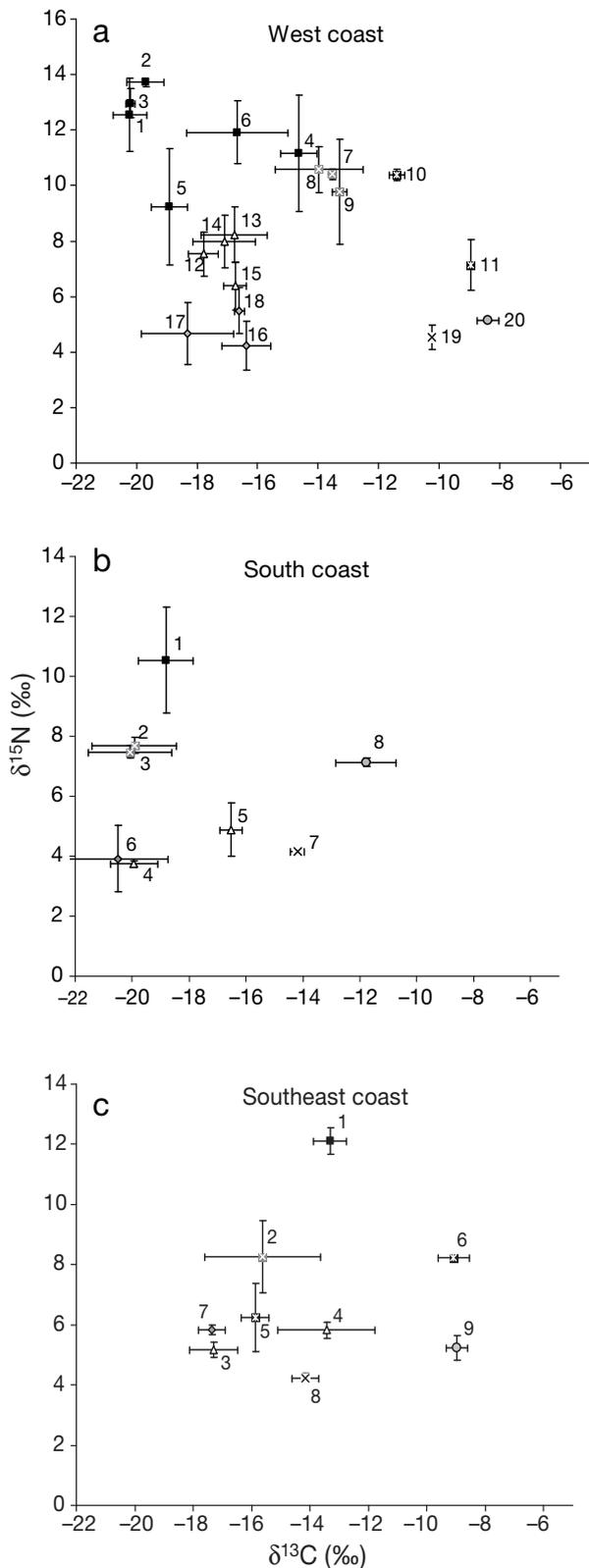


Fig. 4. Mean  $\pm$  SD of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  signatures of a number of species associated with *Zostera* beds off the (a) west, (b) south, and (c) southeast coasts of Sweden. See Table 5 for key to species for each panel

role of omnivorous grass shrimp appeared to differ between the regions.

At the west coast sites, the linear mixing model analysis of  $\delta^{13}\text{C}$  suggested that the amphipod grazers *Gammarus locusta* and *Microdeutopus gryllotalpa* mainly assimilated filamentous algae (Table 4), which is also supported by the finding of significantly higher  $\delta^{15}\text{N}$  signatures for the amphipods than for the algae (Fig. 4a, Tables 5 & 6). In contrast, the mixing model results indicated that *Zostera* constituted the main food source for the dominant gastropods of the genus *Rissoa* (Table 4). *Rissoa* spp. showed an average  $\delta^{15}\text{N}$  enrichment of 2‰ compared to *Zostera* (Fig. 4a, Table 5). The mixing model also disclosed that amphipods and gas-

Table 5. Each species and total length (TL), carapace length (CL), or carapace width (CW) for the data points in Fig. 4

