

**What is the diet
of *Palaemon elegans*
Rathke, 1837
(Crustacea, Decapoda),
a non-indigenous species
in the Gulf of Gdańsk
(southern Baltic Sea)?***

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Abstract

Palaemon elegans, a new component of the Gulf of Gdańsk macrozoobenthos, colonised the southern Baltic coastal zone in the late 20th and early 21st century. Analysis of the stomach contents of *P. elegans* revealed 16 plant and animal taxa that these prawns had fed on. The principal dietary component was detritus, with a mean frequency of occurrence in stomachs of > 80%. The most frequently occurring plant components in the diet were algae from the genus *Cladophora* and the family Ectocarpaceae, while the most significant animal components were Harpacticoida, Chironomidae, Ostracoda and *Gammarus* spp. The results of the study show that the dietary composition of *P. elegans* differed significantly between stations and months. The foraging area consisted of two distinctive regions – the Inner Puck Bay, and the Outer Puck Bay together with the Dead Vistula River; two of the stations – Gdynia and Sopot – were distinct from all the others. However, no obvious seasonality in the food composition could be demonstrated.

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1. Introduction

Alien species are regarded as a threat to global biodiversity (e.g. Leppäkoski 2002, Streftaris et al. 2005, Galil 2007). The appearance of a new species in an ecosystem may alter its structural and functional biodiversity. There are reports, from the Baltic as well, on the adverse influence of alien species on native ones, and even on whole assemblages (Kotta & Ólafsson 2003, Szaniawska et al. 2005, Karlson et al. 2007). On the other hand, one cannot rule out the positive effect of a new species on a biocoenosis: it may enhance species richness or expand the functioning of an ecosystem by the addition of new ecological traits or the intensification of existing ones (Bonsdorf 2006, Reise et al. 2006, Wallentinus & Nyberg 2007).

The prawn *Palaemon elegans* Rathke, 1837 (syn. *Leander squilla* var. *elegans* (Rathke, 1837)) is a recent coloniser of the southern Baltic, having arrived in this region around 2000 (Janas et al. 2004, Grabowski 2006). It is not yet known if this is a natural range extension of the population inhabiting the North Sea, or, as suggested by Köhn & Gosselck (1989), an introduction into German waters from ballast waters offloaded from ships.

P. elegans has become the most numerous representative of the family Palaemonidae on the Polish coast (Jażdżewski et al. 2005). The presence of *P. elegans* in the southern Baltic, especially on such a massive scale, may significantly affect the native flora and fauna. Very probably, this new prawn species plays a significant role in the trophic web in that it forages on certain food components and is itself consumed by predators. Only general data on an omnivorous type of feeding have been obtained for the species in other areas (Forster 1951b, Berglund 1980), and nothing is known about the composition of the food taken by *P. elegans* in the Baltic Sea.

It is known that mobile epibenthic crustaceans may play an important role in the reduction of infaunal and epifaunal density (Pihl & Rosenberg 1984, Möller et al. 1985, Pihl 1985, Gregg & Fleeger 1998). They may also influence ambient communities by selective feeding on certain species (Nelson 1979, Sitts & Knight 1979).

This study aimed to find answers to two questions: 1) What is the diet of *P. elegans* in its new habitat – the Gulf of Gdańsk? 2) Is there any spatial and seasonal variability in the species' diet? With this knowledge, it should be possible to state which species could be affected by *P. elegans* individuals through their diet.

2. Material and methods

The study area was located in the Gulf of Gdańsk (southern Baltic Sea). This consists of the Inner Puck Bay (Puck Lagoon) and the Outer Puck Bay, which are separated by a shallow underwater sandbank known as the Rybitwia Mielizna. The shallow, Inner Puck Bay is covered mainly by medium- or fine-grained sands; gravels and large cobbles occur sporadically and are associated with cliffs (Jankowska 1993). In the littoral zone, the main components of the macrophytobenthos are green algae and brown algae from the family Ectocarpaceae (Pliński & Florczyk 1993, Pliński & Józwiak 2004). In many parts of the Gulf of Gdańsk, e.g. Hel or Sobieszewo, the substrate is artificial – the shore is reinforced with concrete or boulders and groynes. Such localities are particularly suitable for *Palaemon elegans*, as are timber structures like the Sopot pier, or port areas (Gdynia). The hard substrate down to a depth of 1 m is overgrown, mostly by green algae from the genera *Cladophora* and *Enteromorpha*.

Specimens of *P. elegans* were collected from 10 stations in the littoral zone of the Gulf of Gdańsk in July and August 2004 (Figure 1). Further specimens were taken from the yacht marina in Gdynia from June to

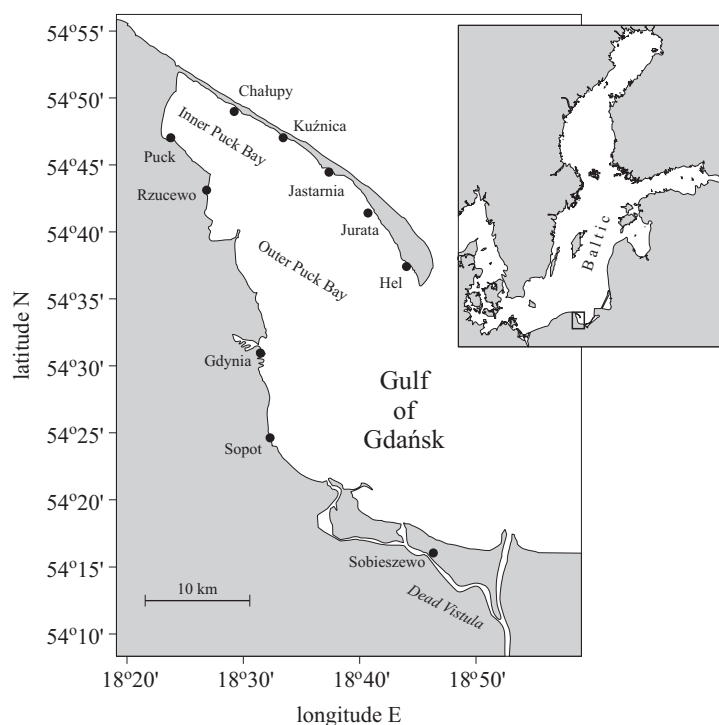


Figure 1. Location of the sampling stations in the Gulf of Gdańsk

December 2004 and in May 2005. The surface water temperature and salinity were measured with a conductometer (WTW, Germany). The animals were caught with a hand net (mesh diameter 3 mm) from a depth of 1 m and immediately deep-frozen.

