Energy values and energy resources of two prawns in Baltic coastal waters: the indigenous *Palaemon adspersus* and the non-indigenous *Palaemon elegans*

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Abstract

Until recently only two palaemonid species inhabited the southern Baltic: *Palaemon adspersus* and *Palaemonetes varians*. Soon after the year 2000 a new species – *Palaemon elegans* – arrived and quickly established itself as a new component in the trophic web. The objects of this research were to define the energy value and energy resources of *P. elegans* and to compare them with the corresponding values for the native *P. adspersus*. These parameters will supply information about this new link in the trophic web and may help to explain the part played by the new prawn and its population in the energy flow. This work demonstrated that the energy values of both prawn species were very much the same: the average energy value of *P. elegans* was 16.5±2.1 J mg^{-1} DW (19.3 ± 2.5 J mg^{-1} AFDW) (N = 150), that of *P. adspersus* was 16.7 ± 2.1 J mg^{-1} DW (19.5 ± 2.5 J mg^{-1} AFDW) (N = 71). No statistically significant differences in energy value were found between the two species with respect to sex, size or season. The results show that *P. elegans* is an energetically valuable food item for predators. Its energy resources in Polish brackish coastal waters can be as high as 150 kJ m^{-2}; the highest among

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the palaemonid species in this area, they constitute a rich supply of food for other organisms.

1. Introduction

Until recently, the southern Baltic was inhabited by two prawn species: *Palaemonetes varians* (Leach, 1814) and *Palaemon adspersus* Rathke, 1837. The occurrence of the former is restricted to the Dead Vistula River (Martwa Wisła) – one arm of the Vistula delta (Jażdżewski & Konopacka 1995, Grabowski 2006). The latter species was once widespread throughout the Polish coastal zone (Jażdżewski & Konopacka 1995). However, the degradation of underwater meadows led to a drastic reduction in its numbers in the 1980s and 1990s (Wiktor 1993); now it is present only in the Gulf of Gdańsk (Grabowski et al. 2005). Soon after the year 2000, a new species – *Palaemon elegans* Rathke, 1837 – turned up in the southern Baltic, which has since become the most numerous and most widespread prawn in the region (Janas et al. 2004, Grabowski 2006). Thus, the presence of *P. elegans* in the southern Baltic could have a significant impact on benthic energy resources.

Prawns like *P. adspersus* and *P. elegans* play an important role in coastal waters as a food item for many fish species, e.g. European eel *Anguilla anguilla* and cod *Gadus morhua* (Rasmussen 1973, Berglund & Bengtsson 1981). Both these prawn species, and *P. adspersus* in particular, are caught for human consumption in, for example, the Danish Belt Sea, the Mediterranean and the Black Sea (Kobyakova & Dolgopol'skaya 1969, Holthuis 1980, Barnes 1994). They are also a valuable live food source for aquaculture (Salama & Hartnoll 1992, Yiğit et al. 2005).

One parameter testifying to the value of an organism as a potential source of food is its energy value. While much is known about the energy value of native crustaceans in the Baltic Sea (e.g. Szaniawska 1983, 1984a, b, 1991, Dobrzycka & Szaniawska 1993, Normant & Szaniawska 1993, Dobrzycka & Szaniawska 1995, Gorokhova & Hansson 2000), much less is known about the alien species in the region (Wiszniewska et al. 1998, Normant et al. 2002). The energy value of *P. adspersus* from the Gulf of Gdańsk was investigated in Puck Bay in the 1970s and was found to be one of the highest such values recorded for Baltic crustaceans (Szaniawska 1984b). Currently, however, no information is available on the energy value and resources of *P. adspersus*. All we can find in the literature are fragmentary data on the energy value of *P. elegans* from the British coast (Cummins & Wuycheck 1971).

There are interspecific differences in energy values, which are the result, among other things, of the different life strategies of the animals involved.

In general, benthic species have a lower energy value than nektobenthic or planktonic species (Salonen et al. 1976, Norrbin & Bamstedt 1984, Szaniawska 1991, Company & Sardà 1998). The energy value of organisms within a population is governed by endogenous factors like size, sex or life cycle stage (Szaniawska 1991, Gorokhova & Hansson 2000). Moreover, exogenous factors such as food availability, temperature and salinity may have a considerable influence on the energy value of a species (Prus 1970, 1993). In addition to the above factors, the energy resources of a population are affected by the size and sex structure of the population as well as its density.

