



A neighbour is a neighbour? Consumer diversity, trophic function, and spatial variability in benthic food webs

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ARTICLE INFO

Article history:

Received 3 March 2010

Received in revised form 10 June 2010

Accepted 14 June 2010

Keywords:

Functional diversity

Niche complementarity

Predator–prey interactions

Stable isotopes

$\delta^{13}\text{C}$

$\delta^{15}\text{N}$

ABSTRACT

The short ecological history and the environmental conditions characterising the Baltic Sea make it inhabitable for only few species, resulting in a functional poverty of the system (number of functional groups and number of species within each group). Thus, it is a well-suited system for studies on biodiversity and ecosystem functions, particularly when moving from observation of patterns to determination of mechanisms behind observed relationships, such as the importance of species richness for trophic functioning. Predators in the benthic community are predominately generalists, with a potential for overlap in trophic function. Through analysis of stable isotope ratios ($^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$), we determined the trophic position of epibenthic consumers and estimated spatial variability in isotope ratios of food web components at nine shallow sandy sites. There were significant differences in isotope ratios both within species and for species assemblages between bays. The secondary consumer signatures in bivariate δ -space showed a partly overlapping transition from benthivores (*Crangon crangon*, *Pomatoschistus microps*) to more pelagically feeding predators (*Gasterosteus aculeatus*). At two sites (one sheltered, one moderately exposed), the gut contents of generalist predators revealed feeding on abundant prey and confirmed the potential for overlap in diets. Focusing on members of the benthic trophic pathway, we assessed the influence of secondary consumer diversity on trophic transfer, with temporal separation of resource use as a mediator of biodiversity effects. In a laboratory experiment, we were able to show temporally separated foraging for two epibenthic carnivores and that mechanisms behind the biodiversity effect differed in time. Many food web properties, such as function, resilience and resistance are linked to the diversity and characteristics of nodes and links in the food web (e.g. degree of redundancy, connectedness and trophic level) and our study provides information on some dimensions of the trophic niches of abundant species in shallow soft-bottom food webs.

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1. Introduction

Positive relationships between biodiversity and ecosystem functions have been reported from a range of ecosystems and trophic levels (Loreau et al., 2000; Balvanera et al., 2006; Cardinale et al., 2006; Stachowicz et al., 2007). For primary producers of temperate grasslands (Tilman et al., 1996), detritivores in streams (Jonsson and Malmqvist, 2000), and secondary consumers on marine shores (Griffin et al., 2008), species richness influences ecosystem functions, such as stability, biological production, and resource acquisition. Currently, focus has shifted to the functions provided by consumers and the potential consequences of diversity changes within consumer trophic levels (Duffy, 2002; Ives et al., 2005). Higher-level consumers are likely to be strong interactors within the food web, but are also prone to local extinction (Petchey et al., 2004; Byrnes et al., 2007). Members of a

feeding guild use the same resources in similar ways and may in a trophic sense be functionally equivalent (Blondel, 2003). However, the trophic niche includes several dimensions of feeding, including *on what*, *where*, and *when* foraging takes place, and such niche segregation may be of importance for trophic functioning (Fridley, 2001).

On shallow marine sandy bottoms in northern Europe, several sympatrically occurring predators (crustaceans, gobiids and flatfishes) show a dietary overlap, feeding on invertebrate infauna (Pihl, 1985; Aarnio et al., 1996). The diet of generalist predators depends on which food items are spatially or temporally available (Evans, 1983), causing variability in realized feeding links. Acknowledging such variability, we evaluated epibenthic predator positions in trophic pathways by studying stable isotope ratios ($^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$, expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) (Peterson and Fry, 1987) between and within secondary consumers at a set of shallow sandy sites. Stable isotopes are useful for determining trophic structure when the isotope ratios of a consumer reflect those of its diet in a fairly predictable manner. $\delta^{13}\text{C}$ provides an indication of carbon sources used by an organism, as its value changes relatively little (0–1‰) between diet and consumer. $\delta^{15}\text{N}$ shows a

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stepwise increase (2–4%) from one trophic level to the next (McCutchan et al., 2003; Fry, 2006). Together, these two variables provide a time-integrated measure of trophic position (Peterson and Fry, 1987), integrating realized feeding relationships (Layman, 2007). Trophic pathways can be strongly linked to spatial attributes and many studies point to connections between species trophic interactions and the immediate surroundings (Deegan and Garritt, 1997; Guest et al., 2004; Connolly et al., 2005; Kanaya et al., 2007). The sites included in this study range in exposure from relatively sheltered to exposed, a characteristic known to influence energy flow (Möller et al., 1985). By depicting the spatial consistency of position in bivariate δ -space of benthic species, we assessed their relative position in major trophic pathways, accounting for site-specific diets. For comparative purposes we also studied gut contents of epibenthic predators at two sites (geographically close, differing in exposure).

For predators feeding on the same set of prey species (belonging to the same trophic pathway), aspects of the trophic niche other than prey preferences may be important for coexistence, e.g. habitat preferences and in particular the time of active foraging. Foraging at different times of the day could decrease niche overlap and increase total resource use in diverse predator assemblages. Such mechanisms constitute the rationale for the niche complementarity hypothesis, which is one of the proposed explanations for heightened functioning in high-diversity assemblages (Loreau and Hector, 2001; Karlson et al., 2010). Although the theory of resource partitioning has been generally accepted for decades (Schoener, 1974), there is a lack of experimental evidence to support that predator diversity effects on prey capture are mediated through niche complementarity (Bruno and Cardinale, 2008; Griffin et al., 2008).

Two of the epibenthic predator species commonly found at shallow sandy sites in the northern Baltic Sea are known to feed at different times: the flounder, *Platichthys flesus* L., is a visual hunter and feeds during daytime (Mattila and Bonsdorff, 1998), whereas the brown shrimp, *Crangon crangon* L., feeds mainly in lower light conditions (night, dusk and dawn) (Pihl and Rosenberg, 1984). Using this pair of co-occurring generalist predators and two types of prey in a laboratory experiment, we tested the following hypotheses: (1) higher diversity in a predator assemblage results in high predation efficiency; and (2) the diversity effect is mediated through differences in time of feeding.

A consensus on significant relationships between biodiversity and ecosystem functioning is now established, and the next challenge is to identify the mechanisms behind the observed patterns (Hector et al., 2009). Comparing process rates observed in species mixtures against the rates in the average monoculture and the highest performing monoculture assesses non-transgressive and transgressive overyielding, respectively (Fridley, 2001; Griffin et al., 2008). Additive partitioning of biodiversity effects identifies two categories of mechanisms: complementarity effects (resource partitioning, facilitative or interference interactions), and selection effects (including positive and negative sampling effects, connecting to dominance or subordination of species with particular traits) which together amount to the net biodiversity effect (Loreau and Hector, 2001). Fox's (2005) subsequent development of a tripartite partitioning yields a component of trait-independent complementarity (equal to the complementarity effect of Loreau and Hector, 2001), and further splits the previously mentioned selection effect into trait-dependent complementarity and dominance. Identification of mechanisms underpinning biodiversity and ecosystem functioning patterns are needed for future predictions of consequences following species loss or gain, but formal comparisons of the available measures are rare (Hector et al., 2009), and to the best of our knowledge, no estimates of diel variation in biodiversity effects are available.