After thawing in the laboratory, 20 specimens were picked at random from every station and every month; if less than 20 specimens had been caught, then the whole material was investigated. The samples included both males and females. The total length of each specimen was measured from the tip of the rostrum to the tip of the telson. The length of the animals used for the spatial and seasonal variations of dietary composition ranged from 19 to 53 mm. In accordance with Dall (1968), the anterior chamber of the proventriculus (stomach) from *P. elegans* individuals was dissected with a scalpel and the contents placed on a microscope slide for qualitative analysis. A total of 239 animals with full stomachs were subjected to such analysis. All food items were identified to the lowest possible taxon under a microscope. These included well-preserved fragments of higher plants and algae, which were identified according to Ringer (1972) and Pliński (1988a, b, c, d). The benthic animals were identified from intact body parts according to Hayward & Ryland (eds.) (1996) and Rybak (2000). These parts were mostly thoracic segments, parts of jaws or legs (Chironomidae, *Gammarus* spp.) or chaetae (*Hediste diversicolor* (O.F. Müller, 1776)). Larger fragments or whole bodies of prey items were intact where these were small: Ostracoda, Harpacticoida, Hydracarina. Detritus has been defined by Velmirov et al. (1981) as dead material of unrecognisable origin. Into this category was placed a mass of unidentified, comminuted matter, digested food, and all other animal and plant parts too small to permit identification.

A quantitative analysis of the various categories of food was also carried out. The significance of a given dietary component was assessed on the basis of two parameters: frequency of occurrence, and contribution to the stomach content. Frequency of occurrence indicated the percentage of prawns that had eaten the prey at every station and in every month. The percentage of each separate dietary component was determined by microscopic examination of the stomach contents. The volume of the entire stomach contents placed on the slide was taken to be 100%; then, the area occupied by the various organisms or their parts was estimated. This was not done if the parts were very small, e.g. chironomid claws or algal cells.

All multivariate analyses were carried out using PRIMER v.6 (Clarke & Gorley 2006). Prior to the statistical analyses, datasets were square-root transformed, and similarity matrices were constructed using the Bray-Curtis similarity coefficient. The percentage of the total stomach contents of each dietary category for individual prawns (separately for each individual) from

each station and each month were used to determine whether their dietary compositions differed between stations and/or seasons. For this purpose, one-way Analysis of Similarities (ANOSIM) was performed on the similarity matrices. For each ANOSIM test, the null hypothesis that there were no significant differences between groups was rejected when the significance level p was < 0.05 .

When seeking similarities between stations/months, hierarchical cluster analysis was applied to the food composition/frequency data in order to distinguish groups of samples of similar dietary composition. The SIMPROF permutation procedure was used to test the significance of the clusters. The null hypothesis of no internal group structures in the full set of samples was rejected when the significance level p was < 0.05 . Similarity percentages (SIMPER) were used to determine which dietary categories typified particular groups and were most responsible for any dissimilarity between groups.

3. Results

The water temperature at the time of sampling was 4.0–22.5°C. The salinity varied in a very narrow range from 6.2 to 6.9 PSU; in the Dead Vistula River it was 5.6 PSU.

Altogether 15 aquatic plant and animal taxa made up the diet of *Palaemon elegans*. Detritus and pine pollen grains were also found (Tables 1 and 2).

ANOSIM demonstrated that the dietary composition of *P. elegans* differed significantly among the studied stations (global $R = 0.40$, $p < 0.001$). Pairwise tests showed a significant difference between pairs of stations ($p = 0.001$ – 0.040), except for those between all pairs of three stations: Kuźnica, Chałupy and Rzucewo ($p > 0.05$). Pairwise comparison showed that the greatest differences in diet composition were between the two stations at Sopot and Puck ($R = 0.785$), whereas the least difference was detected between two adjacent stations: Puck and Rzucewo ($R = 0.086$).

Cluster analysis indicated a successive split into two groups of stations and two stations: Gdynia and Sopot were distinct from all the others (SIMPROF global test $\pi = 2.82$, $p < 0.05$) (Figure 2). One group consisted of prawns foraging in the Inner Puck Bay (Puck, Rzucewo, Kuźnica, Chałupy), the other group sought food in the Outer Puck Bay (Jastarnia, Jurata, Hel) and in the Dead Vistula River (Sobieszewo). The animals from the Inner Puck Bay displayed the greatest variation in their diet, which consisted of 13 components, whereas those from the other areas of the Gulf of Gdańsk

Table 1. Frequency of occurrence (F) and mean contribution by volume (V) of the dietary categories to the overall diet of *Palaeomon elegans* at stations situated in different areas of the Gulf of Gdańsk, produced by hierarchical clustering of stations (Figure 2); N – number of stomachs examined

