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Research Article

Trophic position and basal energy sources of the invasive prawn *Palaemon elegans* in the exposed littoral of the SE Baltic Sea

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Abstract

We investigated the abundance, trophic position, and linkages to basal energy sources of the non-indigenous prawn *Palaemon elegans* in shallow (0.5–1.6 m) stony habitats of the exposed coast of the SE Baltic Sea. Prawn abundance at the site with artificial stone was higher than that in the natural stony habitats. Stable isotope analysis (SIA) suggested similarity in feeding between different size classes of *P. elegans*. However, SIA of stomach contents showed greater variability of ingested food among large individuals (body length > 25 mm). Trophic position was estimated at 3.0 ± 0.8 suggesting the prevalence of animal prey in the assimilated diet of *P. elegans*. However, filamentous green algae was also consumed by large-sized individuals, as indicated by their isotopic signature and the elemental (C:N) ratio of their stomach contents. Modeling of the contribution of *Cladophora* and particulate organic matter, as basal food sources, to the diet of *P. elegans* (two end-member mixing model) revealed that only 40% of the assimilated biomass was derived from macroalgae, either directly or through intermediate consumers. This finding suggests that pelagic production was the main carbon source supporting prawn's nutrition. In an experimental study, *P. elegans* readily consumed mysids, suggesting that this prey may be the prawn's link to the pelagic food chain.

Key words: artificial habitats, filamentous macroalgae, littoral mysids, stable isotope analysis

Introduction

Stony substrates play a key role in maintaining species diversity in littoral communities along exposed coastal areas of the SE Baltic Sea. Hydrodynamic forcing and eutrophication induce extreme conditions that may result in a decline of macroalgae and associated fauna from these habitats (Bučas et. al. 2009). Availability of this habitat type in the open sand areas might be significantly improved by the construction of artificial reefs or other artificial structures (Jensen 2002). In turn this may change the structure of benthic communities and alter the ecosystem functioning (Chojnatski 2000). Artificial substrate habitats may also become a stepping stones for the spread of fauna associated with macroalgae and potentially change the patterns of invasive species colonization.

The arrival of non-indigenous species is a crucial driver of biodiversity in coastal communities of the Baltic Sea (Leppäkoski et al. 2002). Crustaceans represent one of the most successful groups of aquatic invaders due to their broad environmental tolerances, omnivorous feeding habits, and r-selected life-history traits (Bij de Vaate et al. 2002; Hänfling et al. 2011). They may substantially affect local communities through predation or competitive exclusion of native species (Hänfling et al. 2011). A recent invader of the littoral zone of the Baltic Sea coast is the rock pool prawn *Palaemon elegans*, Rathke 1837. *P. elegans* colonized western coasts of the southern Baltic Sea decades ago (Berglund 1985), and recent molecular investigations suggest that human-mediated invasion played a role in its dispersal (Reuschel et al. 2010). The prawn has spread to the southern (Janas et al. 2004; Grabowski et al. 2005; Jażdżewski et al. 2005) and southeastern Baltic coasts (Daunys and Zettler 2006), and its distribution is currently expanding northwards (Lavikainen and Laine 2004; Grabowski 2006; Kotta and Kuprijanov 2012; Katajisto et al. 2013). *P. elegans* was observed in the Lithuanian coastal waters for the first time in 2002 (E. Bacevičius personal communication).

Palaemon elegans is a characteristic species of open habitats in the tidal zone, on sandy and stony bottom, covered with macroalgae or seagrass (Berglund 1980). In newly invaded areas of the Baltic Sea, it has been found in a wide range of habitats with different exposure, vegetation and sediment types (Lapinska and Szaniawska 2006; Katajisto et al. 2013). *P. elegans* has become an important component of fish diet in these areas (Gruszka and Więcaszek 2011) and is considered among the major threats leading to population decline in the native palaemonid *Palaemon adspersus* Rathke, 1837 (Grabowski 2006). *P. elegans* is characterized as an omnivore, thus its feeding activities have the potential to directly affect both herbivores and algae (Eriksson et al. 2010). Site-specific variation in the diet of *P. elegans* has been reported in relation to the abundance of invertebrate prey and filamentous algae (Berglund 1980; Janas and Baranska 2008; Jephson et al. 2008). Our limited understanding of the species trophic role hampers prediction of the consequences of invasion for local communities.