No.	Species	Measurement (mm)	n
<b>West coast</b>			
1	<i>Gadus morhua</i>	TL ~110	5
2	<i>Syngnathus typhle</i>	TL ~150	1
3	<i>Gobiusculus flavescens</i>	TL ~40	4
4	<i>Gobius niger</i>	TL 50 to 60	4
5	<i>Gobius niger</i>	TL 92 to 98	2
6	<i>Gasterosteus aculeatus</i>	TL ~50	4
7	<i>Carcinus maenas</i>	CW 30 to 40	2
8	<i>Palaemon elegans</i>	CL 3 to 10, TL 26 to 48	3
9	<i>Palaemon adspersus</i>	CL 3 to 10, TL 26 to 48	2
10	<i>Littorina littorea</i>	TL 20	2
11	<i>Rissoa</i> sp.	TL ~4	5
12	<i>Microdeutopus gryllotalpa</i>	TL 0.5 to 3	2
13	<i>Erichtonius difformis</i>	TL 0.5 to 3	6
14	<i>Corophium insidiosum</i>	TL 0.5 to 3	3
15	<i>Gammarus locusta</i>	TL ~5	7
16	<i>Ectocarpales</i>		4
17	<i>Ulva</i> sp.		4
18	<i>Polysiphonia</i> sp.		4
19	Detritus		2
20	<i>Zostera marina</i>		2
<b>South coast</b>			
1	<i>Spinachia spinachia</i>	TL 70 to 100	3
2	<i>Palaemon elegans</i>	CL >7, TL >39	2
3	<i>Palaemon adspersus</i>	CL >7, TL >39	2
4	<i>Gammarus locusta</i>	TL ~7	2
5	<i>Idotea baltica</i>	TL ~9	2
6	Filamentous algae		6
7	Detritus		2
8	<i>Zostera marina</i>		2
<b>Southeast coast</b>			
1	<i>Gobius niger</i>	TL ~100	1
2	<i>Palaemon adspersus</i>	CL 3 to 10, TL 26 to 48	4
3	<i>Gammarus locusta</i>	TL ~10	5
4	<i>Idotea baltica</i>	TL ~10	6
5	<i>Radix baltica</i>	TL 5 to 10	3
6	<i>Theodoxus fluventalis</i>	TL ~4	2
7	Filamentous algae		3
8	Detritus		3
9	<i>Zostera marina</i>		4

tropods, in turn, were the main food of the grass shrimp *Palaemon elegans* and *P. adspersus*, and the shrimp had mean  $\delta^{15}\text{N}$  signatures between 1.6 and 4.2‰ higher than those noted for the amphipods and gastropods (Fig. 4a, Table 5). The  $\delta^{15}\text{N}$  signatures of the 2 shrimp species did not differ significantly (Table 6). The fish *Gobius niger* also appeared to be an important predator of amphipods, because it had a significantly higher  $\delta^{15}\text{N}$  signature than the amphipods did (Fig. 4a, Tables 5 & 6). The 2 different size classes of *G. niger* that were analyzed (TL 50 to 60 and 92 to 98 mm) had similar  $\delta^{15}\text{N}$  signatures, suggesting that both groups fed on the same trophic level, but they had different carbon isotope signatures (Table 6) and thus probably also different diets. Furthermore, the smaller *G. niger* had a nitrogen isotope signature closer to that of the grass shrimp (Fig. 4a, Table 5), indicating a higher proportion of gastropods in the diet. In the west coast beds, the fish *Gadus morhua*, *Gobiusculus flavescens*, *Syngnathus typhle*, and *Gasterosteus aculeatus* had the highest mean  $\delta^{15}\text{N}$  isotope signatures, which might demonstrate predation on a higher trophic level.