Food items	Gulf of Gdańsk																			
	Inner Puck Bay								Outer Puck Bay and Dead Vistula River											
	Kuźnica (N = 10)		Chałupy (N = 13)		Puck (N = 17)		Rzucewo (N = 14)		Hel (N = 12)		Jurata (N = 18)		Jastarnia (N = 17)		Sobieszewo (N = 11)		Gdynia (N = 15)		Sopot (N = 14)	
	F[%]	V[%]	F[%]	V[%]	F[%]	V[%]	F[%]	V[%]	F[%]	V[%]	F[%]	V[%]	F[%]	V[%]	F[%]	V[%]	F[%]	V[%]	F[%]	V[%]
Cyanophyta	10	0.2	46.0	6.5	53.0	1.0	21.0	0.5	0	0	0	0	0	0	0	0	0	0	0	0
Bacillariophyceae	0	0	0	0	70.5	5.0	21.4	1.0	0	0	64.0	7.2	0	0	0	0	0	0	0	0
<i>Dinophysis</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	60.0	2.5	0	0
<i>Cladophora</i> spp.	60.0	31.5	61.5	14.2	35.5	9.0	54.2	16.4	41.6	11.2	88.0	29.0	82.3	16.0	36.4	7.7	53.3	12.0	0	0
<i>Enteromorpha</i> spp.	20.0	2.0	0	0	76.4	20.5	42.8	13.5	25.0	3.3	39.0	16.0	17.6	2.0	54.4	17.7	20.0	1.0	0	0
Ectocarpaceae	40.0	1.5	7.7	0.2	11.7	1.0	21.4	4.6	16.6	1.0	39.0	4.4	64.7	9.0	0	0	66.6	20.0	50.0	15.3
<i>Ceramium</i> spp.	10.0	3.0	15.3	2.0	0	0	21.4	2.8	0	0	0	0	0	0	0	0	6.6	1.5	0	0
<i>H. diversicolor</i>	0	0	23.0	5.7	0	0	21.4	3.0	0	0	0	0	0	0	0	0	0	0	0	0
Ostracoda	80.0	5.8	92.0	22.5	76.0	12.0	71.4	9.3	0	0	0	0	0	0	0	0	0	0	0	0
Harpacticoida	30.0	1.0	38.5	2.0	41.0	3.4	28.5	2.0	33.3	2.0	22.2	2.7	70.5	6.0	45.5	3.1	20.0	1.5	7.0	1.5
<i>Gammarus</i> spp.	0	0	0	0	0	0	0	0	50.0	10.4	39.0	7.7	41.2	10.5	81.8	31.3	0	0	64.2	13.2
Chironomidae	70.0	6.0	77.0	7.7	82.0	14.3	85.0	10.0	66.6	20.8	50.0	4.0	47.0	7.0	27.3	2.2	0	0	0	0
Hydracarina	0	0	0	0	0	0	0	0	25.0	10	0	0	0	0	0	0	6.6	2.5	14.2	1.0
Bryozoa	40.0	7.5	15.3	1.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32.7	6.5
Pine pollen	10.0	0.5	23.0	0.6	0	0	21.4	0.2	0	0	0	0	0	0	0	0	40.0	1.5	21.4	2.2
Detritus	80.0	41.0	92.0	37.2	94.0	33.8	92.8	36.7	91.6	41.3	94.0	29.0	100.0	49.5	100.0	38.0	100	57.5	93.0	60.3
total	11		11		9		12		8		8		7		6		9		7	

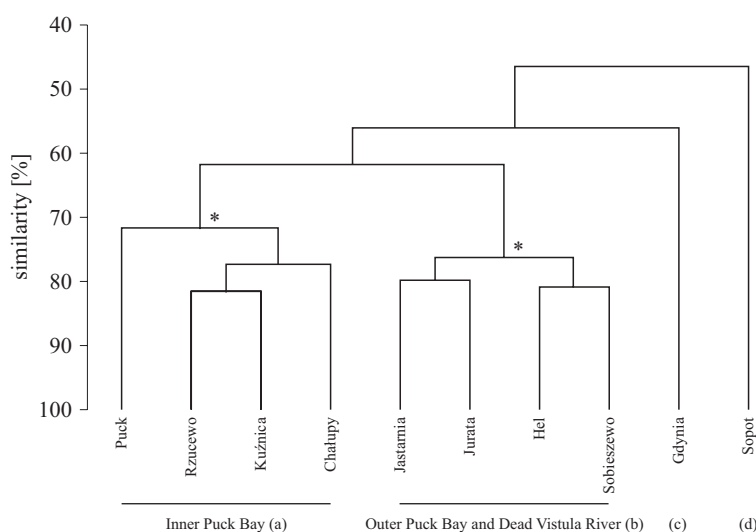


Figure 2. The similarity of the stations in the Gulf of Gdańsk as compared by the frequency of occurrence of *Palaemon elegans* food items. Dendrogram for the hierarchical clustering of the ten stations, using group-average linking of Bray-Curtis similarities calculated from square-root transformed frequency data; *significant evidence of structure (SIMPROF test, $p < 0.05$)

had consumed no more than 9 (Table 1). The SIMPER similarity average for these two groups of stations was 77.78 and 75.24% respectively. Six food components accounted for 80% of the species composition in the Inner Puck Bay: detritus 18.46%, Ostracoda 17.18%, Chironomidae 17.15%, *Cladophora* spp. 13.68%, Harpacticoida 11.01%, *Enteromorpha* spp. 5.10%, and five in the Outer Puck Bay and the Dead Vistula River: detritus 23.45%, *Cladophora* spp. 16.04%, *Gammarus* spp. 15.63%, Chironomidae 14.60%, Harpacticoida 13.15%. Sopot and the Outer Puck Bay together with the Dead Vistula River were the most distinctive areas (SIMPER, dissimilarity average = 60.70%). The similarities were greatest between the Inner Puck Bay and the Outer Puck Bay (SIMPER, dissimilarity average = 38.13%). The taxa most responsible for dissimilarity between these two groups were Ostracoda 17.01%, *Gammarus* spp. 15.88%, Bacillariophyceae 7.94%, Cyanophyta 7.68%, Ectocarpaceae 6.91%, pine pollen 6.88%, *Ceramium* spp. 6.40%, *Enteromorpha* spp. 5.73% and Bryozoa 5.73%.