The energy values of various taxa are used to assess the energy resources of the population under study, to evaluate the bioproductivity of a system, and to construct energy flow models (Szaniawska 1991, Prus 1993). In the Baltic Sea alien species are a highly significant component of its communities. In Puck Bay (southern Baltic Sea), for example, up to 33% of benthic species are non-indigenous (Janas & Rzemykowska, in preparation). The prawn *P. elegans*, a new arrival in the southern Baltic, has become part of the food web, altering existing trophic relationships.

The study aimed to find out whether non-native *P. elegans* and native *P. adspersus* differ in their energy value and to calculate the energy resources of both populations in the Polish coastal waters, which depend on density, body size and sex structure.

2. Material and methods

Individuals of *P. elegans* and *P. adspersus* were collected in the yacht marina at Gdynia each month from July to December 2005, and also in June 2006 and February 2007. During this period, the temperature varied from 1.0 to 23.5°C and the salinity from 5.8 to 6.9 PSU. The animals were caught with a 30x25 cm 3 mm-mesh hand net from depths down to 1 m. All the prawns were taken to the laboratory within 60 min of capture in cool boxes and frozen. In addition, in order to estimate density, size and sex structure, and energy resources, prawns were collected in the coastal zone of the Gulf of Gdańsk at stations differing primarily in salinity and the type of substratum inhabited (6 stations: Hel, Jastarnia, Chałupy, Osłonino, Rewa, Gdynia), in the Dead Vistula River (Martwa Wisła) (1 station) and in the Vistula Lagoon (Zalew Wiślany) (4 stations: Frombork, Tolkmicko, Krynica Morska, Piaski) in early July 2005 (Figure 1, Table 1). During this study period water temperatures were 16.2–20.5°C (Gulf of Gdańsk), 22.0°C (Dead Vistula) and 20.4–23.0°C (Vistula Lagoon); the respective salinities were 6.5–6.8, 5.1, and 1.8–2.1 PSU. The same net was always used for catching the prawns, which were frozen immediately after capture. At

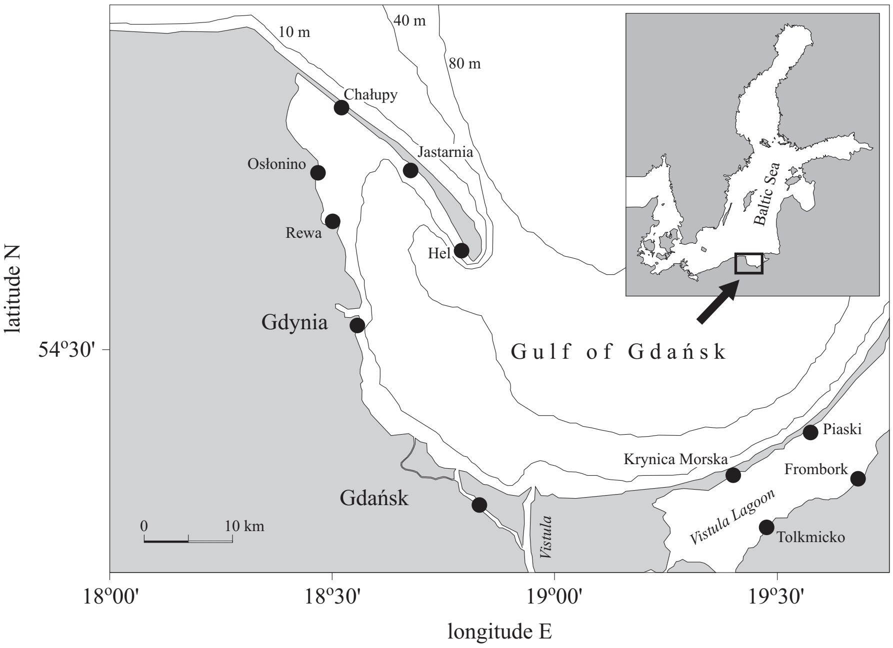


Figure 1. Locations of the sampling stations in Polish coastal waters

each station the prawn samples were taken from a surface area of 10–50 m^2 down to a depth of l m.