The overall study objective was to assess aspects of the trophic ecology of an assemblage of benthic generalist consumers. More specifically, we wanted to (1) determine species-specific positions in

trophic pathways, (2) assess effects of predator diversity and temporal feeding habits on predation efficiency, and (3) identify mechanisms behind potential biodiversity effects. By combining spatial variation-inclusive estimates of predator positions in trophic pathways with a short-term functional experiment, we elucidated realized trophic patterns as well as a temporal manifestation of mechanisms behind main predator–prey relationships in the low-diversity study system.

2. Methods

Organisms for the stable isotope analysis, dietary analysis and laboratory experiment were collected from shallow (<1.5 m) sediment sites using the following methods: Macrozoobenthos using a 1 mm sieve, predatory epibenthic fauna using a beach seine (2 mm net) and a push net (2 mm net). Surface sediment cores (top 2 cm) were collected by snorkelling. Organisms for stable isotope analysis were sampled in nine bays (Table 1) around the Åland Islands, northern Baltic Sea (Fig. 1). All sites were shallow with sandy substrate and sparse vegetation. The degree of exposure assigned to each bay varied from relatively sheltered (sites A1, A3 and B4) via moderately exposed (B5, B6, C8 and C9) to exposed (A2 and C7). Predators for dietary analysis were collected at sites B4 and B5, which are geographically close but differ in exposure to wind and waves.

2.1. Epibenthic consumer trophic positions, stable isotope analysis

We evaluated epibenthic predator trophic positions using $\delta^{13}\text{C}$ as an indicator of carbon source (base of food web) and $\delta^{15}\text{N}$ as a proxy for trophic level. We studied epibenthic predators (fishes and *C. crangon*) and included infaunal macroinvertebrates and sediment organic matter (SOM) for comparison. Sampling was performed during a time interval of 12 days (Table 1) to minimize the effect of temporal changes in stable isotope values (Nordström et al., 2009). Macroinvertebrates were overnight placed in filtered seawater (20 μm) to allow gut evacuation. Organisms (determined to lowest possible taxon) and sediment were stored frozen (-20°C) and later oven-dried (60°C , 48 h) and ground, after which an aliquot of the homogenous sample was packed in a tin capsule. Samples of fishes and shrimp were muscle tissue. Other invertebrates were analyzed whole, molluscs after removing the shell. Samples were composites of several individuals, and were not acidified since this could affect stable isotope ratios (Cabel et al., 2006). Also, the amphipod *Bathyporeia pilosa* Lindström, which constitutes the samples likely most affected by acidification, is consumed entirely by the predators, whereby exoskeleton isotopes contribute to consumer ratios. Analysis of stable isotope ratios $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$ was conducted at the Stable Isotope Facility, UC California, Davis. Carbon and nitrogen isotope ratios are expressed in per mille (‰) delta (δ) values according to:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left[\left(R_{\text{sample}} / R_{\text{standard}} - 1 \right) \right] \times 10^3$$

where R is $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$. The international standards for C and N are Vienna-PDB and atmospheric N_2 , respectively (Fry, 2006). Data accuracy was estimated by analyzing sets of subsamples in triplicate from all bays. The reproducibility for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was 0.2‰ or better. When possible, we analyzed three replicate samples per species per site.

When sampling for stable isotope analysis, we also measured water temperature ($^\circ\text{C}$) and took samples for water chemistry. Dissolved O_2 (mg l^{-1} , %) was measured by Winkler titration, salinity from conductivity on a Metrohm 712, and pH on a Metrohm 691. Levels of total P and total N ($\mu\text{g l}^{-1}$) were determined spectrophotometrically after persulfate oxidation, and Chl-*a* ($\mu\text{g l}^{-1}$) after filtration and acetone extraction (Chl-*a*). Sediment samples for analysis of organic content (loss on ignition, 3 h at 500°C) ($n=3$) and grain size distributions were

Table 1
Description of sites visited for collection of surface sediment, primary and secondary consumers for stable isotope analysis. Degree of exposure calculated from the Baardseth Exposure Index modified for archipelago conditions (Berglund et al., 2003). n/a = data not available.

Area, site nr	Site name	Date of sampling	Coordinates	Exposure: degree and direction	Sediment organic content (%)	Sediment grain size	Vegetation observed during sampling	Salinity	pH	Temp (°C)	Chl- <i>a</i> (µg l ⁻¹)	Tot-N (µg l ⁻¹)	Tot-P (µg l ⁻¹)
A1	Norrsandvik	7.6.2007	60°22 N 19°36 E	18° NE	0.51 ± 0.04	Medium and coarse sand	<i>Fucus vesiculosus</i> , <i>Cladophora glomerata</i> and <i>Chorda filum</i> found on stones and boulders. Sparse vegetation (<i>Potamogeton pectinatus</i> , <i>Chara aspera</i>) characterized the bottom.	5.3	8.5	17.4	1.3	260	12
A2	Finbo	7.6.2007	60°21 N 19°36 E	90° E	0.23 ± 0.01	Mostly very coarse sand, also granules, coarse and medium sand	<i>Fucus vesiculosus</i> , <i>Cladophora glomerata</i> and <i>Chorda filum</i> found on stones and boulders. Sparse vegetation (<i>Potamogeton pectinatus</i> , <i>Chara aspera</i>) characterized the bottom.	5.5	8.5	15.2	n/a	n/a	n/a
A3	Äppelö, Södersand	9.6.2007	60°22 N 19°42 E	36° S	0.37 ± 0.02	Medium sand	<i>Cladophora glomerata</i> on rocks, <i>Chara aspera</i> , <i>Potamogeton pectinatus</i> , <i>Chorda filum</i> , <i>Potamogeton perfoliatus</i>	5.3	8.1	15.6	1.0	300	22
B4	Skeppsvik	11.6.2007	60°11 N 19°31 E	18° W	0.30 ± 0.02	Medium and fine sand	Mostly bare sandy bottom, but <i>Chara aspera</i> , <i>Potamogeton pectinatus</i> and loose-lying <i>Pylaiella littoralis</i> present	6.0	8.7	17.4	1.1	300	28
B5	Hinderbengtsviken	11.6.2007	60°10 N 19°32 E	63° SW	0.20 ± 0.01	Coarse sand	Bare sand, some loose-lying filamentous algae (e.g. <i>Pylaiella littoralis</i>)	6.0	8.5	13.6	1.2	270	17
B6	Degersand	11.6.2007	60°09 N 19°36 E	54° S	0.14 ± 0.01	Mostly medium sand, also fine sand	Bare sand, some loose-lying filamentous algae (e.g. <i>Pylaiella littoralis</i>)	5.7	8.3	13.2	1.7	290	24
C7	Maren	16.6.2007	60°11 N 20°15 E	81° S	0.27 ± 0.03	Medium and fine sand	Close to the shore almost uniform <i>Chara aspera</i> , further out moderate amounts of <i>Potamogeton pectinatus</i> . On rocks mostly <i>Pylaiella littoralis</i> and/or <i>Cladophora glomerata</i>	5.5	8.4	19.7	0.9	260	13
C8	Prästö	16.6.2007	60°12 N 20°15 E	54° SW	0.18 ± 0.01	Mostly medium sand, also fine sand	Bare sand, only sparse occurrence of <i>Potamogeton pectinatus</i>	5.2	8.2	15.9	1.6	310	18
C9	Mickelsö	19.6.2007	60°12 N 20°17 E	45° W	0.24 ± 0.01	Mostly medium sand, also fine sand	Bare sand, small amounts of <i>Chara aspera</i> , <i>Potamogeton pectinatus</i> , single <i>Potamogeton perfoliatus</i> individuals, also <i>Cladophora glomerata</i> on small rocks.	5.6	8.3	17.4	1.3	420	24