Detritus was the dominant food item with respect to both frequency of occurrence ($> 80\%$) and volume ($> 29\%$) (Table 1, Figure 3). *Cladophora* spp. was the most frequent plant component in the whole study area except for Sopot. Its frequency of occurrence varied from 36% at Sobieszewo to 88% at Jurata; at the same time it made up a substantial part of the stomach volume (8–32%). The next most important plant component consisted of

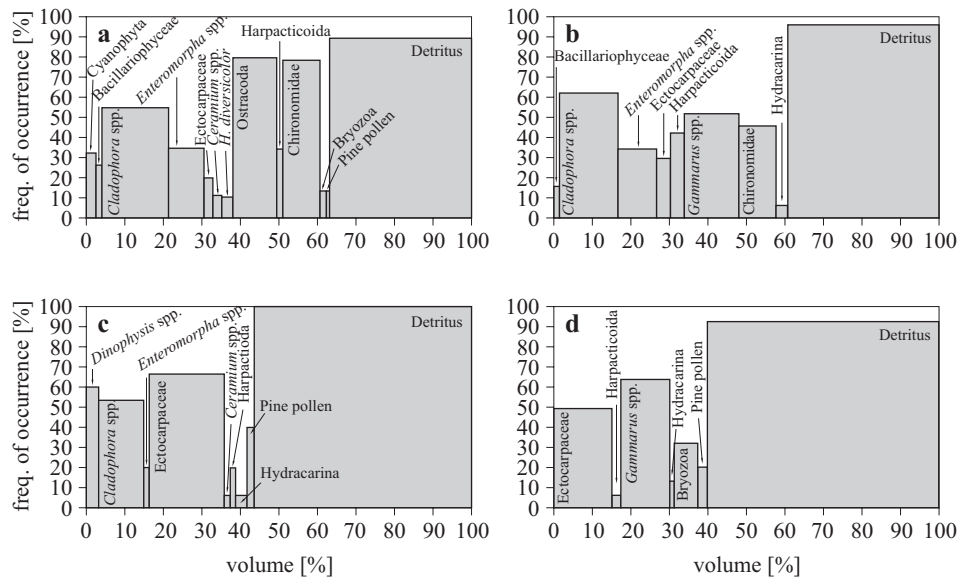


Figure 3. Parallelograms of the importance of *Palaemon elegans* food items. Mean contribution by volume [%] and frequency of occurrence [%] of the dietary categories to the overall diet in four areas of the Gulf of Gdańsk created by hierarchical clustering (Figure 2): a) Inner Puck Bay (N = 54), b) Outer Puck Bay and Dead Vistula River (N = 58), c) Gdynia (N = 15), d) Sopot (N = 14); N – number of stomachs examined

Ectocarpaceae algae with a frequency of occurrence from 8–40% of stomachs at stations situated in the Inner Puck Bay to 67% at Gdynia. These brown algae were a particularly conspicuous dietary item throughout the study area and during the whole study period. Of the benthic crustaceans that turned up in the stomachs, the most frequent were Harpacticoida – from 7% at Sopot to > 20% elsewhere in the Gulf of Gdańsk. They, too, were ever present throughout the study period. Significant items in the diet in the Outer Puck Bay and at Sopot were *Gammarus* spp., with a frequency of occurrence from 39 to 82% of stomachs. Ostracoda and Chironomidae were also frequent, especially in the Inner Puck Bay: these were found in > 70% of stomachs, occupying from 6 to 23% of the stomach volume.

Analysis of the stomach contents of *P. elegans* inhabiting the Gdynia port basin between June and December 2004 and in May 2005 revealed the presence of 15 dietary components (Table 2). Only at this station were *Zostera marina* L. and *Dinophysis* spp. present in the diet of *P. elegans*.

ANOSIM statistics confirmed that the dietary composition of the prawns differed significantly among the studied months (global R = 0.42, $p < 0.001$). Differences were also found between almost each pair of those months

($p=0.001-0.030$), except for those between all pairs of three months: July, November and December, and additionally the pair October and December ($p > 0.05$).

Cluster analyses of the samples collected in Gdynia show no clear evidence of seasonality in the dietary composition of *P. elegans* (global SIMPROF test, $p > 0.05$). Although the results point to considerable similarities in the diet throughout the study period, the groups produced by clustering contain certain characteristic components. Clustering distinguished two principal periods – an early warm season (May and June), and a warm/cold season (July, September, October, November and December) – besides the month of August, which differed from the other two periods (Figure 4). The similarity within the two principal periods was very considerable, the SIMPER similarity averages being 81.89 and 71.76% respectively. The greatest similarities were observed between the two groups (SIMPER, dissimilarity average = 32.26%), whereas August was the most distinct from the early warm season group (SIMPER, dissimilarity average = 48.72%).

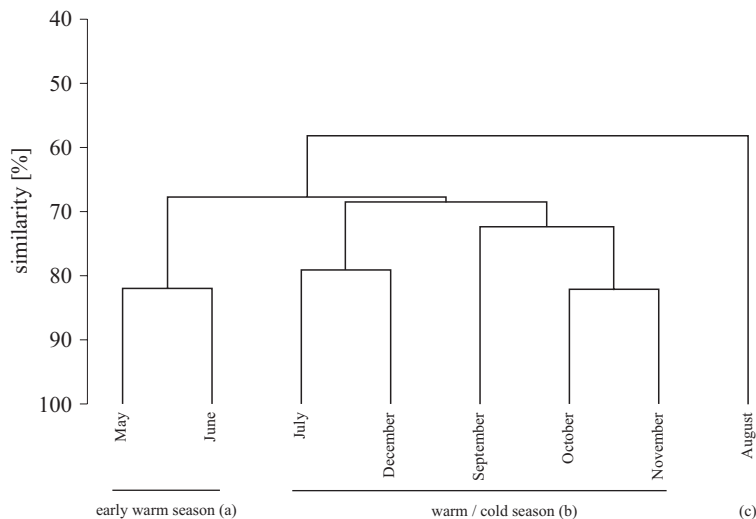


Figure 4. The similarity of months at Gdynia as compared by the frequency of occurrence of *Palaemon elegans* food items. Dendrogram for hierarchical clustering of eight months using group-average linking of Bray-Curtis similarities calculated from square-root transformed frequency data

