



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

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### 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  $\delta$ -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  $\delta$ -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  $\mu\text{m}$ ) to allow gut evacuation. Organisms (determined to lowest possible taxon) and sediment were stored frozen ( $-20^\circ\text{C}$ ) and later oven-dried ( $60^\circ\text{C}$ , 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 ( $\delta$ ) 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  $\text{N}_2$ , 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  $\text{O}_2$  ( $\text{mg l}^{-1}$ , %) 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  $500^\circ\text{C}$ ) ( $n=3$ ) and grain size distributions were

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