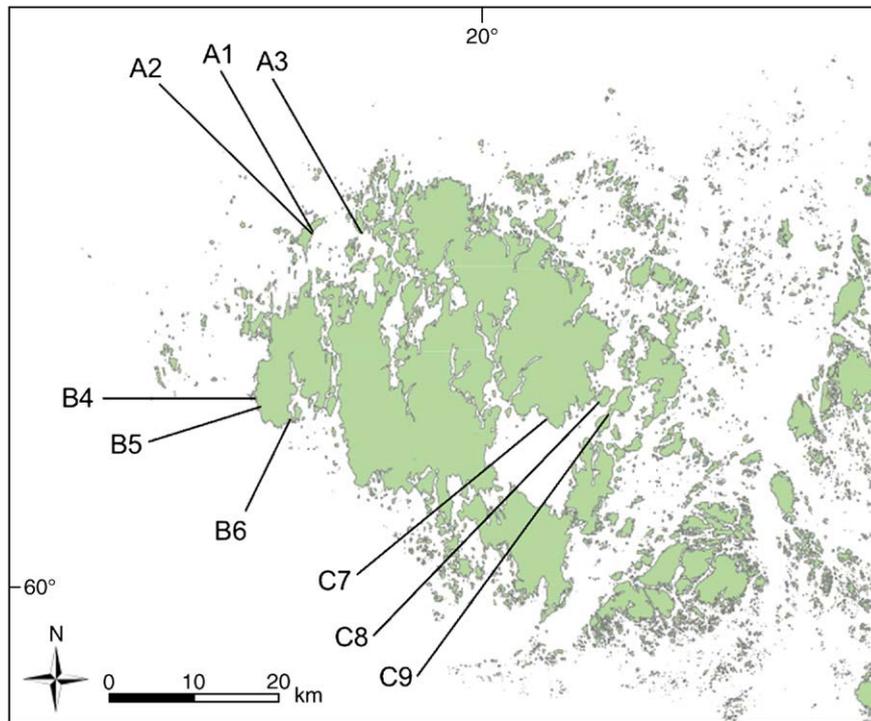


Fig. 1. Study sites at the Åland Islands, northern Baltic Sea. Letters indicate geographical grouping of sites.

also collected from all localities. The data are presented with other site characteristics in Table 1.

2.2. Epibenthic consumer diets, gut content analysis

The epibenthic predators, *Crangon crangon*, *Pomatoschistus microps* Krøyer, *Pomatoschistus minutus* Pallas, and *Platichthys flesus* were collected for dietary analysis in two bays (B4 and B5; Table 1), in July, August and September. Predator densities varied greatly and some species were absent at one site on some occasions. Only *P. flesus* gut contents are presented for each sampling event, the rest are given as an average for the whole season. Each individual predator was weighed and its total length measured (0.01 g and 1 mm accuracy), and then stored in 70% alcohol for analysis of contents of stomach and/or intestine. Prey items were determined to lowest possible taxon and counted.

2.3. Predation efficiency in differing predator assemblages, laboratory experiment

We used juvenile flounder, *Platichthys flesus*, and brown shrimp, *Crangon crangon*, as predators. The flounder is the most common flatfish in the northern Baltic Sea, where its juveniles are sympatric to the brown shrimp on shallow sandy bottoms (Aarnio et al., 1996). Two prey species were used, juvenile *Macoma balthica* L. (Bivalvia), and *Bathyporeia pilosa* (Amphipoda), which are both among the dominant infauna of the biotope, and are eaten by the predators used in this experiment (Pihl, 1985; Aarnio et al., 1996; this study).

The experiment used a two-factor design. The factor, 'Predator assemblage', had three levels: (1) *P. flesus*, (2) *C. crangon*, and (3) *P. flesus* + *C. crangon*. The other factor, 'Time', had two levels: (1) day, and (2) night. This design allowed us to study the independent and interactive effects of diversity and time of feeding, i.e. to take into account potential temporal resource partitioning. The different predator treatments constituted a substitutive design equalizing density over single species and combination treatments. In our experiment, density equalled two predators per replicate and the ecological function of

interest, namely predation efficiency, was measured as per capita consumption rate. A control treatment without predators was used to check for mortality unrelated to predation. Each treatment consisted of six replicates.

Flounders were 56–72 mm (average 63 ± 7 mm) and shrimp 49–62 mm (average 55 ± 5 mm) in total length. The prey species averaged 1.9 mm (*M. balthica*) and 2.7 mm (*B. pilosa*) in length. 30 individuals per prey were added to each aquarium, 1102 ind. m^{-2} per species and a total of 2204 ind. m^{-2} , corresponding well to natural densities (Blomqvist and Bonsdorff, 1986; Bonsdorff et al., 1995). A high density of predators was used, as the effects of diversity are most pronounced at high predator densities (Griffin et al., 2008).

All trials were conducted in a temperature-regulated room (12.0–14.6 °C). During trials, salinity and pH were about 4.8 and 7.9, respectively. High oxygen levels ($\geq 92\%$) were maintained by air bubbling. The substrate was 3 cm deep dried, sieved ($\leq 500 \mu\text{m}$) sand (organic content 0.2%). Predators were starved for 48 h prior to trials to equalize hunger levels. A fine net prevented predators from escaping. Prey were acclimatised to the trial tanks before predators were added and trials started. The predators were allowed to forage for 5 h (09–14, 21–02) in either light or dark conditions. After completion of trials, the sand was sieved and remaining prey counted. The short trial duration also enabled us to conduct gut contents analysis on *P. flesus*. Gut contents were studied under a microscope and retrieved prey counted. Prey were difficult to distinguish in the gut of *C. crangon* and prey that were unaccounted for (found neither in the sediment nor in the gut of *P. flesus*) were counted as eaten by the brown shrimp.

2.4. Data analyses

To evaluate if spatial variation in stable isotope ratios was present within species, means of the measured ratios were tested over sites using one-way ANOVA or t-tests, if assumptions of normality and homogeneity of variances were fulfilled, otherwise the non-parametric Kruskal–Wallis test was used. Multivariate analyses (ANOSIM and nMDS based on Euclidean distances) tested for differences in stable

isotopes among sites ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$). We focused on a subset of species (*Crangon crangon*, *Pomatoschistus minutus*, *Pomatoschistus microps*, *Gasterosteus aculeatus* L., *Macoma balthica*) and sites (A1–B4, C7 and C9) in order to get a balanced analysis. Relationships between environmental variables and site stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ separately) were evaluated using the BEST procedure in PRIMER 6 (Clarke, 1993; Clarke and Gorley, 2006). Comparisons between epibenthic secondary consumer species ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were made using ANOSIM, where the R statistics of pairwise tests were considered 'low' if <0.5 . Interspecific comparisons were made using two-way ANOVA (factors 'Site' and 'Species') for organisms not included in multivariate analysis.