Detritus was the most significant dietary component in the prawns from the Gdynia station, with a frequency of occurrence from 47 to 100% and occupying from 17 to 58% of the stomach volume (Table 2, Figure 5). In the early warm season, pine pollen turned out to be an important component: it

Table 2. Frequency of occurrence (F) and mean contribution by volume (V) of the dietary categories to the overall diet of *Palaemon elegans* in the studied months at the Gdynia station in different periods, produced by hierarchical clustering of months (Figure 2); N – number of stomachs examined

Food items	Early warm season				Warm/cold season											
	May (N = 19)		June (N = 14)		July (N = 15)		September (N = 14)		October (N = 14)		November (N = 14)		December (N = 8)		August (N = 15)	
	F [%]	V [%]	F [%]	V [%]	F [%]	V [%]	F [%]	V [%]	F [%]	V [%]	F [%]	V [%]	F [%]	V [%]	F [%]	V [%]
Cyanophyta	0	0	0	0	0	0	50.0	15.0	0	0	0	0	37.5	2.0	0	0
Bacillariophyceae	0	0	0	0	0	0	21.4	3.5	0	0	0	0	0	0	73.3	14.5
<i>Dinophysis</i> spp.	0	0	0	0	60.0	2.5	0	0	0	0	0	0	0	0	0	0
<i>Cladophora</i> spp.	84.2	19.5	28.5	8.0	53.3	12.0	35.7	5.5	50.0	30.0	35.7	5.3	50.0	13.0	73.3	27.6
<i>Enteromorpha</i> spp.	0	0	0	0	20.0	1.0	0	0	0	0	0	0	25.0	7.5	33.3	9.5
Ectocarpaceae	52.6	2.0	85.7	31.0	66.6	20.0	100.0	45.0	35.7	5.7	64.3	15.3	62.5	12.5	33.3	7.5
<i>Ceramium</i> spp.	0	0	0	0	6.6	1.5	0	0	0	0	0	0	0	0	0	0
<i>Z. marina</i>	84.2	12.5	42.8	9.0	0	0	14.2	2.0	14.2	1.8	0	0	0	0	0	0
Harpacticoida	5.2	0.5	42.8	4.0	20.0	2.5	35.7	2.5	14.2	2.8	42.8	7.0	50.0	11.8	13.3	1.0
<i>Gammarus</i> spp.	0	0	0	0	0	0	0	0	7.0	1.0	28.5	15.3	0	0	26.6	4.6
Chironomidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6.6	1.0
Hydracarina	0	0	0	0	6.6	2.5	0	0	7.0	5.5	0	0	0	0	0	0
Bryozoa	0	0	0	0	0	0	14.2	2.0	28.5	10.7	21.4	6.4	0	0	0	0
Pine pollen	100.0	48.5	85.7	6.0	40.0	1.5	28.5	2.0	14.2	3.5	14.2	0.7	37.5	1.4	0	0
Detritus	47.3	17.0	100.0	42.0	100.0	56.5	78.6	22.5	93.0	39.0	93.0	50.0	87.5	51.8	80.0	34.3
total	6		6		9		9		9		7		7		8	

was found in > 86% of prawns. *Cladophora* spp. and Bacillariophyceae were particularly numerous in August: their frequency of occurrence was 73%, and respectively occupied 28 and 15% of the stomach volume. In the other months the most important plant components were brown algae (Ectocarpaceae), with frequencies of occurrence from 36 to 100% and stomach volumes from 2 to 45%. Harpacticoida and *Gammarus* spp. were the most significant animal components in the diet, with maximum frequencies of occurrence and volume in November and December. Representatives of the Hydracarina and Bryozoa were present only in the warm/cold season.

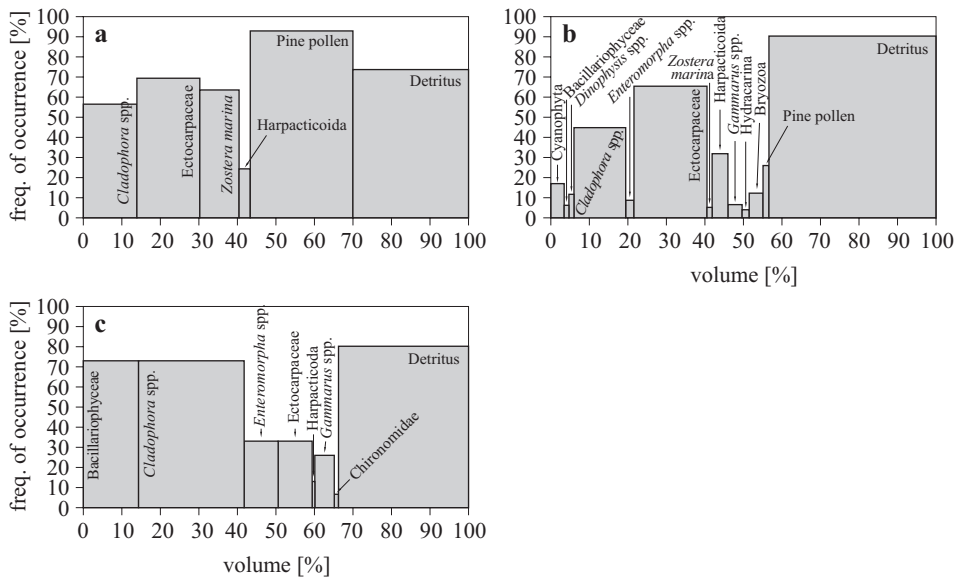


Figure 5. Parallelograms of the importance of *Palaemon elegans* food items. Mean contribution by volume [%] and frequency of occurrence [%] of the dietary categories to the overall diet at Gdynia for three periods produced by hierarchical clustering (Fig. 4): a) early warm season (N = 33), b) warm/cold season (N = 65), c) August (N = 15); N – number of stomachs examined

4. Discussion

Palaemon elegans is omnivorous but, as in most decapod crustaceans, there are differences in the diet of this species from region to region (Forster 1951b, Smaldon 1979, Berglund 1980). Although the diet of *P. elegans* inhabiting the Gulf of Gdańsk contained both plants and animals, it was detritus that occurred with the highest frequency in *P. elegans* stomachs and occupied the largest percentage of the stomach volume. Detritus is reported to be a significant dietary component in this species elsewhere

in Europe, and also in other palaemonid species (Forster 1951b, Berglund 1980, Albertoni et al. 2003).