After defrosting, the total length of each specimen was measured from the tip of the rostrum to the tip of the telson. The endopodite of the second pair of pleopods was used to determine sex (Hayward & Ryland 1996). In the males this endopodite is cleft and forms the *appendix masculina*. At least 5 males and 5 females of each species were picked at random from each month's catch for the energy value analyses; if less than 10 specimens had been caught, then the whole material was investigated.

Prawns were weighed wet, then dried at a temperature of 55°C to constant dry weight (DW). The whole dried individuals were homogenised in a mortar. The energy values of the prawns were determined using a modified Philipson KMB-2 type microbomb calorimeter, described in Klekowski & Bęczkowski (1973) and Prus (1993). The bomb was calibrated using benzoic acid samples with a known caloric content. The energy values were expressed in joules per milligram of dry weight [J mg^{-1} DW] and per milligram of ash-free dry weight [J mg^{-1} AFDW]; afterwards, the energy content per individual [J $indiv.^{-1}$] was computed by multiplying the body DW by the respective energy value.

Table 1. Type of substratum, density, percentage of males, non-ovigerous females and ovigerous females of *Palaemon elegans* and *P. adspersus* at 11 stations in Polish coastal waters in June 2005

Station	Type of substratum	*P. elegans*				*P. adspersus*			
		Density [indiv. m^{-2}]	Males [%]	Females (non-ovigerous) [%]	Females (ovigerous) [%]	Density [indiv. m^{-2}]	Males [%]	Females (non-ovigerous) [%]	Females (ovigerous) [%]
Hel	Cb, Fa	1–10	35	54	11	< 1	50	50	0
Jastarnia	Hq, Fa	< 1	0	100	0	< 1	0	31	69
Chałupy	Sa, Fa	< 1	0	100	0	0			
Osłonino	St, Fa	1–10	51	30	19	0			
Rewa	Sa, Fa	0				0			
Gdynia	Hq, Fa	11–100	44	46	10	< 1	53	47	0
Dead Vistula River	Cb, Cp, Fa	11–100	66	14	20	0			
Krynica Morska	Hq	0				0			
Piaski	Hq, Fa	< 1	0	0	100	0			
Tolkmicko	Hq, Fa	0				0			
Frombork	Hq	< 1	20	0	80	0			

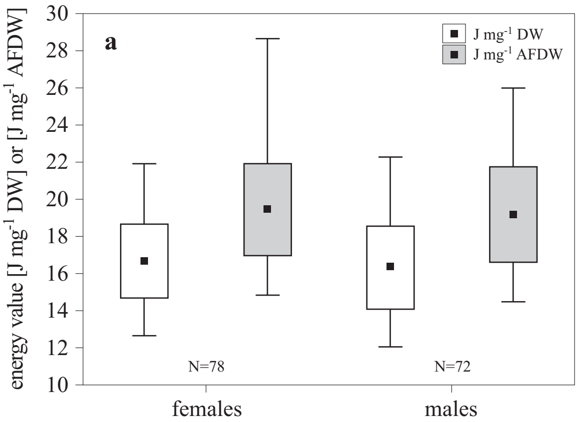
Type of substratum: Cb – concrete blocks, Cp – concrete pier, Fa – filamentous green algae, Hq – harbour quaysides, Sa – sand, St – stones.

The numbers of *P. elegans* and *P. adspersus* per square metre were estimated from catch sizes and observations of the animals in their environment in July 2005. They were classified to the following size groups: 0 – no individuals, < 1 indiv. m^{-2} (less than one individual per square metre), 1–10 indiv. m^{-2} and 11–100 indiv. m^{-2}. The density of the two species as well as the percentage of males, ovigerous females and non-ovigerous females was determined at each station. The overall length and wet weight of individuals were measured, after which mean lengths and mean wet weights were calculated for the individuals inhabiting the entire study area, separately for males, ovigerous females and non-ovigerous females. The body dry weight of individuals was calculated from the average annual water content in the body wet weights of *P. elegans* and *P. adspersus*, obtained from studies of the Gdynia specimens. These latter values were 75% for *P. elegans* and 72% for *P. adspersus*. The energy value of ovigerous females was assumed to be 28.4% higher than that of non-ovigerous females (Szaniawska 1991). The energy resources of the two species were calculated as the product of the number of individuals found on a given area of sea bed and the energy content of average-sized individuals [J indiv.^{-1}], separately for males, ovigerous females and non-ovigerous females, after which these three values were summed.