Gut content analysis of *P. elegans* in Baltic coastal waters have shown that detritus and filamentous algae are the most frequently occurring food items as well as various invertebrates (Janas and Baranska 2008). Quantification of food items in crustacean stomachs is, however, a difficult task, and a large proportion of food items may remain unidentified or undetected. In addition, identifiable food items may vary in gut passage time and have different nutritional value for the organism. For example, nutritional quality in terms of carbon (C):nutrient ratios shows substantial variation in aquatic primary producers whereas it is more stable in animal tissues (Sterner and Elser 2002). Therefore, gut content analysis might not reflect variable nutritional quality and assimilation efficiency of diverse food resources. Lastly, it provides only a 'snapshot' of food consumption and may not show true preferences of an organism in a long-term perspective. In contrast, stable isotope analysis (SIA, ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$) provides information on consumer's diet over longer time scales (e.g., weeks to months for crustaceans; Gorokhova and Hansson 1999; Lesutienė et al. 2008). The carbon isotope is used to reveal the ultimate sources of carbon (i.e. basal energy sources) for a consumer species, whereas the nitrogen isotope is used for assessing consumer's trophic position (Post 2002). The isotopic signature of the consumer reflects the assimilated C and N from their diet and therefore reflects differences in nutritional sufficiency of various dietary components.

The goals of this study were: to assess and compare *P. elegans* abundance in artificial and natural stony habitats; to estimate the trophic position of *P. elegans* using nitrogen stable isotope analysis; and to evaluate the relative contribution of basal energy sources, i.e. macroalgae and particulate organic matter, to the nutrition of *P. elegans*. To accomplish this, we analyzed the stable isotopic composition of gut contents to determine whether macroalgae were consumed, and applied a mixing modelling to assess macroalgae contributions to assimilated diet. Finally, we experimentally investigated the feeding of *P. elegans* on littoral mysids, a prey that may provide a link to the pelagic food chain.

Methods

Study site

The study area was a high-energy coastline exposed to predominating south-westerly winds and high wave activity (Kelpšaitė et al. 2011). The area is influenced by a eutrophic water plume from the Curonian Lagoon. Mean salinity is 6.0 ± 1.2 and chlorophll *a* concentrations vary from 0.7 to 156 mg m^{-3} (Vaičiūtė 2012). The habitat is mostly sandy with solitary large boulders or patches of stony areas. At the 1–15 m depth, hard bottom substrates are covered by red algae (*Furcellaria lumbricalis);* maximum abundance is at 4–10 m depths (Bučas et al. 2009). The shallow upper littoral (<1 m) is colonized by filamentous algal communities dominated by *Cladophora glomerata*, *Bangia atropurpurea* and *Enteromorpha intestinalis* (Labanauskas 1998). Typical hard-bottom macroalgal and associated fauna communities also occur on the artificial substrates (piers and moles; Bučas et al. 2009).

Burrowing infaunal (*Marenzelleria viridis, Pygospio elegans, Macoma baltica*) or actively swimming nectobenthic (*Bathyporeia pilosa, Crangon crangon*) species are the major components of the fauna (Olenin and Daunys 2004). The crustacean fauna colonizing hard substrates includes isopods, gammarids, and mysids (Olenin and Daunys 2004).

Abundance estimates

To compare *P. elegans* abundance in artificial and natural stony habitats, three sampling sites were selected along the 25 km coastline between

Klaipeda and Palanga (Table 1). Sampling sites at Karklė and Nemirseta represent natural stony bottom habitats, whereas the Palanga site is the artificial habitat formed by concrete constructions and stones placed for the protection of the city's pier. Semi-quantitative samples were taken by a hand net (opening size 25×25 cm, mesh size 0.5 mm) in June 2011. Four replicate vertical hauls were performed by scraping the vertical surfaces from the bottom to the top of the large boulder or concrete block at each sampling location. The depth at sampling sites ranged from 0.5 to 1.6 m (Table 1). Collected prawns were preserved in 4% formaldehyde and their abundance expressed as individuals per square meter of the bottom.