Even between individuals of *P. elegans* inhabiting different parts of the Gulf of Gdańsk there were evident differences in dietary composition. Those living in the shallow, littoral zone of Puck Lagoon (the Inner Puck Bay), with its greater biodiversity, consumed far less detritus than those living elsewhere in the Gulf. Benthic animals, like ostracods, chironomids or *Hediste diversicolor*, were much more frequent food items in the Lagoon. These organisms inhabit calm, sheltered spots in the littoral zone (Rybak 2000). Large numbers of small crustaceans or other benthic organisms are probably eaten along with the algae upon which they live. On the other hand, at localities with a far smaller diversity of benthic assemblages, such as ports (Gdynia) or piers (Sopot), brown algae (Ectocarpaceae) are a frequent component of the prawns' diet. Wiktor (1979) reported that brown algae were also consumed by *Palaemon adspersus* Rathke, 1837, another prawn species inhabiting the Gulf of Gdańsk.

Although the dietary composition exhibited no clear seasonality, the observed differences can be explained by the seasonal occurrence of the various components. In the early warm season pine pollen was the main item found in the stomachs of *P. elegans*. Pines release their pollen at this time (Dzwonkowski 2004) and a lot of it ends up on water surfaces. Nevertheless, pollen is of minimal nutritional value and is difficult to digest (Strasburger (ed.) 1967). Epiphytes on underwater plants are known to be a potential food source for prawns (Morgan 1980, Fleeger et al. 1999). In the August sample epiphytic diatoms were recorded in 73% of *P. elegans* stomachs, chiefly from the genera *Achnanthes*, *Cocconeis*, *Epithemia*, *Melosira*, *Navicula*, *Nitzschia*, *Synedra* and the species *Rhoicosphenia curvata* (A. Latała – personal communication). Wiktor (1979) also found Bacillariophyceae in the stomachs of the largest *P. adspersus* females. These tiny algae contain large quantities of nutrients like lipids, so they may be an important component of the diet during the reproductive season. According to Rönnerberg & Lax (1980), these genera of diatoms grow on *Cladophora* spp., which were the second most important component in the diet of *P. elegans* at the Gdynia station in August.

From autumn onwards, the prawns' food resources shrink, chiefly because the growing season is coming to an end (Kozłowski 2001, Kuczyński 2001). A somewhat greater frequency of occurrence and volume of animal components in the diet of *P. elegans* at this time than in the warm period is noticeable. A similar tendency has been observed in other prawns, too (Forster 1951a, Wiktor 1979). In the cold season, there is a decline in food requirements, a situation indicated by earlier studies, which demonstrated

a decrease in activity level, metabolic rate, grazing rate and growth rate of palaemonid species at low temperatures (Hagerman & Østrup 1980, Berglund 1981, Morris & Taylor 1985, Orav-Kotta & Kotta 2003). Moreover, *P. elegans* individuals migrate from the coastal zone of the Gulf of Gdańsk in December and spend the winter at depths from several to several tens of metres, where they are less active (P. Wysocki – personal communication; authors' own observations).

The large-scale occurrence of *P. elegans* in the coastal zone of Gulf of Gdańsk may regulate the densities of the organisms on which it feeds. A positive sign is that it consumes filamentous algae; in doing so, it may help to reduce the biomass of these primary producers, which, in the Baltic, are multiplying in excess. According to Orav-Kotta & Kotta (2003) *P. adspersus* consumes relatively large quantities of *Pilayella littoralis* L. and the basal parts of *Fucus vesiculosus* L. Abundant in the Gulf of Gdańsk, filamentous algae made up a substantial proportion of the diet of the studied prawns: *Cladophora* spp. were particularly frequent and numerous. Off British coasts filamentous algae, especially *P. littoralis* and thalloid algae – most likely *Laminaria* spp. – constitute a large part of the diet of *P. elegans* (Forster 1951a, b). In comparison, this species from pools on the rocky coast of Sweden fed mostly on the alga *Enteromorpha intestinalis* L. (Berglund 1980).

Animal items made an important contribution to the stomach contents in terms of volume and frequency of occurrence. Thus, *P. elegans* feeding on animals, mainly Harpacticoida, Chironomidae, Ostracoda and *Gammarus* spp., could potentially affect their assemblages. The adverse effect of *Palaemonetes pugio* Holthuis, 1949 on the density of meiofauna has been highlighted (Bell & Coull 1978), and the effect of the predation of another prawn *Palaemonetes vulgaris* (Say, 1818) on gammarids has also been demonstrated (Nelson 1979). Amphipods were also the main food component (75%) of *P. adspersus* off the Swedish coast (Möller et al. 1985). Some *Palaemon* species have been shown to be predominantly carnivorous (Sitts & Knight 1979, Guerao 1995, Guerao & Ribera 1996).

Although no fish eggs were found in the stomachs of prawns from the Gulf of Gdańsk, they are a potential component of their diet (Köhn & Gosseck 1989). The eggs of the round goby *Neogobius melanostomus* (Pallas, 1814), laid on hard bottom substrates, appear to be excellent food, the more so that in the laboratory prawns have been observed to eat them (M. Normant – personal communication).