The Shapiro-Wilk test was used to test for normality. The significance of the differences obtained was tested using an unpaired t-test or one-way ANOVA. Linear regressions were employed to describe the relationship between energy value and the total length of prawns. The significance of the differences between slopes and intercepts was determined using multiple regression (Townend 2002). Differences were considered significant if P values (significance level) were < 0.05. The analyses were performed using STATISTICA 8 PL (StatSoft, Poland). The average, standard deviation and the range of the data from minimum to maximum values are presented.

3. Results

The average energy values, both per unit of dry weight and organic matter, of the females of both *P. elegans* and *P. adspersus* were slightly higher than those of the males, but the differences were not statistically significant (t-test, $P > 0.05$). The differences in the energy values among the females and among the males of both species were not statistically significant either. The average energy values were as follows: *P. elegans* – females 16.7 ± 2.0 J mg^{-1} DW (19.5 ± 2.5 J mg^{-1} AFDW) (N =78), males 16.3 ± 2.2 J mg^{-1} DW (19.2 ± 2.6 J mg^{-1} AFDW) (N = 72); *P. adspersus* – females 17.0 ± 2.2 J mg^{-1} DW (19.6 ± 2.5 J mg^{-1} AFDW) (N = 37), males 16.5 ± 2.0 J mg^{-1} DW (19.4 ± 2.5 J mg^{-1} AFDW) (N = 34), (Figure 2). The



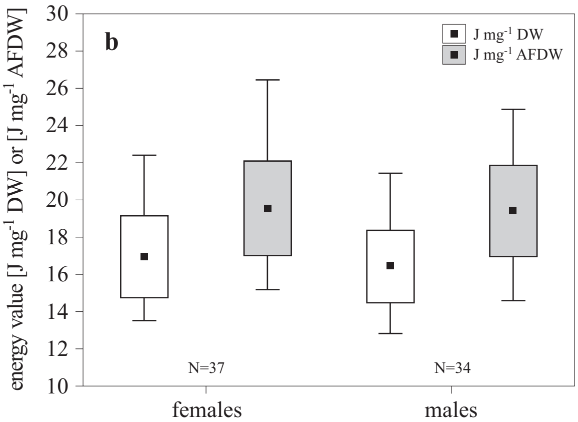


Figure 2. Energy value of dry weight [J mg^{-1} DW] and energy value of organic matter [J mg^{-1} AFDW] of females and males of a) *Palaemon elegans* and b) *P. adspersus* collected at Gdynia from December 2005 to February 2007. Square – average; box – standard deviation; whiskers – range of data, N – number of individuals studied

average energy value of *P. elegans* (males and females combined) was 16.5 ± 2.1 J mg^{-1} DW (19.3 ± 2.5 J mg^{-1} AFDW) (N = 150), that of *P. adspersus* was 16.7 ± 2.1 J mg^{-1} DW (19.5 ± 2.5 J mg^{-1} AFDW) (N = 71). No statistically significant differences were found in the energy value per unit of body weight between the two species (t-test, $P > 0.05$).

There was, however, a strong, positive and statistically significant relationship between the energy value of the organic matter and the energy value of the dry weight of both prawn species: the line of best fit for *P. elegans* is described by $y = 1.11x + 1.01$, $R^2 = 0.88$, $P < 0.0001$ (N = 150) and for *P. adspersus* by $y = 1.05x + 1.88$, $R^2 = 0.78$, $P < 0.0001$ (N = 71), where y – energy value of organic matter [J mg^{-1} AFDW], x – energy value of dry weight [J mg^{-1} DW]. The differences between the intercepts and slopes of the two lines were not statistically significant (P > 0.05).