All specimens in the samples were counted and measured. Body length (BL) was estimated from the tip of the rostrum to the end of the telson to the nearest millimeter. For biomass (dry weight), the length to weight relationship was estimated using measurements of 34 individuals. Prawns were measured and dried individually at 60°C to the constant weight and weighed with a precision of ± 0.2 mg. The best model for the relationship between body weight (BW) and length relationship was: $BW = 0.002\ BL^{2.98}$ (BL range 22–47 mm, $r^2 = 0.99$, $n = 34$, $P < 0.001$).

Samples for Stable Isotope Analysis

Samples for SIA were collected at the Smiltyne site in September 2011 (Table 1). The littoral community at this site is represented by similar macroalgal and crustacean assemblages as found at the prawn sampling locations typical for the Lithuanian exposed coast. Macroalgae (*Cladophora*) were collected from stones, washed to remove debris and epiphytes, and stored frozen. A hand net was used to collect littoral crustaceans. *P. elegans* were frozen immediately, whereas the smaller crustaceans were kept overnight in filtered sea water for gut content evacuation (Hill and McQuaid 2011) and then stored frozen. All samples were maintained at -20°C temperature.

For SIA preparation, field samples were defrosted at 4°C. Crustaceans were identified, sorted, and measured. Individuals of *P. elegans* were divided into four size classes: BL < 15, 15–25, 26–35, 36–45 mm. Samples of muscle (abdominal body part) and stomach content for SIA were prepared from individual prawns. The stomach was dissected and the bolus removed to obtain the sample. Three to six replicates of muscle and eight to fifteen stomachs of several pooled individuals were prepared for each size class. Samples were dried at 60°C for 48 h, ground to fine powder in an agate mortar, and 0.5–1 mg of sample weighed into tin capsules for SIA.

Amphipods (*Gammarus* spp.; BL < 8 mm) and isopods (*Idotea* spp.; 7–20 mm) were used as baseline grazer species (Kotta et al 2006) for assessing the trophic position of *P. elegans*. Each sample consisted of 3–5 pooled individuals and six samples of each baseline species was prepared for SIA as described above.

Water samples for determination of SIA of particulate organic material (POM) were screened through 200 µm Nitex to remove mesozooplankton. Seston was concentrated on precombusted and preweighted glass fiber filters (Whatmann GFF, 47 mm diameter), dried for 48 h at 60 ˚C and weighed. From each filter, two subsamples were prepared by cutting a 7 mm diameter circle using a puncher, and packed into tin capsules.

Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ as well as %C and %N in the samples were determined using continuous-flow isotope mass spectrometry provided in Automated NC Analysis (ANCA) SL 20–20, PDZ Europa at the Stable Isotope Facility (University of California, Davis, USA). The standard reference materials were Vienna Pee Dee Belemnite and atmospheric N_2. Isotope ratios were expressed as parts-per-thousands (‰) differences from the standard reference material (Peterson and Fry 1987).

Experimental study of mysid consumption

Consumption of mysids (*Neomysis integer*) by *P. elegans* was quantified in the presence and absence of alternative (algal) food sources. The experiment was performed in June 2012 using laboratory facilities at the Lithuanian Sea Museum (Klaipeda). Food sources (mysids and *Cladophora*) and individuals of *P. elegans* were collected at the Smiltyne site. Prawns and mysids were placed into separate aquaria for acclimatization to room temperature and kept without food for 24 h. Feeding experiments were performed in aerated mesocosms (3.3 L buckets, 0.02 m^2 bottom area) filled with sea water, which was prefiltered to remove POM. A two-level factorial design was used to test the effects of prey density and the presence of alternative algal food on prawn consumption of mysids. Mysids used in these experiments had a body size of 8 to 20 mm (mean 16 ± 2 mm). Prey densities used in these experiments were 10, 15 and 20 individuals per mesocosm; equivalent to 500, 750 and 1000 ind. m^{-2}. These densities were somewhat higher