Predation efficiency was measured as per capita consumption per trial for each prey species. Total consumption was calculated as the sum for both prey species. The expected prey-specific consumption in the combination treatment was calculated as the sum of observed per capita consumption in monocultures divided by the number of predator species (in this experiment: 2) (Griffin et al., 2008). The proportional deviation from expected predator effects was expressed as [(observed consumption – expected consumption)/expected consumption] \times 100. For evaluation of non-transgressive overyielding, prey consumption in the combination treatment was compared with the average of monocultures (Fridley, 2001). Efficiency data from the experiment were analyzed with two-way ANOVA using R 2.7.2 (R Development Core Team, 2008). Tukey's honestly significant difference (HSD) was used for *a posteriori* multiple comparisons. Data were tested for normality and homogeneity of variances prior to analyses and transformed if not meeting the assumptions. The tripartite partition (trait-independent complementarity, trait-dependent complementarity, and dominance) of the net biodiversity effect was calculated according to Fox (2005), and each effect type was tested for deviation from 0 (no significant effect) using a one-sample t-test.

3. Results

3.1. Consumer stable isotope ratios and spatial variability

Stable isotope ratios $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$ were studied in the species in a benthic food web of nine shallow soft-bottom bays. The lowest average consumer $\delta^{13}\text{C}$ was recorded for the bivalve *Macoma balthica*, -22.1‰ (site C8), and the highest for the ragworm *Nereis diversicolor*

Müller, -14.9‰ (site A2) (Fig. 2). The corresponding values for $\delta^{15}\text{N}$ were 3.4‰ for *M. balthica* (site B4) and 11.9‰ for *Pomatoschistus minutus* (site C7). Unfortunately, the sediment samples contained too little N and C to give reliable estimates of isotope ratios. The SOM isotope values are given in Fig. 2, but excluded from further analyses.

Sites differed in assemblage $\delta^{13}\text{C}$ composition (ANOSIM; global $R=0.715$, $p\leq 0.001$, Table 2). A cluster analysis based on $\delta^{13}\text{C}$, separated the two most sheltered sites A1 and B4 from the other sites, meaning that they had assemblages more similar in C isotope composition than some bays located geographically closer to each other (e.g. sites A1 and A2). A site-specific composition of nitrogen ratios was also identified (ANOSIM global $R=0.773$, $p\leq 0.001$), with site C7 primarily separated from the other bays by clustering. Geographical distance between sites was thus not consistent in influencing the stable isotope values of food web components. There were no significant correlations between matrices constructed from abiotic variables and $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (BEST, $p>0.05$).

Significant intraspecific differences in stable isotopes ratios for both C and N were found (Fig. 2, Table 2). Some species showed large ranges in $\delta^{13}\text{C}$, e.g. *Macoma balthica* differed up to 5.0‰ between site-averages, whereas for *Bathyporeia pilosa* the largest between-site difference was 1.5‰. The corresponding ranges for $\delta^{15}\text{N}$ were 2.7‰ and 1.4‰ for *M. balthica* and *B. pilosa* respectively. Among the secondary consumers, *Crangon crangon* showed the largest range and differed up to 2.4‰ in $\delta^{13}\text{C}$, and 2.5‰ $\delta^{15}\text{N}$, whereas *Gasterosteus aculeatus* showed significant differences only for $\delta^{13}\text{C}$ by up to 1.4‰.

Secondary consumer trophic signatures differed between species when including spatial variation (ANOSIM Global $R=0.691$, $p\leq 0.001$, Table 2). The three-spined stickleback, *G. aculeatus*, showed isotope ratios indicating a diet consisting of pelagic prey (Fig. 2), separating this species from other secondary consumers. The stable isotope ratios of *Crangon crangon* differed significantly from those of the sand goby, *Pomatoschistus minutus*, but overlapped with the common goby, *Pomatoschistus microps* (Table 2). The two gobiid species showed an intermediate but significant separation ($R=0.511$, $p\leq 0.001$). In all, this suggests that *P. microps* utilizes benthic food sources to a greater degree than *P. minutus*. There was no significant spatial difference in flounder $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ between the two sites (B5 and B6) where *Platichthys flesus* was caught in sufficient amounts for stable isotope analysis. However, *P. flesus* was isotopically separated from *C. crangon* at both sites ($\delta^{13}\text{C}$: two-way ANOVA, 'Species' F_1 ,

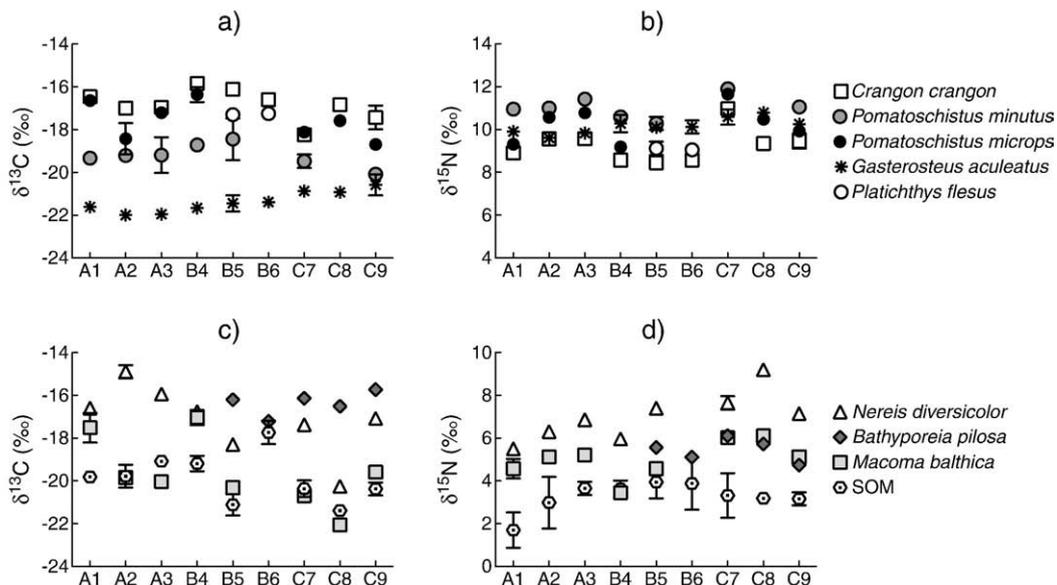


Fig. 2. Stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, ‰) of benthic food web components for sites A1–C9. a)–b) secondary consumers: *Gasterosteus aculeatus*, *Crangon crangon*, *Pomatoschistus minutus*, *Pomatoschistus microps*, *Platichthys flesus*; and c)–d) lower trophic levels: *Nereis diversicolor*, *Bathyporeia pilosa*, *Macoma balthica*, SOM.

Table 2

Results from univariate analyses (A = ANOVA; K–W = Kruskal–Wallis; t = t-test) on intra-specific (between-site) stable isotope values, and multivariate analyses (ANOSIM) on inter-specific and site-specific differences in stable isotope values. Significant values are presented in **bold**.