No relationship was found between the energy value of *P. elegans* and its total length ($P > 0.05$) (Figure 3a). In contrast, a positive, linear relationship, albeit a very weak one, was found in *P. adspersus* individuals between their energy value and total length ($R^2 = 0.07$, $P < 0.05$, $N = 71$); the line of best fit is described by $y = 0.139x + 12.62$, where y – energy value [J mg^{-1} DW] and x – total length [mm] (Figure 3b).

The average energy values of *P. elegans* in the separate months varied only slightly from 15.9 J mg^{-1} DW to 17.2 J mg^{-1} DW (Figure 4a), and

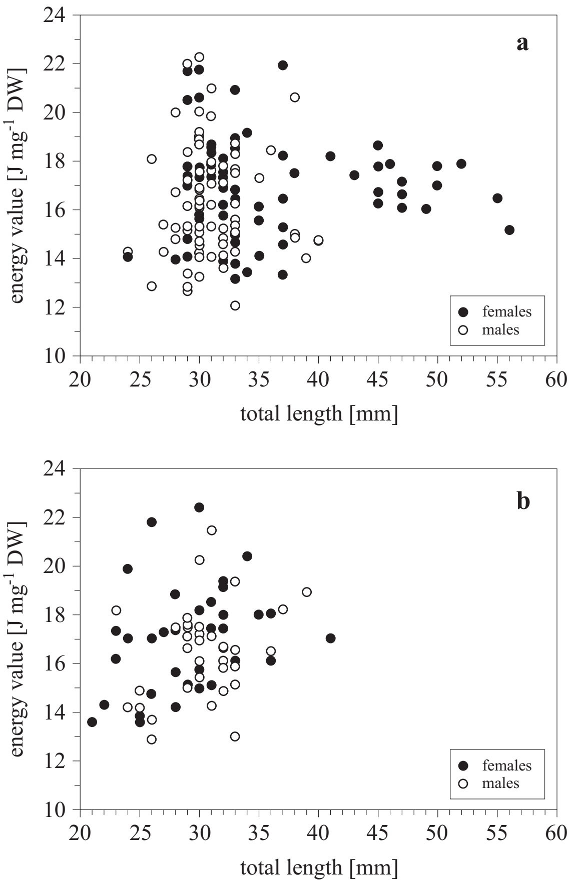


Figure 3. Dependence of the energy value of a) *Palaemon elegans* (N = 150) and b) *P. adspersus* (N = 71) on the total length of prawns collected at Gdynia from December 2005 to February 2007

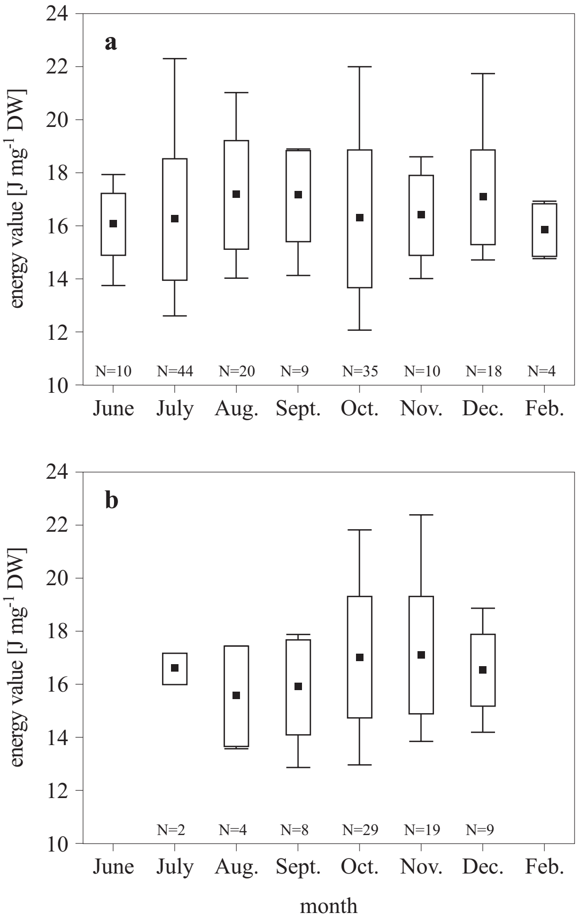


Figure 4. Seasonal changes in energy value [J mg^{-1} DW] of a) *Palaemon elegans* and b) *P. adspersus* at Gdynia. Square – average; box – standard deviation; whiskers – range of data, N – number of individuals studied