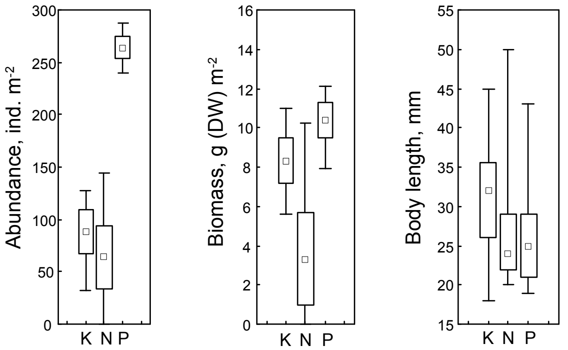

Figure 1. Abundance (ind. m^{-2}), biomass (g (DW) m^{-2}) and body length (mm) of *Palaemon elegans* in three study sites (K – Karkle, N – Nemirseta, P – Palanga). Mean values, SE as a boxes and Min-Max as a whiskers are presented for abundance and biomass, and medians, percentiles (25–75%) as a boxes and Min-Max as a whiskers are given for body length. Estimates of abundance and biomass were based on 4 measurements at each study site, and body length variation assessed from measurement of 32, 17 and 66 specimens at K, N, P sites, respectively.

than those observed at the study sites. Mixed food treatments included mysids and *Cladophora* (~5 g wet weight); 4 replicates were used for each treatment. A single prawn (mean BL = 37 ± 4 mm) was placed into each bucket. Experiment lasted for 24 h at 15.6°C and was performed at constant, dim light. At the termination of experiment, all remaining mysids, both alive and dead, were counted to determine the number of consumed mysids. At experiment termination, the percentage of dead mysids did not differ among treatments (mean = 23 ± 13%; ANOVA, $F_{5,18}$ = 0.57, P = 0.72), indicating that prey viability was comparable under all experimental conditions.

Statistical procedures and stable isotope mixing models

Differences in stable isotope (SI) composition between crustacean taxa and the various size groups of *P. elegans* were tested using *t*-tests or one-way ANOVA's followed by post-hoc tests, if required. Levenes test was applied to test for homogeneity of variances. A Mann-Whitney U test was used in cases where transformations did not improve homogeneity of variances. A Kolmogorov-Smirnov test was used to compare body size distributions, i.e. size structure of prawns, between study sites. The effect of alternative food and prey density on consumption rate was examined using two-way ANOVA and linear regression analysis. Pearson correlation was used to evaluate the relationships between variables.

An SI mixing model was applied to estimate the proportional contributions from the two carbon sources: littoral macroalgae (*Cladophora* spp.) and POM. The software package SIAR (Stable Isotope Analysis in R) was used to estimate probability distributions of contribution from each source (Parnell et al. 2010). The trophic enrichment factor (TEF) was set at 0.4 ± 1.3 ‰ for δ^{13}C (Post 2002) and multiplied by the number of trophic transfers (α). The number of trophic transfers was calculated as $\alpha = TP - 1$, where TP is the trophic position of the consumer of interest. The TP of *P. elegans* was calculated using the δ^{15}N values of the prawn and the baseline animals, i.e. primary consumers representing the 2nd trophic level, by the equation: $TP = (\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/3.4 + 2$ (Post 2002). For the baseline, we used δ^{15}N signatures of *Gammarus* spp. and *Idotea spp.*

Results

Abundance and body size of P. elegans

The abundance of *P. elegans* ranged from 0 to 213 ind. m^{-2} and differed significantly between sites (ANOVA, $F_{2,9}$ = 24.7, P < 0.001).The highest abundance was recorded at Palanga on stones chain protecting the city's pier. On average, abundance was 3 fold higher at this site compared to the natural stones occurring in Nemirseta and Karkle (Tukeys HSD tests, P < 0.001, Figure 1), whereas there were no significant differences of abundance at Nemirseta and Karkle (Tukeys HSD test, P = 0.73).