Competition for food may affect the densities of other populations. Occupying the same habitat as two other prawn species – *P. adspersus* and *Palaemonetes varians* (Leach, 1814) (Grabowski 2006; authors' own

observations) – as well as that of the three-spined stickleback *Gasterosteus aculeatus* L. (Kotwicki 1993), *P. elegans* may compete with them for food. Other species drawing from similar food resources are crustaceans of the genus *Gammarus*, among which the alien species *Gammarus tigrinus* Sexton, 1939 is currently dominant (Szaniawska et al. 2005).

The dietary compositions of *P. elegans* have demonstrated that plants may well be a significant component of this species' food. On the other hand, laboratory observations have shown that this is a highly active and voracious species (Berglund 1980, Berglund & Bengtsson 1981; authors' own observations). Individual prawns are capable of detecting the flesh of fish or mussels within a few seconds of these being placed in the aquarium (authors' own observations). Further research into dietary preferences and feeding rates are necessary before any definitive statement can be made on the extent to which *P. elegans* regulates the biomass of algae and animals, and whether this new prawn species competes for food with other animals in the littoral zone of the Gulf of Gdańsk.

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References

- Albertoni E. F., Palma-Silva C., Esteves F. A., 2003, *Natural diet of three species of shrimp in a tropical coastal lagoon*, Braz. Arch. Biol. Techn., 46 (3), 395–403.
- Bell S. S., Coull B. C., 1978, *Field evidence that shrimp predation regulates meiofauna*, Oecologia, 35 (2), 141–148.
- Berglund A., 1980, *Niche differentiation between two littoral prawns in Gullmar Fjord, Sweden: Palaemon adspersus and P. squilla*, Holarctic Ecol., 3 (2), 111–115.
- Berglund A., 1981, *Sex dimorphism and skewed sex ratios in the prawn species Palaemon adspersus and P. squilla*, Oikos, 36 (2), 158–162.
- Berglund A., Bengtsson J., 1981, *Biotic and abiotic factors determining the distribution of two prawn species: Palaemon adspersus and P. squilla*, Oecologia, 49 (3), 300–304.
- Bonsdorff E., 2006, *Zoobenthic diversity-gradients in the Baltic Sea: Continuous post-glacial succession in a stressed ecosystem*, J. Exp. Mar. Biol. Ecol., 330 (1), 383–391.
- Clarke K. R., Gorley R. N., 2006, *Primer v. 6: User manual/tutorial*, PRIMER-E Ltd., Plymouth U.K., 192 pp.

- Dall W., 1968, *Food and feeding of some Australian penaeid shrimp*, FAO Fish. Rep., 57 (2), 251–258.
- Dzwonkowski R. J., 2004, *Przyroda polska*, Wyd. Mozaika, Warszawa, 277 pp.
- Fleeger J. W., Carman K. R., Webb S., Hillbun N., Pace M. C., 1999, *Consumption of microalgae by the grass shrimp Palaemonetes pugio*, J. Crustacean Biol., 19 (12), 324–336.
- Forster G. R., 1951a, *Notes on Leander squilla L.*, J. Mar. Biol. Assoc. U.K., 30 (2), 361–367.
- Forster G. R., 1951b, *The biology of the common prawn Leander serratus Pennant*, J. Mar. Biol. Assoc. U.K., 30 (2), 333–360.
- Galil B. S., 2007, *Loss or gain? Invasive aliens and biodiversity in the Mediterranean Sea*, Mar. Pollut. Bull., 55 (7–9), 314–322.
- Grabowski M., 2006, *Rapid colonization of the Polish Baltic coast by an Atlantic palaemonid shrimp Palaemon elegans Rathke, 1837*, Aquat. Invas., 1 (3), 116–123.
- Gregg C. S., Fleeger J. W., 1998, *Grass shrimp Palaemonetes pugio predation on sediment- and stem-dwelling meiofauna: field and laboratory experiments*, Mar. Ecol.-Prog. Ser., 175, 77–86.
- Guerao G., 1995, *Locomotor activity patterns and feeding habits in the prawn Palaemon xiphias (Crustacea: Decapoda: Palaemonidae) in the Alfacs Bay, Ebro Delta (northwest Mediterranean)*, Mar. Biol., 122 (1), 115–119.
- Guerao G., Ribera C., 1996, *Locomotor activity patterns and feeding habits in the prawn Palaemon Serratus (Pennant, 1977) (Decapoda, Palaemonidae) in the Alfacs Bay, Ebro Delta, Spain*, Crustaceana, 69 (1), 101–112.
- Hagerman L., Østrup J., 1980, *Seasonal and diel activity variations in the shrimp Palaemon adspersus from a brackish, non-tidal area*, Mar. Ecol.-Prog. Ser., 2, 329–335.
- Hayward P. J., Ryland J. S. (eds.), 1995, *Handbook of the marine fauna of North-West Europe*, Oxford Univ. Press, New York, 816 pp.
- Janas U., Zarzycki T., Kozik P., 2004, *Palaemon elegans – a new component of the Gulf of Gdańsk macrofauna*, Oceanologia, 46 (1), 143–146.
- Jankowska H., 1993, *The bottom deposits of Puck Bay*, Stud. Mater. Oceanol., 64, 163–171.
- Jażdżewski K., Konopacka A., Grabowski M., 2005, *Native and alien malacostracan Crustacea along the Polish Baltic Sea coast in the twentieth century*, Oceanol. Hydrobiol. Stud., 34 (Suppl. 1), 175–193.
- Karlson A. M. L., Almqvist G., Skóra K. E., Appelberg M., 2007, *Indication of competition between non-indigenous round goby and native flounder in the Baltic Sea*, ICES J. Mar. Sci., 64 (3), 479–486.
- Kotta J., Ólafsson E., 2003, *Competition for food between the introduced polychaete Marenzelleria viridis (Verrill) and the native amphipod Monoporeia affinis Lindström in the Baltic Sea*, J. Sea Res., 50 (1), 27–35.