Species, between sites	Test	df	MS	F/ χ^2 /t	p
$\delta^{13}\text{C}$					
<i>Crangon crangon</i>	A	8, 18	1.526	6.656	≤ 0.001 ***
<i>Pomatoschistus minutus</i>	A	6, 11	0.574	2.209	0.121
<i>Pomatoschistus microps</i>	K–W	6	16.069	0.013	*
<i>Platichthys flesus</i>	t	4	–0.189	0.859	
<i>Gasterosteus aculeatus</i>	K–W	8	17.953	0.022	*
<i>Nereis diversicolor</i>	K–W	5	16.064	0.007	**
<i>Macoma balthica</i>	K–W	7	21.28	0.003	**
<i>Bathyporeia pilosa</i>	A	4, 10	3.668	38.121	≤ 0.001 ***
$\delta^{15}\text{N}$					
<i>Crangon crangon</i>	A	8, 18	1.847	13.106	≤ 0.001 ***
<i>Pomatoschistus minutus</i>	A	6, 11	0.699	5.338	0.008 **
<i>Pomatoschistus microps</i>	A	6, 14	2.264	33.135	≤ 0.001 ***
<i>Platichthys flesus</i>	t	4	0.207	0.846	
<i>Gasterosteus aculeatus</i>	A	8, 18	0.407	2.451	0.054
<i>Nereis diversicolor</i>	K–W	5	15.316	0.009 **	
<i>Macoma balthica</i>	K–W	7	18.981	0.008 **	
<i>Bathyporeia pilosa</i>	A	4, 10	3.428	6.286	0.009 **
ANOSIM				R	p
Secondary consumers, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$					
Global				0.691	≤ 0.001 ***
<i>G. aculeatus</i> , <i>C. crangon</i>				0.975	≤ 0.001 ***
<i>G. aculeatus</i> , <i>P. minutus</i>				0.896	≤ 0.001 ***
<i>G. aculeatus</i> , <i>P. microps</i>				0.911	≤ 0.001 ***
<i>C. crangon</i> , <i>P. minutus</i>				0.768	≤ 0.001 ***
<i>C. crangon</i> , <i>P. microps</i>				0.064	0.083
<i>P. minutus</i> , <i>P. microps</i>				0.511	≤ 0.001 ***
Sites, $\delta^{13}\text{C}$					
Global				0.715	≤ 0.001 ***
Sites, $\delta^{15}\text{N}$					
Global				0.773	≤ 0.001 ***

$s = 17.693$, $p = 0.003$; $\delta^{15}\text{N}$: two-way ANOVA, 'Species' $F_{1, 8} = 8.414$, $p = 0.020$, no significant interactions between 'Site' and 'Species').

Regarding primary consumers, *B. pilosa* was consistently more enriched in ^{13}C than *M. balthica* ($\delta^{13}\text{C}$: two-way ANOVA, 'Species' $F_{1, 16} = 7.230$, $p < 0.001$, no significant interaction, Fig. 2), but only at site B5 for $\delta^{15}\text{N}$ (two-way ANOVA, 'Site' \times 'Species' $F_{3, 16} = 6.670$, $p = 0.004$). *Nereis diversicolor* also had significantly higher $\delta^{13}\text{C}$ values than *M. balthica*, except at site A1 (two-way ANOVA, 'Site' \times 'Species': $F_{5, 24} = 14.681$, $p < 0.001$, Tukey's HSD for A1 $p = 0.428$, site B1 with only one replicate was not included in analysis). The high $\delta^{15}\text{N}$ of *N. diversicolor* is in agreement with its predatory nature (two-way ANOVA, 'Species': $F_{1, 24} = 10.111$, $p < 0.001$, no significant interaction between 'Site' and 'Species').

3.2. Epibenthic consumer diets

The dietary analyses provided us a snapshot of active predation on benthic macroinvertebrates and revealed some differences in the contribution of prey taxa to consumer diets at two sites. Of 429 guts examined, 217 guts contained material, from which 20 prey taxa were identified. At site B4, *Pomatoschistus microps* had fed on meiofauna and Chironomidae, whereas *Pomatoschistus minutus* also consumed molluscs and crustaceans (Fig. 3). Meiofauna was a significant part of the diet of most predators ($\geq 43.2\%$ of prey objects found in gut). The diet of *Crangon crangon* consisted mostly of macrozoobenthos, although this may be connected to the large number of empty guts noted for *C. crangon*, i.e. most ingested prey were already digested. Crustaceans

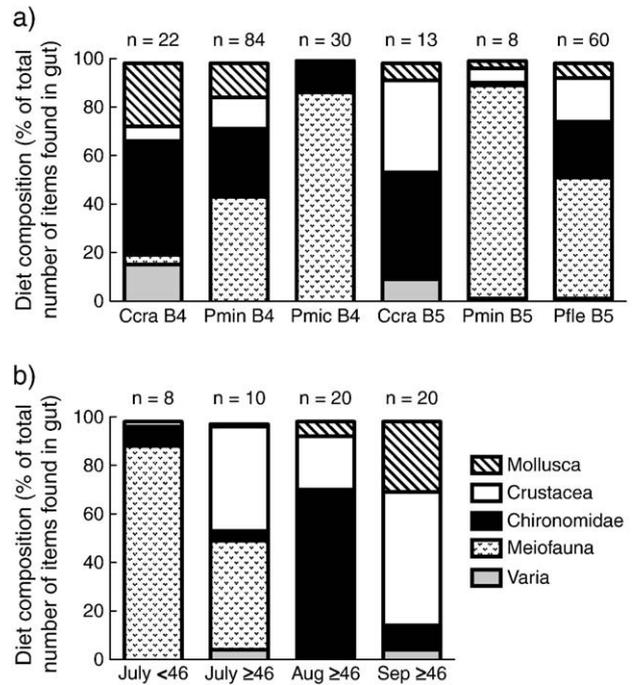


Fig. 3. Dietary composition (n of prey objects, %) of epibenthic predators at sites B4 and B5: Ccra = *Crangon crangon*, Pmin = *Pomatoschistus minutus*, Pmic = *Pomatoschistus microps*, Pfle = *Platichthys flesus*. a) Interspecific predator diets averaged for the entire season. b) Monthly dietary composition of *Platichthys flesus* (size classes separated at 46 mm; Aarnio et al., 1996) at site B5.

quantity (mainly *Bathyporeia pilosa*) were more important in the diet of *C. crangon* at the exposed site, B5, where amphipods dominates the faunal community. At this site, *Platichthys flesus* seemed to switch consumption from meiofauna to macrofauna (e.g. *B. pilosa* and Chironomidae) as it grew during the season (Fig. 3). Yield-effort curves suggest that only *P. minutus* at B4 was sufficiently sampled, as the curves for other consumers did not approach an asymptote. Nevertheless, the gut analyses show that the generalist predators in the bays studied have the potential to use abundant or profitable prey groups that may differ between life stages or sites. All benthic predators consumed the most abundant prey taxa (pers. obs.), confirming that interspecific dietary overlap occurs.

3.3. Consumer diversity and temporal predation efficiency

The laboratory experiment showed that temporal separation in foraging activity determined the level of predation efficiency and the manifestation of biodiversity effects. Average survival of prey in the control treatment was 99%, indicating negligible non-predatory mortality. Predation efficiency differed between predator assemblages depending on the time of the trial ('Predator assemblage' \times 'Time': $p < 0.001$, Table 3a). The combination treatment showed consistently high predation efficiency whereas the monocultures alternately showed decreased per capita consumption in accordance with predator-specific temporal feeding habits: *Platichthys flesus* foraged almost exclusively during daytime, *Crangon crangon* mostly at night (Fig. 4). When the predation efficiency was separated into prey-specific effects, some differences were observable. During daytime, all predator assemblages showed a comparable consumption of *Bathyporeia pilosa* (Tukey's HSD: $p > 0.05$) (Fig. 4c), while more *Macoma balthica* were consumed in the *P. flesus*-treatment than in the *C. crangon* assemblage (Tukey's HSD: $p < 0.001$). In the combination treatment, predation efficiency was independent of time (Tukey's HSD: $p > 0.05$). However, the gut content analyses show that the two predator species foraged in temporally

Table 3

Two-way ANOVA results for a) predation efficiency (number of prey consumed), b) predation efficiency (number of prey found in gut) in the combination treatment, and c) non-transgressive overyielding. Significant values presented in **bold**.