At the south coast site, the proportional contribution of  $\delta^{13}\text{C}$  revealed that filamentous algae was the most important food source for *Gammarus locusta* (Table 4), although  $\delta^{15}\text{N}$  signature was not significantly higher for *G. locusta* than for the algae (Fig. 4b, Tables 5 & 6). We also found that the  $\delta^{15}\text{N}$  signature of the isopod *Idotea baltica* did not differ significantly from that of *G. locusta*; even though the mixing model suggested that filamentous algae represent an important part of the diets of those species, it seems that they also consume detritus and *Zostera* (Table 4). The mean  $\delta^{15}\text{N}$  signatures of *G. locusta* and *I. baltica* were 2.6‰ to 4.0‰ lower than those of *Palaemon elegans* and *P. adspersus*, indicating that the shrimp consumed these grazers (Fig. 4b, Tables 5 & 7). However, according to the mixing model, filamentous algae constituted the most important food source for *P. elegans* and *P. adspersus* in the south coast bed (but not in the west and southeast beds; Table 7), since the shrimp had mean  $\delta^{15}\text{N}$  signatures 3.8 and 3.6‰ higher than the signature in the algae (Fig. 4b, Table 5). No significant difference in  $\delta^{15}\text{N}$  was found between *P. elegans* and *P. adspersus* (Table 7). Fish of the species *Spinachia spinachia* had  $\delta^{15}\text{N}$  signatures 2.8 and 3.1‰ higher than the values for *P. adspersus* and *P. elegans*, respectively, indicating that *S. spinachia* preyed on those shrimp in the south coast bed.

The mixing model analysis of  $\delta^{13}\text{C}$  at the southeast sites suggests that filamentous algae constituted the most important food source for both *Gammarus locusta* and the gastropod *Radix baltica* (Table 4), although the  $\delta^{15}\text{N}$  signatures of those animal species could not reveal any enrichment compared to the algae (Fig. 4c,

Table 5). The  $\delta^{15}\text{N}$  signature of the isopod *Idotea baltica* differed significantly from that of *G. locusta* (Table 6), and the mixing model indicated that the food consisted of algae, detritus, and *Zostera*, although in highly varying proportions (Table 4). *Theodoxus fluviatilis* showed 3.0‰ enrichment of  $\delta^{15}\text{N}$  compared to *Zostera* in the southeast coast beds, and the mixing model findings suggest *Zostera* is the most important food source for that gastropod (Table 4). The mixing model results for the southeast sites also indicated that *Palaemon adspersus* consumed mainly *G. locusta* and *I. baltica*, since those 2 species had significantly lower  $\delta^{15}\text{N}$  signatures (3.1 and 2.4‰, respectively) than the shrimp did (Fig. 4c, Tables 5 & 7). The fish *Gobius niger* had the highest  $\delta^{15}\text{N}$  isotope signature, and it was 3.9‰ higher than the  $\delta^{15}\text{N}$  signature of *P. adspersus*, indicating that the former species may be a predator on the latter in the southeast coast beds.

## DISCUSSION

The present study assessed structural aspects and trophic relationships in *Zostera* communities in 3 regions that are affected in different ways by eutrophication-related overgrowth of macroalgae. The results revealed striking dissimilarities in the communities with regard to the biomass of fast-growing filamentous algae and the biomass and size structure of the grazers. There was a significant negative correlation between the mean biomasses of the filamentous algae and the grazers at each site. This observation is not consistent with the 'production ceiling hypothesis', which suggests that plant production controls the biomass of motile epifauna (Edgar & Aoki 1993, Edgar & Klumpp 2003), but instead it indicates that the algal biomass is controlled by grazers, which in turn may also be controlled by top-down processes. Although we measured the standing stock of algal biomass and not the production of algae in the present study, previous observations showing high biomass of filamentous algae in eelgrass beds off the Swedish west coast do suggest that algal production is higher in that region than in the eelgrass systems along the Swedish south and southeast coasts (S. P. Baden unpubl. data). However, our data do not allow us to adequately assess the effect of grazer biomass on algal biomass, because the presence of filamentous algae is also determined by exposure to prevailing winds, which may have a greater impact on the south and southeast beds. That assumption is supported by the low organic content we found in the sediment in the south and southeast beds.