The BL of prawns ranged from 18 to 51 mm with a median of 26 mm indicating the prevalence of small-sized individuals (Figure 1). The size structure of prawns significantly varied between Karkle and Palanga sites and they were larger at the Karkle site (Kolmogorov-Smirnov test, $n_1 = 32$, $n_2 = 66$, $p < 0.025$; mean BL (±SD): 31.4 ± 6.5 vs. 26.2 ± 6.1 mm). Whereas differences in size structure between Nemirseta and Palanga sites were absent (Kolmogorov-Smirnov test, $n_1 = 17$, $n_2 = 66$, $p > 0.1$; mean BL in Nemirseta: 27.4 ± 7.9 mm).

There was a significant site effect on biomass (ANOVA, $F_{2,9}$ = 5.26, P = 0.031). Biomass was highest in the artificial habitat, i.e. Palanga site, and significantly differed from Nemirseta (Turkey

Table 1. Description of *Palaemon elegans* study sites; prawn abundance was measured on natural (Karkle and Nemirseta) and artificial (Palanga) substrates, prawns for SIA were collected at Smiltyne site.

	Karkle	Nemirseta	Palanga	Smiltyne
Coordinates	55°48'40.30" N 21°03'55.04" E	55°51'55.23" N 21°03'26.13" E	55°55'12.32" N, 21°02'55.87 E"	55°43'19.50" N 21°05'38.53" E
Depth, m	1.6	1	0.5	1–1.5
Habitat	boulders	boulders	pier	harbor mole

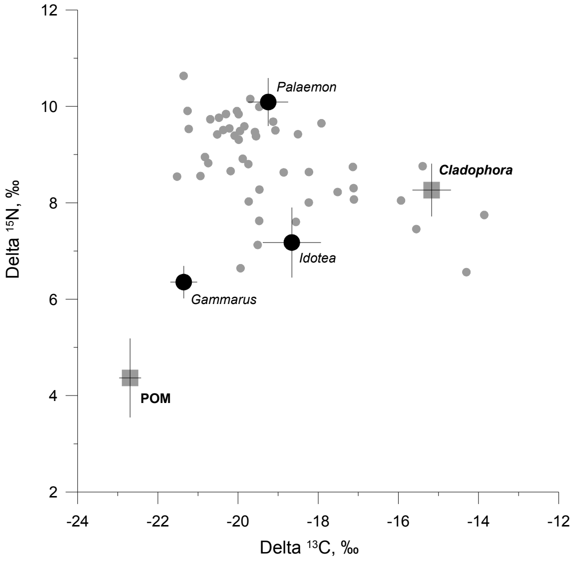

Figure 2. Mean (± SD) δ^{13}C versus δ^{15}N values of basal organic matter sources (squares), and consumers (circles). Grey circles denote individual values of stomach content in *Palaemon elegans.*

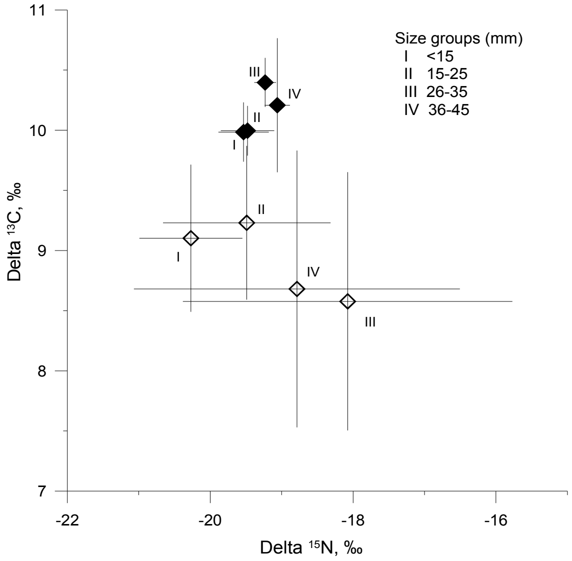

Figure 3. The mean (± SD) stable δ^{13}C and δ^{15}N isotope composition of *Palaemon elegans* (filled symbols) and their stomach content (open symbols) among size classes.