Source	df	MS	F	p
a)				
Total prey consumption				
Predator assemblage	2	4.797	5.111	0.012 *
Time	1	1.284	1.369	0.251
Predator assemblage × time	2	27.262	29.047	≤0.001 ***
Error	30	0.939		
Consumption of <i>Macoma balthica</i>				
Predator assemblage	2	0.466	1.450	0.251
Time	1	1.068	3.323	0.078
Predator assemblage × time	2	10.925	34.000	≤0.001 ***
Error	30	0.321		
Consumption of <i>Bathyporeia pilosa</i>				
Predator assemblage	2	2.791	9.526	0.001 ***
Time	1	0.010	0.034	0.855
Predator assemblage × time	2	3.943	13.458	≤0.001 ***
Error	30	0.293		
b)				
Total prey consumption				
Predator species	1	315.400	4.467	0.047 *
Time	1	0.400	0.005	0.943
Predator species × time	1	4732.000	67.018	≤0.001 ***
Error	20	70.600		
Consumption of <i>Macoma balthica</i>				
Predator species	1	92.040	2.570	0.125
Time	1	18.380	0.513	0.482
Predator species × time	1	737.040	20.583	≤0.001 ***
Error	20	35.810		
Consumption of <i>Bathyporeia pilosa</i>				
Predator species	1	66.670	4.237	0.053
Time	1	24.000	1.525	0.231
Predator species × time	1	1734.000	110.212	≤0.001 ***
Error	20	15.730		
c)				
Total prey consumption				
Predator assemblage	1	3.880	4.063	0.057
Time	1	0.440	0.461	0.505
Predator assemblage × time	1	0.618	0.647	0.431
Error	20	0.955		
Consumption of <i>Macoma balthica</i>				
Predator assemblage	1	0.683	1.821	0.192
Time	1	0.718	1.912	0.182
Predator assemblage × time	1	0.0001	0.001	0.987
Error	20	0.375		
Consumption of <i>Bathyporeia pilosa</i>				
Predator assemblage	1	1.307	5.440	0.030 *
Time	1	0.034	0.141	0.712
Predator assemblage × time	1	0.634	2.638	0.120
Error	20	0.240		

distinct ways also in this treatment, just as in the monocultures (Table 3b, Fig. 5a).

Comparing the performance of the combination treatment with that of the average monoculture and the highest performing monoculture assesses non-transgressive and transgressive overyielding, respectively. Transgressive overyielding was not evident in our trials, as the combination treatment did not differ significantly from the most efficient predator assemblage, irrespective of time of day (Fig. 4a). Based on consumption in monocultures, predators in the combination treatment were expected to show a predation efficiency of 1.2–1.8 prey $\text{ind}^{-1} \text{h}^{-1}$. The observed consumption of *M. balthica* was 23 and 29% higher than expected values. The predation on *B. pilosa* differed in deviations from expected values during daytime and nighttime trials. Amphipod consumption during daytime exceeded expected values by 8%, while the nighttime trial resulted in values 50% higher than expected (Fig. 5d). All deviations were positive and indicate that prey sources were used to a comparable or even higher degree by the more diverse predation assemblage, in particular *B. pilosa* during night (Table 3c). The

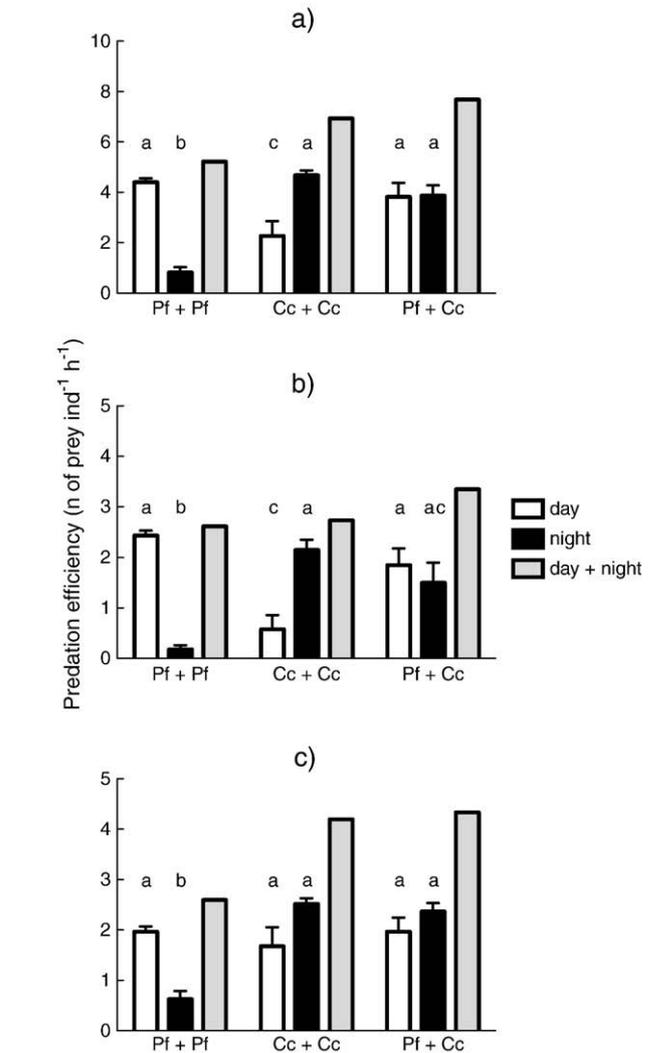


Fig. 4. Predation efficiency (n of prey consumed $\text{ind}^{-1} \text{h}^{-1}$, mean + SE): the number of a) total prey, b) *Macoma balthica*, and c) *Bathyporeia pilosa*, consumed in predator assemblages *Platichthys flesus* (Pf), *Crangon crangon* (Cc), *Platichthys flesus* and *Crangon crangon*, during day and night. Grey bars show overall predation effect (day and night values added). Data show significant interactions for 'Predator assemblage' and 'Time' for all prey groups. Different letters indicate significant differences (Tukey HSD: $p < 0.05$). Note the different scales on the y-axes.

more diverse predator assemblage showed a significantly higher amphipod consumption rate, indicating non-transgressive overyielding (Fig. 5d). No such effect was found for *M. balthica* (Fig. 5c). The net biodiversity effect was positive in all predator mixture treatments, but significantly so only for nighttime predation on *B. pilosa* ($t = 4.490$, $df = 5$, $p = 0.007$) (Fig. 6). Dominance ($t = 3.450$, $df = 5$, $p = 0.018$, regarded as marginally significant after correction for multiple tests) was the driving mechanism behind the net effect, found also for nighttime predation on *M. balthica* ($t = 16.360$, $df = 5$, $p < 0.001$), but counteracted by negative (non-significant) trait-independent complementarity and trait-dependent complementarity. Dominance corresponds to the selection effect (Loreau and Hector, 2001) when trait-dependent complementarity is zero (Hector et al., 2009), and the selection effect was significant for nighttime predation on both *B. pilosa* ($t = 4.997$, $df = 5$, $p = 0.004$) and *M. balthica* ($t = 5.431$, $df = 5$, $p = 0.003$). Our experiment shows that diversity effects on an ecological function can occur through temporal resource use as well as predator-specific preferences for certain prey species.