the differences were not statistically significant (ANOVA, $P > 0.05$). In *P. adspersus*, the average energy values in the different months varied from 15.9 to 17.1 J mg^{-1} DW (Figure 4b), the differences between them not being statistically significant (ANOVA, P $>$ 0.05). There were no statistically significant differences in the energy values in the separate months between the two species either (t-test, P $>$ 0.05).

At the beginning of July, *P. elegans* occurred at eight of the eleven stations, whereas *P. adspersus* was present at only three (Table 1). The third palaemonid species *P. varians* was not found anywhere in the study area. *P. adspersus* made up no more than 10% of the overall palaemonid density, except for the harbour at Jastarnia, where 68% of the prawns belonged to

Table 2. Average total length, wet weight, dry weight, energy value per dry weight and energy content per individual in *Palaemon elegans* and *P. adspersus* males, non-ovigerous females and ovigerous females sampled in Polish coastal waters in June 2005

Species and sex	Number of individuals	Total length [mm]	Wet weight of individuals [mg WW]	Dry weight of individuals [mg DW]	Energy value [J mg^{-1}DW]	Energy content [J indiv.$^{-1}$]
P. elegans						
males	170	29 ± 4	182 ± 83	45.5 ± 20.8	16.5	751 ± 343
females (non-ovigerous)	155	31 ± 5	257 ± 119	64.3 ± 29.8	16.5	1061 ± 492
females (ovigerous)	55	44 ± 6	785 ± 303	196.3 ± 75.0	21.2*	4162 ± 1590
P. adspersus						
males	12	27 ± 4	139 ± 61	38.9 ± 17.2	16.5	641 ± 283
females (non-ovigerous)	15	37 ± 12	536 ± 468	150.0 ± 131.0	17.0	2550 ± 2227
females (ovigerous)	9	52 ± 2	1342 ± 253	375.6 ± 70.8	21.8*	8200 ± 1545

* Energy value of non-ovigerous females increased by 28.4% (after Szaniawska 1991).

this species. *P. elegans* was found mainly on hard substrates covered with filamentous green algae (principally *Enteromorpha* spp.). The density of the species at Gdynia and in the Dead Vistula River was the highest of all the stations investigated – from over a dozen to several tens of individuals per square metre. But near Osłonino and Hel, the density was no higher than a few individuals per square metre. Only one individual per several square metres was found near Chałupy and on the three harbour quaysides. The density of *P. adspersus* at all the three stations where it occurred was only one individual per several square metres.

The proportions of *P. elegans* males at the various stations ranged from 20% at Frombork to 66% in the Dead Vistula (Table 1). At the stations located on the Gulf of Gdańsk and on the Dead Vistula the proportions of ovigerous females did not exceed 20%, whereas in the Vistula Lagoon they ranged from 80 to 100%. Males made up about 50% of *P. adspersus* populations, except at Jastarnia, where 69% of this species consisted of ovigerous females.

In summer in Polish brackish waters, males of both species with their small size (<30 mm) and weight (<50 mg DW) had a low energy content (<1000 J indiv.$^{-1}$) (Table 2). Non-ovigerous females of *P. elegans* had less than half the energy content (1061 J indiv.$^{-1}$) of non-ovigerous females of *P. adspersus* (2550 J indiv.$^{-1}$). The energy contents of ovigerous females were 4162 J indiv.$^{-1}$ (*P. elegans*) and 8200 J indiv.$^{-1}$ (*P. adspersus*).