The dramatic differences between the 3 regions with regard to biomass and mean size of the large mesograzers *Gammarus* spp. and *Idotea* spp. are consistent

Table 6. Results of independent *t*-test used to analyze differences in  $\delta^{15}\text{N}$  between species (see Table 3 for species names in full). -: species not found in the area

Species	West coast			South coast			Southeast coast		
	p	df	t	p	df	t	p	df	t
<i>R. baltica</i> vs. algae	–	–	–	–	–	–	>0.05	3	0.46
<i>I. baltica</i> vs. algae	–	–	–	>0.05	8	1.36	>0.05	4	0.09
<i>M. gryllotalpa</i> vs. algae	<0.05	18	2.00	–	–	–	–	–	–
<i>G. Locusta</i> vs. algae	<0.05	23	2.36	>0.05	6	0.29	<0.05	3	3.20
<i>G. locusta</i> vs. <i>I. baltica</i>	–	–	–	>0.05	4	1.98	<0.05	9	3.11
<i>P. elegans</i> vs. algae	<0.05	20	7.50	<0.05	8	6.25	–	–	–
<i>P. adspersus</i> vs. algae	<0.05	19	6.73	<0.05	8	6.67	0.056	4	2.67
<i>Palaemon</i> sp. vs. <i>I. baltica</i>	–	–	–	<0.05	10	10.38	<0.05	6	3.94
<i>Palaemon</i> sp. vs. <i>G. locusta</i>	<0.05	12	14.52	<0.05	8	24.69	<0.05	5	4.25
<i>Palaemon</i> sp. vs. <i>E. difformis</i>	<0.05	11	5.25	–	–	–	–	–	–
<i>Palaemon</i> sp. vs. <i>M. gryllotalpa</i>	<0.05	7	6.82	–	–	–	–	–	–
<i>Palaemon</i> sp. vs. <i>C. insidiosum</i>	<0.05	8	6.35	–	–	–	–	–	–
<i>P. adspersus</i> vs. <i>R. baltica</i>	–	–	–	–	–	–	0.07	5	2.25
<i>P. elegans</i> vs. <i>P. adspersus</i>	>0.05	4	0.19	>0.05	6	1.68	–	–	–
<i>G. niger</i> (TL 50 to 60 mm vs. <i>G. niger</i> (TL 92 to 98 mm)	>0.05	9	1.90	–	–	–	–	–	–

Table 7. Proportional contribution of food sources (using  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  combined) for *Palaemon elegans* and *P. adspersus*, as given by the IsoSource linear mixing model (Phillips & Gregg 2003). Values (%) are mean and distribution of feasible solutions (1st to 99th percentile). Source increment was set at 1%. Tolerance was 0.1‰ with the following exceptions: 0.2% for *P. elegans* in the south coast bed and 0.5% for *P. adspersus* in the southeast coast beds; *P. elegans* was not found at the southeast sites

Consumer	Food source	Percent contribution to diet
<b>West coast</b>		
<i>Palaemon elegans</i>	<i>Gammarus locusta</i>	10 (0–32)
	<i>Microdeutopus gryllotalpa</i>	15 (0–47)
	<i>Erichtonius difformis</i>	16 (0–38)
	<i>Corophium insidiosum</i>	15 (0–43)
	<i>Rissoa</i> sp.	39 (0–42)
<i>Palaemon adspersus</i>	Filamentous algae	5 (0–16)
	<i>Gammarus locusta</i>	9 (0–30)
	<i>Microdeutopus gryllotalpa</i>	5 (0–18)
	<i>Erichtonius difformis</i>	4 (0–12)
	<i>Corophium insidiosum</i>	4 (0–14)
	<i>Rissoa</i> sp.	48 (46–50)
<b>South coast</b>	Filamentous algae	31 (20–39)
	<b>South coast</b>	
	<i>Palaemon elegans</i>	
<i>Palaemon elegans</i>	<i>Gammarus locusta</i>	2 (0–4)
	<i>Idotea baltica</i>	19 (19–19)
	Filamentous algae	79 (77–81)
<i>Palaemon adspersus</i>	<i>Gammarus locusta</i>	8 (0–22)
	<i>Idotea baltica</i>	10 (7–13)
	Filamentous algae	82 (67–91)
<b>Southeast coast</b>		
<i>Palaemon adspersus</i>	<i>Gammarus locusta</i>	73 (72–76)
	<i>Idotea baltica</i>	26 (23–28)
	<i>Theodoxus fluviatilis</i>	0.1 (0–1)
	<i>Radix baltica</i>	0.3 (0–1)
	Filamentous algae	0.5 (0–2)