HSD test, P = 0.029) but no significant difference was observed when compared with Karkle site (P = 0.65) (Figure 1). If biomass values between artificial and natural habitats are compared using planned comparisons, biomass in natural habitats was significantly lower ($F_{1,9}$ = 5.49, P = 0.044).

Isotopic and elemental composition of food sources

The basal organic matter sources, i.e. macroalgae and POM, significantly differed in SI composition (*t*-test. for δ^{13}C, *t* = 23.6, df = 4, P < 0.001 and δ^{15}N, *t* = 6.9, df = 4, P = 0.002). *Cladophora* had 7.5‰ higher δ^{13}C and 3.9‰ higher δ^{15}N values (Table 2, Figure 2). The C:N ratio was 2.8 fold higher in *Cladophora* than POM (*t*-test, *t* = 13.5, df = 4, P < 0.001, Table 2).

The two grazers (*Idotea* and *Gammarus*) had similar δ^{15}N values (Mann-Whitney U test, df = 10, P = 0.051) but significantly differed in δ^{13}C (*t* test, *t* = 8.9, df = 10, P < 0.001). *Idotea* had more enriched δ^{13}C signatures (approaching that of *Cladophora*), whereas *Gammarus* exhibited stronger reliance on more depleted in ^{13}C sources (Figure 2). The estimated proportion of carbon from *Cladophora* (mixing model) was 16 ± 7%, whereas POM contributed 84 ± 7% to the assimilated diet of *Gammarus*. In the isopod, the contribution of *Cladophora* was substantially greater (48 ± 6%) and comparable to that from POM (52 ± 6%).

Isotopic composition of ingested food and body tissues in P. elegans

δ^{13}C of stomach contents from prawns spanned the range of values observed in their food sources (Figure 2). Large individuals (BL > 25 mm) exhibited greater variability in δ^{13}C values of ingested food than smaller individuals (Levene's test for homogeneity of variances, $F_{3,41}$ = 4.74, P = 0.006, Figure 3). For large prawns, depleted

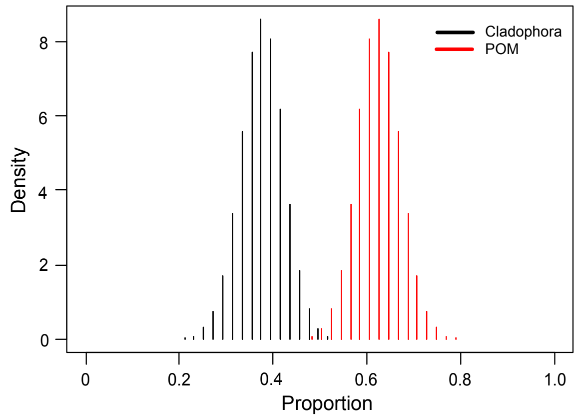

Figure 4. Density histograms showing the distribution of feasible contributions from each basal carbon source (macroalgae and POM) to the assimilated diet of *Palaemon elegans* estimated by the mixing model (SIAR).

Table 2. Stable isotope composition (mean ± SD, ‰) and C:N (molar) ratios of organic matter sources and crustaceans. N – sample size.

	$\delta^{13}C$, ‰	$\delta^{15}N$, ‰	C:N	N
Cladophora	-15.2 ± 0.5	8.26 ± 0.6	17.7±1.0	3
POM	-22.7 ± 0.3	4.4 ± 0.8	6.2 ±1.1	3
Idotea spp.	-18.7 ± 0.6	7.2 ± 0.7	5.7 ±0.7	6
Gammarus spp.	-21.4 ± 0.6	6.2 ± 0.1	6.2 ±0.3	6
Palaemon elegans	-19.2 ± 0.3	10.1 ± 0.5	4.1 ±0.1	25

$\delta^{15}N$ signatures of gut contents coincided with the enriched $\delta^{13}C$ as was also observed in *Cladophora*. This give an overall negative relationship between nitrogen and carbon isotopic composition in the stomach contents (Pearson's r = –0.57, n = 45, $P < 0.05$). A strong correlation between $\delta^{13}C$ and C:N values (Pearson's r = 0.73, n = 45, $P < 0.05$) indicates co-occurrence of $\delta^{13}C$ enrichment and low nutritional quality (high C:N) in food items. This also supports the presence of *Cladophora* among ingested items in large prawns.