The highest energy resources of *P. elegans*, of the order of 10 –150 kJ m^{-2}, were recorded at Gdynia and in the Dead Vistula (Table 3). Somewhat lower values, from a few to a dozen kJ m^{-2}, were found at Osłonino and Hel. The lowest energy resources (< 5 kJ m^{-2}) were observed in the Vistula Lagoon, and at Jastarnia and Chałupy. The resources of *P. adspersus* at the three stations where it was present did not exceed 7 kJ m^{-2}.

Table 3. Energy resources of *Palaemon elegans* and *P. adspersus* at 11 stations in Polish coastal waters in June 2005

Station	Energy resources [kJ m^{-2}]	
	P. elegans	*P. adspersus*
Hel	1–15	< 2
Jastarnia	< 2	< 7
Chałupy	< 2	0
Osłonino	1–15	0
Rewa	0	0
Gdynia	11–124	< 2
Dead Vistula River	13–150	0
Krynica Morska	0	0
Piaski	< 5	0
Tolkmicko	0	0
Frombork	< 4	0

4. Discussion

The energy values of *P. elegans* and *P. adspersus* per unit body weight were very similar and typical of benthic crustaceans in the Baltic (Table 4). The former species had the highest energy values of all the non-indigenous nektobenthic crustaceans in the Baltic studied to date. Similar energy values were recorded in the common shrimp *Crangon crangon* (Szaniawska 1991), and also in *P. elegans* from British coastal waters 4.0 ± 0.2 cal mg^{-1} DW ($= 16.8 \pm 0.8$ J mg^{-1} DW; N = 6); in addition, somewhat higher values (from 4.2 to 4.5 cal mg^{-1} DW ($= 17.6 - 18.8$ J mg^{-1}DW; N = 23)) were calculated for *Palaemon serratus*, another prawn from the same region (see Cumminis & Wuycheck 1971).

The present energy values of *P. adspersus* were 34% less than those recorded in the 1970s (Szaniawska 1984a) (Table 4). These differences may be due to a change in diet. Previously, the most frequent food items

Table 4. Dry weight of individuals 33–35 mm in size, mean energy value, organic matter content, energy value of organic matter and energy content per individual of selected Baltic crustacean species

Species	Total length [mm]	Dry weight of individuals [mg]		Energy value [J mg^{-1} DW]	Organic matter [%]	Energy value [J mg^{-1} AFDW]	Energy content [J indiv.$^{-1}$]		Source
		Females	Males				Females	Males	
Rhithropanopeus harrisii				8.0 ± 1.5	62	12.7 ± 2.1			Wiszniewska et al. 1998
Eriocheir sinensis				11.0 ± 2.1	60	15.3 ± 2.4			Normant et al. 2002
Saduria entomon	35	177	150	10.9	61	18.9	2171	1636	Szaniawska 1991
Palaemon elegans	35	96	59	16.5 ± 2.1	86	19.3 ± 2.5	1816	1258	this study
Palaemon adspersus	35	87	70	16.7 ± 2.1	86	19.5 ± 2.5	1451	1370	this study
Crangon crangon	33	46	37	17.0 ± 1.8	85	20.1 ± 2.3	766	596	Szaniawska 1983, 1991
Palaemon adspersus	35	105	74	19.8 ± 1.8	87	22.5 ± 1.8	2192	1461	Szaniawska 1984a, 1991

were crustaceans (Wiktor 1979). The present diet of *P. adspersus*, besides crustaceans, consists largely of green algae from the genus *Cladophora*, polychaetes, molluscs and detritus; as such it closely resembles the diet of *P. elegans* (Janas & Barańska 2008, Barańska et al. 2009). This would explain the marked similarity in the energy values of the two prawn species.

In the populations of *P. elegans* and *P. adspersus* from the Gulf of Gdańsk it was found that females had somewhat higher energy values than males, although these differences were not statistically significant. In *P. adspersus* similar observations had been made earlier by Szaniawska (1984a), and also in other crustaceans from the southern Baltic (Szaniawska 1984b, Wiktor & Szaniawska 1989, Szaniawska 1991, Wiszniewska et al. 1998). Only in the case of *P. adspersus* was there a weak positive relationship between energy value and total length. The increase in energy value with increasing body size was more conspicuous in *C. crangon* (Szaniawska 1983). No relationship between energy value and individual size was reported for the mud crab *R. harrisii* (Wiszniewska et al. 1998) or the blue mussel *Mytilus edulis* (Szaniawska 1991).