with top-down control of such species and expected high, intermediate, and low abundance of small predators at the west, south, and southeast coast sites, respectively. Size-specific fish predation on amphipods has been found to cause a shift in the population size structure towards smaller individuals in many aquatic systems (Edgar & Aoki 1993, Blumenshine et al. 2000), including the eelgrass beds along the Swedish west coast (Moksnes et al. 2008). There is little information available at present regarding the abundance of small fish predators at the Baltic sites we studied. However, recent cage experiments carried out by Moksnes et al. (2008) using the same sites as we did have suggested that predation pressure on mesograzers is markedly higher in the 2 west coast *Zostera* beds than in the 2 southeast beds. Moksnes et al. (2008) observed that *G. locusta* can reach a large size and very high biomass in the absence of local predators, and hence that species can control the growth of filamentous green algae, even during periods of nutrient enrichment. However, those investigators also noted that local predators reduced the mean size and abundance of gammarids to very low levels, resulting in increased algal

growth. Similar cage experiments at the southeast sites did not reveal any effect of predators (S. P. Baden unpubl. data). On the west coast the fish species *Gobius niger* and *Gasterosteus aculeatus* are among the most abundant primary predators (Pihl et al. 2006), and the isotope assimilation data suggest that these species prey on the amphipod assemblage.

The mixing model analysis in the present study indicated that *Gammarus locusta* is an important grazer on filamentous algae. Algae also constituted the main source of food for the amphipod *Microdeutopus gryllotalpa*, whereas the isopod *Idotea baltica* and the gastropod *Radix baltica* appeared to feed only partly on algae, which agrees with other results in the literature (Duffy et al. 2001, Jormalainen et al. 2001, Goecker & Kåll 2003, Andersson 2005). The nitrogen isotope signatures of the grazers did not reveal clear enrichment compared to algae. However, recent studies have also detected considerable variation in nitrogen enrichment by marine invertebrates (McCutchan et al. 2003, Svensson et al. 2007), and consumers feeding mainly on detritus tend to exhibit lower  $\delta^{15}\text{N}$  discrimination than do carnivores or herbivores (Vanderklift & Ponsard 2003). This may also apply to *I. baltica* in the beds at our south and southeast sites. Only 2 small gastropods (*Rissoa* sp. and *Theodoxus fluviatilis*) had carbon and nitrogen signatures indicating assimilation of *Zostera* as their main source of food. It is plausible that *Zostera* epidermis is ingested by animals as they browse on the film of microalgae and bacteria on the surface of the leaves (Fredriksen et al. 2004).

Our isotope analyses of the omnivorous grass shrimp suggest that these species are more carnivorous in the beds off the west and southeast coasts than at the site off the south coast, and thus they may play different trophic roles in the 3 regions. This deduction is supported by a recent study of *Zostera* beds along the Swedish west coast (Persson et al. 2008), in which it was found that *Palaemon elegans* preferred to feed on small gammarids rather than algae, resulting in a positive net effect on algal growth. However, if the gammarids were more than 5 mm in length, *P. elegans* shifted towards consuming algae. The low abundance of small amphipod prey in our south coast *Zostera* bed may explain why *P. elegans* mainly assimilated algae. Analysis of the stomach contents of the south coast shrimp confirmed that the animals had chiefly ingested filamentous algae (T. Jephson unpubl. data).

In conclusion, this study identified *Gammarus locusta*, *Microdeutopus gryllotalpa*, and *Radix baltica* as the most important grazers of macroalgae, and *Idotea* sp. and *Palaemon* spp. (on the south coast) probably have a negative impact on algal growth as well. *G. locusta* and *Idotea baltica* showed greater biomass and mean sizes in the Baltic Sea beds (south and south-

east coasts) compared to the west coast beds, where *G. locusta* individuals were <5 mm and *Idotea* spp. were missing, even though we found the highest algal biomass at those sites. Therefore, it can be expected that the grazing pressure on algae will be lower in the west coast *Zostera* beds than in the south and southeast coast beds. Lower grazing pressure on algae at the west coast sites may be the result of top-down control of grazers due to a trophic cascade effect. In short, that means that overfishing and a decrease in large predators may have increased the density of intermediate predators, which in turn has lowered the biomass of algal mesograzers, and such a reduction in grazing control has then allowed the filamentous algae to flourish during periods of nutrient pollution. Also, the isotope signatures indicate that *Zostera* was used only to a limited extent as a source of energy by the predominant invertebrates.

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