- Kotwicki S., 1993, *Food of stickleback in spring months*, Stud. Mater. Oceanol., 64 (3), 273–281.
- Kozłowski G., 2001, *Skład gatunkowy, rozmieszczenie oraz biomasa zielenic bentosowych Zatoki Gdańskiej (w latach 1999–2000)*, M.Sc. thesis, Univ. Gdańsk, Gdynia, 95 pp.
- Köhn J., Gosselck F., 1989, *Identification key for the Malacostraca of the Baltic Sea*, Mitt. Zool. Mus. Berl., 65 (1), 3–114.
- Kuczyński R., 2001, *Skład i rozmieszczenie brunatnic, krasnorostów i roślin naczyniowych w zachodniej części Zatoki Gdańskiej w latach 1999–2000*, M.Sc. thesis, Univ. Gdańsk, Gdynia, 97 pp.
- Leppäkoski E., 2002, *Harmful non-native species in the Baltic Sea – an ignored problem*, [in:] *Baltic coastal ecosystems: structure, function and coastal zone management*, G. Schernewski & U. Schiewer (eds.), CEEDES, Springer-Verlag, Berlin–Heidelberg, 253–275.
- Morgan M. D., 1980, *Grazing and predation of the grass shrimp Palaemonetes pugio*, Limnol. Oceanogr., 25 (5), 896–902.
- Morris S., Taylor A. C., 1985, *Oxygen consumption by Palaemon elegans (Rathke) in response to temperature change: a determinant of distribution*, J. Exp. Biol., 44 (4), 255–268.
- Möller P., Pihl L., Rosenberg R., 1985, *Benthic faunal energy flow and biological interaction in some shallow marine soft bottom habitats*, Mar. Ecol.-Prog. Ser., 27, 109–121.
- Nelson W. G., 1979, *Experimental studies of selective predation on amphipods: Consequences for amphipod distribution and abundance*, J. Exp. Mar. Biol. Ecol., 38, 225–245.
- Orav-Kotta H., Kotta J., 2003, *Seasonal variations in the grazing of Gammarus oceanicus, Idotea baltica, and Palaemon adspersus on benthic macroalgae*, Proc. Estonian Acad. Sci. Biol. Ecol., 52 (2), 141–148.
- Pihl L., 1985, *Food selection and consumption of mobile epibenthic fauna in shallow marine areas*, Mar. Ecol.-Prog. Ser., 22, 169–179.
- Pihl L., Rosenberg R., 1984, *Food selection and consumption of the shrimp Crangon crangon in some shallow marine areas in western Sweden*, Mar. Ecol.-Prog. Ser., 15, 159–168.
- Pliński M., 1988a, *Glony Zatoki Gdańskiej: klucz do oznaczania gatunków. Cz. I. Sinice*, Skr. uczeln., Uniw. Gd., Gdańsk, 82 pp.
- Pliński M., 1988b, *Glony Zatoki Gdańskiej: klucz do oznaczania gatunków. Cz. IV. Okrzemki*, Skr. uczeln., Uniw. Gd., Gdańsk, 183 pp.
- Pliński M., 1988c, *Glony Zatoki Gdańskiej: klucz do oznaczania gatunków. Cz. VI. Zielenice*, Skr. uczeln., Uniw. Gd., Gdańsk, 83 pp.
- Pliński M., 1988d, *Glony Zatoki Gdańskiej: klucz do oznaczania gatunków. Cz. VII. Brunatnice, krasnorosty*, Skr. uczeln., Uniw. Gd., Gdańsk, 62 pp.
- Pliński M., Florczyk I., 1993, *Macrophytobenthos*, [in:] *Puck Bay*, K. Korzeniewski (ed.), Fund. Uniw. Gd., Gdańsk, 416–421, (in Polish).

- Pliński M., Józwiak T., 2004, *The distribution of water vegetation on the Polish coast of the Baltic Sea in 1996–2000*, Oceanol. Hydrobiol. Stud., 33 (2), 29–40.
- Reise K., Olenin S., Thielges D. W., 2006, *Are aliens threatening European aquatic coastal ecosystems?*, Helgoland Mar. Res., 60 (2), 77–83.
- Ringer Z., 1972, *Rośliny Bałtyku*, PZWS, Warszawa, 150 pp.
- Rönnerberg O., Lax P. E., 1980, *Influence of wave action on morphology and epiphytic diatoms of *Cladophora glomerata* (L.) Kütz, Ophelia*, Suppl. 1, 209–218.
- Rybak J. I., 2000, *Bezkregowe zwierzęta słodkowodne*, PWN, Warszawa, 87 pp.
- Sitts R. M., Knight A. W., 1979, *Predation by the estuarine shrimps *Crangon franciscorum* Stimpson and *Palaemon macrodactylus* Rathbun*, Biol. Bull., 156 (3), 356–368.
- Smaldon G., 1979, *British coastal shrimps and prawns: keys and notes for the identification of the species*, Syn. Brit. Fauna (N. S.), Vol. 15, Acad. Press, London, 126 pp.
- Strasburger E. (ed.), 1967, *Botanika*, PWRiL, Warszawa, 1095 pp.
- Streftaris N., Zenetos A., Papathanassiou E., 2005, *Globalisation in marine ecosystems: the story of non-indigenous marine species across European seas*, Oceanogr. Mar. Biol. Ann. Rev., 43, 419–453.
- Szaniawska A., Normant M., Łapucki T., 2005, *Gammarus tigrinus* Sexton 1939 (crustacea, amphipoda) – a new immigrant in the Puck Bay, southern Baltic Sea, Oceanol. Hydrobiol. Stud., 34 (2), 71–78.
- Velimirov B., Ott J. A., Novak R., 1981, *Microorganisms on macrophyte debris: biodegradation and its implication in the food web*, Kieler Meeresforsch., 5, 333–334.
- Wallentinus I., Nyberg C. D., 2007, *Introduced marine organisms as habitat modifiers*, Mar. Pollut. Bull., 55 (7–9), 323–332.
- Wiktor K., 1979, *Skład pokarmu *Palaemon adspersus* (Rathke) z wód Zatoki Puckiej*, Zesz. Nauk. BINOZ UG, 6, 147–154.