There was a significant effect of body length on $\delta^{13}C$ signatures in *P. elegans* suggesting ontogenetic dietary shifts (ANOVA, $F_{3,21} = 4.96$, P = 0.004). The two largest size groups had ~0.4‰ higher $\delta^{13}C$ values (Tukey HSD unequal N tests, $P < 0.05$, Figure 3). As a result, large individuals had greater contributions to their diet from *Cladophora* (40 ± 6%) than smaller individuals (36 ± 7%). The contribution of POM carbon to the assimilated diet of large and small individuals was 64 ± 7 and 60 ± 6 %, respectively (Figure 4).

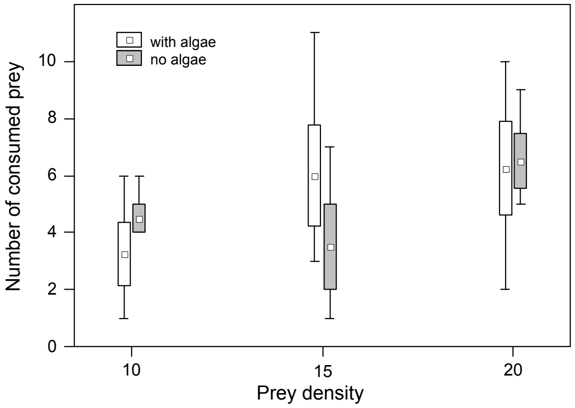

Figure 5. Numbers of mysids consumed by *Palaemon elegans* in treatments with varying prey densities (10, 15 and 20 mysids per bucket) and presence or absence of *Cladophora* as alternative food. Mean values, SE as a boxes and Min-Max as a whiskers are presented.

There were no significant differences in $\delta^{15}N$ values among the size groups of prawns (ANOVA, $F_{3,21} = 1.12$, P = 0.371). Using the average $\delta^{15}N$ value of grazers (amphipods and isopod: 6.7 ± 0.7 ‰) as an isotopic baseline, the trophic position of *P. elegans* was estimated at 3.0 ± 0.8. This value suggests that prawns are secondary consumers (i.e., predators).

Consumption of mysids

The number of consumed mysids varied from 1 to 11 with an average per capita consumption of 5.0 ± 2.7 ind. day^{-1}. There was no significant effect of the presence of algae, as alternative food, and the prey density on mysid consumption by *P. elegans* (two-way ANOVA, alternative food effect $F_{1,18} = 0.09$, P = 0.76, prey density effect $F_{2,18} = 1.83$, P = 0.19, Figure 5). However, there was a marginally significant trend in the increase of consumption with increasing prey density (linear regression analysis, Consumption = 12 + 0.6 × Prey Density, $r^2 = 0.11$, n = 24, P = 0.06).

Discussion

This study documents the importance of hard-bottom macroalgal-colonized substrates to the distribution and feeding of *P. elegans* in the exposed coast of the SE Baltic Sea. The prawns were more abundant in artificial habitats than in natural stone habitats, likely because of higher structural diversity and availability of more spatial refugees in artificial habitat.

Although prawns were abundant in macroalgal-colonized habitats, the source of energy sustaining prawns was from POM. Results from the stable isotope mixing model, suggest that more than 60% of their assimilated carbon was derived from the pelagic food chain. The trophic position of *P. elegans* (3.0 ± 0.8) indicates that they feed on intermediate consumers, rather than directly on algae. The trophic linkages between *P. elegans* and pelagic food sources may be mediated through two pathways: via planktonic (zooplankton, mysids) or benthic consumers of POM. Our data show that *P. elegans* readily prey on mysids, however invertebrates associated with overgrowths of macroalgae, such as amphipods, are also largely depending on POM; therefore, distinguishing of these pathways warrants further investigation.