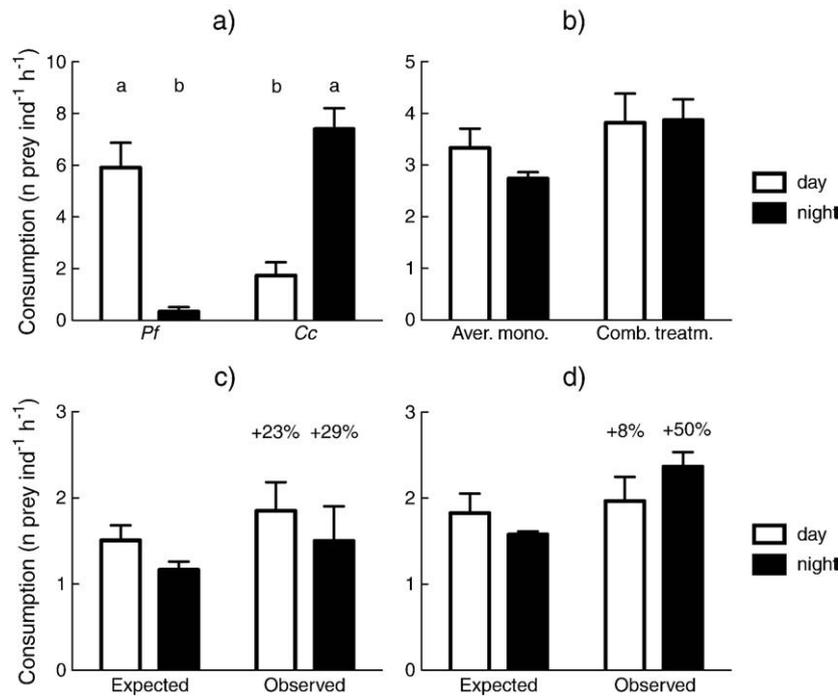


Fig. 5. Species-specific predation efficiency in the predator combination treatment: a) Total number of prey found in gut of predators *Platichthys flesus* (Pf) and *Crangon crangon* (Cc). b) Non-transgressive overyielding did not occur for total prey as predation efficiency (n of prey consumed ind⁻¹ h⁻¹, mean + SE) in the combination treatment did not differ significantly from the average monoculture. c) Expected and observed consumption (n of prey ind⁻¹ h⁻¹, mean + SE) of *Macoma balthica* and d) *Bathyporeia pilosa* in the combination treatment. Percentages show deviation from expected values. Different letters indicate significant differences (Tukey HSD: $p < 0.05$). Note the different scales on the y-axes.

4. Discussion

Benthic consumer positions in major trophic pathways were identified and described through analyses of stable isotope ratios and gut contents. In a laboratory predation experiment we evaluated the temporal separation of epibenthic predator foraging, and found biodiversity effects to manifest temporally. Even though large-scale, spatial patterns suggest stable interspecific relationships, other dimensions of the trophic niche can enable food web components to function dynamically within the framework of the web.

4.1. Spatial isotope patterns

Local processes influence element transfer in benthic food webs (Guest et al., 2004; Norkko et al., 2007) and isotope ratios are a result of site-specific element flows. Specific pathways have been identified on scales of tens of meters to a few 100 m, where differing δ -values may occur within a locality, e.g. within or between habitats (Guest et al.,

2004; Kanaya et al., 2007; Riera et al., 2009). Variation also occurs at larger scales (up to hundreds of km; Jennings and Warr, 2003), e.g. in connection to spatial subsidies of organic matter (Norkko et al., 2007) or proximity to nutrient discharges (Hansson et al., 1997; Savage and Elmgren, 2004). Spatial differences in phyto- and zoobenthos stable isotope ratios can be larger than seasonal differences for the same species (Jennings and Warr, 2003; Kanaya et al., 2007; Nordström et al., 2009).

In general, the trophic structure of the sampled species assemblages in terms of the vertical distribution ($\delta^{15}\text{N}$) was consistent in space. There were significant differences in $\delta^{15}\text{N}$ values among localities, both regarding the whole sample assemblages and within-species comparisons over sites, but since the trophic shift, $\Delta\delta^{15}\text{N}$, is variable (McCutchan et al., 2003) and the separation between an obligate primary consumer and secondary consumers in our dataset generally was large, between-site differences in $\delta^{15}\text{N} < 3\%$ are perceived as resulting from e.g. local nitrogen dynamics rather than indicating changes in trophic level. For one of the study sites, vertical stability on a temporal scale was previously demonstrated (Nordström et al., 2009), supporting the pattern reported here.

Spatial differences in $\delta^{13}\text{C}$ were not clearly related to the geographical placement of sites, nor did any relationship between abiotic site characteristics and $\delta^{13}\text{C}$ emerge. Variables fluctuating on a short-term basis are not believed to be major structuring factors for the isotope ratios in the studied organisms. The separation of sheltered sites from more exposed bays in our analysis has at least two hypothetical, not mutually exclusive, explanations: (1) spatial differences in isotope ratios are manifested at basal resource level; and (2) exposure to waves and wind changes the relative importance of organic matter produced benthically and pelagically (Möller et al., 1985; Newsome et al., 2007). The shift in $\delta^{13}\text{C}$ was especially evident for the facultatively suspension- and deposit-feeding bivalve *Macoma balthica* as its $\delta^{13}\text{C}$ values were up to 5‰ higher at sheltered sites than in more exposed bays (Fig. 7). As $\Delta\delta^{13}\text{C}$ is considered to be $< 2\%$ between the consumer and its diet (McCutchan et al., 2003), a

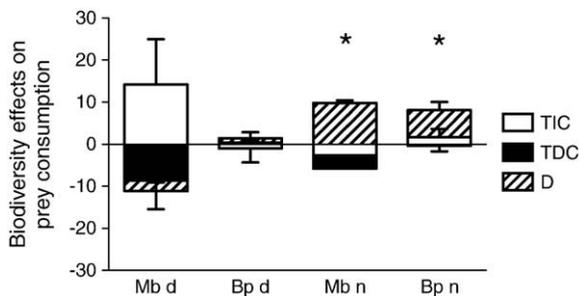


Fig. 6. The net effect on prey consumption partitioned into diversity components; trait-independent complementarity (TIC), trait-dependent complementarity (TDC), and dominance (D); mean + SE. *Macoma balthica* (Mb), *Bathyporeia pilosa* (Bp), day (d), night (n). Asterisks (*) indicate significant ($p < 0.05$) dominance effects. No other partitioned diversity effects differed significantly from zero. Significant net effect found only for Bp n.