Reliance of *P. elegans* on macroalgae and algal-associated amphipods has been demonstrated in experimental as well as field studies (Persson et al. 2008; Eriksson et al. 2011). The prawn prefers animal prey over algae (Persson et al. 2008); however, in the absence of amphipods, it grazes on algae (Eriksson et al. 2011). Gut content analysis of *P. elegans* from the Gulf of Gdańsk (SE Baltic) showed detritus and filamentous algae are the most frequently occurring food items (Janas and Barańska 2008). Filamentous brown algae *Pilayella littoralis* was especially attractive to the prawn in the Gulf of Finland (Kotta and Kuprijanov 2012). Our study showing that 40% of assimilated C was derived from littoral macroalgae is consistent with these previous findings. Further, our analysis of gut contents revealed enriched δ^{13}C and high C:N values, suggesting that macroalgal carbon is directly consumed by prawns. However the stable isotope values of body tissues were rather distant from the values of gut contents, which suggest low macroalgae assimilation by prawns. The most plausible explanation for this discrepancy might be that ingested filamentous green algae such as *Cladophora* are of relatively low nutritional value (high C:N) for prawns.

Accurate estimation of the trophic position of prawns is highly dependent on selection of baseline consumers. Relatively high uncertainty in TP estimate (3.0 ± 0.8) of the prawn is propagating from the variation of δ^{15}N in the baseline organisms. In our study *Gammarus* and *Idotea* were used to represent the second trophic level for the food chain based on macroalgae, as both taxa are known to graze on littoral perennial and ephemeral filamenthous macroalgae (Kotta et al. 2006). However both grazers contained in their body large portions of carbon derived from the phytoplankton or from another alternative food source depleted in ^{13}C. POM exported from the Curonian Lagoon may be important in sustaining littoral communities in the plume zone. Moreover high hydrodynamic activity might increase access of suspended solids to the fauna living inside macrophytes. Amphipods and isopods are known to use epiphytic microalgae as a food source (Jaschinski et al. 2011) and epiphytic diatoms are known to contribute to the ingested diet of *P. elegans* (Janas and Barańska 2008). However, benthic microalgae usually have more enriched δ^{13}C values than their planktonic counterparts due to boundary-layer effect (France 1995). Therefore, their importance at the base of the food chain exploited by *P. elegans* remains questionable.

As shown by nitrogen isotopes of stomach contents, the food ingested by prawns mostly included primary consumers, which hypothetically could be based on phytoplankton. Wave action restricts the presence of mesozooplankton in the upper littoral (Thomasen et al. 2013), whereas mysids are more resistant to hydrodynamic forces. The diet of littoral mysids is mainly composed of zooplankton and phytoplankton depending on availability of each source (Lehtiniemi and Nordström 2008); therefore, mysids are a very likely prawn linkage to pelagic carbon. This study demonstrated that *P. elegans* is an effective predator on mysids and were capable of consuming individuals, up to ~ 20 mm long. Moreover, the presence of macroalgae did not affect the prey consumption. In contrast, when feeding on amphipods, *P. elegans* becomes inefficient as prey size exceeds 8 mm, and switches to algal consumption (Persson et al. 2008). The same pattern also has been detected in the natural environment by using SIA; at sites with high abundance of small amphipods *P. elegans* was carnivorous, whereas at sites where dominated large-bodied species it shifted to grazing on macroalgae (Jephson et al. 2008).

Generally, results of this study agree with previous research using gut content analysis and reporting high variability of dietary components in *P. elegans* diet (Janas and Barańska 2008). However our findings, which combine isotopic and gut content analysis, suggest that gut content data might overestimate the importance of filamentous algae in the assimilated diet of *P. elegans*. A propensity to carnivory of this prawn should be considered when predicting its effects on food webs following invasion. Further investigation is warranted to reveal trophic interactions of *P. elegans* with other components of littoral communities of the Baltic coasts and to understand environmental patterns underlying the species feeding and impacts.

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