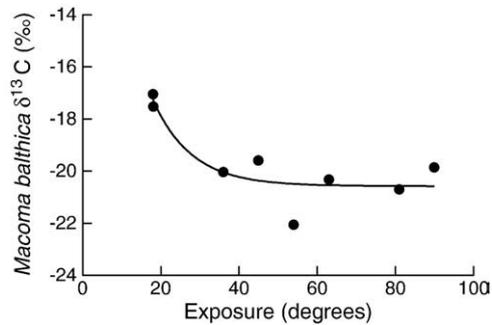


Fig. 7. Degree of exposure and mean *Macoma balthica* $\delta^{13}\text{C}$ values at sampled sites. Line represents best fit (robust regression).

difference of the magnitude observed for *M. balthica* (if not mirrored at basal resource level) indicates a complete switch in feeding habit or food objects between sites, in accordance with the sediment quality-related switch in feeding mode from filtering to deposit-feeding in *M. balthica* found by Ólafsson (1986). The spatial variability observed for $\delta^{13}\text{C}$ exceeds the generally accepted limits of trophic shift, suggesting caution when pooling isotope data from different habitats or over large spatial scales.

4.2. Secondary consumers in the benthic food web

In this study, we evaluated several dimensions of benthic secondary consumer trophic niches: (1) prey preferences or trophic pathway (dietary analysis, stable isotope ratios), and (2) temporal resource use (predation experiment).

4.2.1. Prey preferences/element pathway

The dietary analysis showed that the generalist predators had fed on abundant prey groups irrespective of location suggesting potential overlap in feeding, consistent with gut content-based evaluations conducted elsewhere (Pihl, 1985; del Norte-Campos and Temming, 1994). The specific distinction of stable isotope ratios of the secondary consumers varied, and there was partial overlap between predators relying on pelagic and benthic food. For example, the intermediate separation in bivariate δ -space for two congeneric species, *Pomatoschistus minutus* and *Pomatoschistus microps*, supports previous suggestions of trophic segregation between the gobies (Nellbring, 1988; Salgado et al., 2004) and indicates that *P. microps* is trophically closer to *Crangon crangon*.

One of the assumptions made when using stable isotopes to determine trophic structure is that interspecific differences in δ -space result from dietary separation. However, the stable isotope values of a consumer also depend on physiological processes by which the assimilated nutrients are 'routed' to various tissues, and are thus ultimately a result of the isotope incorporation-rate of a particular tissue (Wolf et al., 2009). Stable isotope analysis has recently been suggested to contribute to niche ecology by depicting aspects of the trophic niche (Bearhop et al., 2004; Layman et al., 2007), but inference from stable isotope δ -values is not straightforward since intra- and interspecific variation depends on fractionation factors, and variability in consumer diet and isotope ratios of food sources (Newsome et al., 2007; Hoenighaus and Zeug, 2008). Clearly, including spatial variation in our approach is a strength, as it identifies the range over which consumer isotopic values vary in similar biotopes at distances of hundreds of meters to tens of kilometres (100 m to 40 km).

4.2.2. Temporal resource use

Resource partitioning can enable co-existence between species. The mechanisms of resource partitioning are multidimensional, and

generally, temporal separation of niches is of less importance than separation by habitat or food-type (Schoener, 1974). Compared to other groups, however, predators are more often separated by specific diel activity patterns (Schoener, 1974) and our study shows that the ecological function, prey capture rate, of juvenile flounder and brown shrimp is similar, but separated temporally. Although systematically separate (different phyla), the brown shrimp, *Crangon crangon*, and juvenile flounder, *Platichthys flesus*, can be considered functionally equivalent on shallow soft bottoms of the Baltic Sea in that they both feed on abundant infaunal invertebrates (Pihl, 1985; Aarnio et al., 1996, this study). Assemblages consisting of functionally equivalent species may maintain resource use through compensation if one species is locally lost (Yachi and Loreau, 1999; Duffy, 2002). For this to occur, the predators should, not only feed on the same prey, but also exert comparable predation pressure. In this study, such redundancy was not found. Instead, the predator species showed a temporal separation in feeding. Intraspecific interactions seemed to have a greater negative impact on predation efficiency than intraspecific ones, as the treatment containing both predator species was able to match the best performing single species treatment irrespective of time of day (Fig. 5). Increased or high predation efficiency in higher-diversity consumer assemblages has previously been found for marine benthos (Boström, 2002; Fodrie et al., 2008; Griffin et al., 2008), although the mechanisms causing this differed between studies.

There are several mechanisms, such as niche differentiation or species interactions, which may result in biodiversity effects. Mechanisms can act simultaneously, and reinforce or counteract each other, making it informative to test for biodiversity effects and, irrespective of the outcome, evaluate underlying mechanisms. The evidence for transgressive overyielding in empirical studies is mixed (Duffy et al., 2007; Bruno and Cardinale, 2008). Our experiment allowed for testing of transgressive overyielding only in day and nighttime trials separately, and no such biodiversity effect was found. Overall (day + night) predation efficiency in the combination treatment was high, but cannot be conclusively interpreted to show transgressive overyielding. However, non-transgressive overyielding was evident for predation on one of the prey species, *Bathyporeia pilosa*, and dominance was the primary mechanism found for consumption on both prey types during nighttime trials. A large and positive dominance effect is expected when species occupy similar niches, and the one with higher monoculture yields dominates at the expense of the species with low monoculture performance (Fox, 2005). Hector et al. (2009) suggested that the contribution of trait-dependent complementarity is normally small because niches are not usually nested. Trait-independent complementarity will occur if individuals of all species perform better in mixtures, due to e.g. facilitation. However, the predators we used are not expected to experience a direct facilitation of the kind observed by Fodrie et al. (2008). The prey in our study are consumed whole by the epibenthic predators, and facilitation would be more likely to originate from altered behaviour or habitat selection of prey.

To conclude, we set out to study aspects of benthic consumer trophic properties, including consumer positions in major trophic pathways and the influence of secondary consumer diversity on predation efficiency, and temporal niche separation as a mediator of biodiversity effects. Our findings show some interspecific divergences in foraging, but also reveal a considerable overlap in trophic function between benthic predators in the northern Baltic Sea, where temporal separation of feeding may lead to biodiversity effects. Short-term studies need to be complemented with studies on biodiversity effects that take longer time to become manifest, and studies using other experimental set-ups, such as additive experimental designs, such as that by Boström (2002), who found *C. crangon* and *P. flesus* to function additively (Sih et al. 1998).

The reduced growth of benthic organisms in the sub-optimal salinity of the northern Baltic Sea skews the size distribution of this entire food web towards small body sizes (e.g. prey smaller than a

few cm). The epibenthic assemblages in the northern Baltic Sea consist of few species, most of them generalists. This results in a prevalence of weak links in the food web, due to mechanisms such as prey switching. Trophically flexible species (wide niches) may promote population stability by incorporating carbon and nutrients from several sources at lower food web levels (Romanuk et al., 2006). Neighbouring bays may differ in relative importance of carbon pathways and species may function differently at different sites, though still linked to the same metacommunity (Leibold et al., 2004). Thus, the “neighbours” within a benthic community can maintain food web structure through variability in trophic functioning. The influence of predator diversity on food web/ecosystem functioning is a challenging, but fruitful, area of research. Incorporation of spatial and temporal scales in this type of work is required if our ultimate aim is to be able to predict consequences of species loss.

Acknowledgements

We thank U. Jacob, and two reviewers for providing helpful comments, which improved the manuscript. Thanks to K. Häggqvist for preparing samples, and to Husö biological station for providing working facilities. Staff and students are acknowledged for all the help. Financial support was received from Stiftelsen för Åbo Akademi. [ST]

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