The energy values of *P. elegans* and *P. adspersus* adults (not including ovigerous females) did not differ significantly with respect to season. The difference between the highest and lowest average values for particular months was no more than 10%. Seasonal changes in energy value were, however, found in many populations of crustaceans (Szaniawska 1991, Dobrzycka & Szaniawska 1995, Wiszniewska et al. 1998). These fluctuations, with the lowest values recorded in winter and the highest in early spring and in summer, were due primarily to changes occurring within the populations, especially the appearance of ovigerous females.

The energy contents of *P. elegans* and *P. adspersus*, both of about the same magnitude, were much higher than those of shrimps *C. crangon* in individuals of similar body length (Table 4) and were comparable to those of the Baltic clam *Macoma balthica* (1376 J indiv.$^{-1}$) (Szaniawska 1991). The energy content per individual prawn was lower than that of *S. entomon*, because the isopods had a much greater body mass. However, it should be stressed that organic compounds make up 61% of the body mass in *S. entomon* (Szaniawska 1991) but ca 86% in the prawns. An animal more often found on the sea bed than prawns, *S. entomon* has a more massive carapace (ca 60% of body DW), which consists in large measure of mineral compounds and poorly digested chitin (Normant & Szaniawska 1993). According to McClintock (1986), the energy of insoluble and indigestible organic compounds (e.g. chitin, collagen) does not constitute energy available to a predator. The proportion of a prawn's carapace in the body is much smaller (8.2 ± 1.7% of body DW; N = 15), which means that a greater quantity of usable energy is available to predators from prawns than from isopods. *P. elegans* prawns are therefore an energetically more valuable food item for other organisms, although they are very active and may be able to escape from predators.

The appearance of the new prawn species *P. elegans* has increased benthic energy resources. In early summer the energy resources of this species in the coastal zone of the Gulf of Gdańsk may reach 150 kJ m^{-2} on a hard, algae-covered substrate. Similar energy resources of *P. elegans* are also available to predators foraging near maritime structures and wrecks in the deeper parts of the Gulf of Gdańsk, where very high densities of the species, reaching several tens of individuals per square metre, have been recorded (Wysocki, personal communication). The energy resources of the new species are currently from 10 to even 70 times higher than those of *P. adspersus*. Until mid-summer they can increase still further because of the greater proportion of ovigerous females, which have the highest energy content in the population (Szaniawska 1991). After this period these resources decline, following the appearance of juveniles and the migration of individuals to deeper waters. It has been demonstrated in many species, e.g. in amphipods, that juveniles have smaller energy resources than adults (Quigley et al. 1989, Hill et al. 1992). In autumn, on the other hand, the resources of *P. adspersus* in the coastal zone of the Gulf of Gdańsk may increase somewhat, since this species is commonly observed there from August to the end of the year (Janas et al., in preparation). The relatively small resources of prawns in the Vistula Lagoon in 2005 increased in later years, but *P. elegans* was still the only prawn species inhabiting those waters (authors' own observations).

Since the arrival of *P. elegans* in the Baltic, these prawns have become the most frequent food item taken by cod during the cold season (Gruszka & Więcaszek, in press). For the winter, prawns migrate to deeper waters; but there they have no shelter on the soft sea bed devoid of vegetation and are far less active, so they are an easy catch for predators. The new prawn may replace the isopod *S. entomon*, which was the main component of the cod's diet in the late 1970s and early 1980s (Załachowski 1986). The energy resources of the population of the non-native *P. elegans* are comparable with those of *S. entomon* estimated in the mid-1980s (119.94 kJ m^{-2}) (Szaniawska 1991). However, current resources of the latter crustacean may be smaller owing to the contraction of its range, also in the Gulf of Gdańsk (Kube et al. 1997, authors' own observations).

In summary, the energy value per unit body mass of the non-indigenous *P. elegans* is almost identical with that of the native *P. adspersus* and exceeds the energy value of many other crustaceans. *P. elegans* is therefore an energetically very valuable source of food for predators. In addition, the current energy resources of *P. elegans* in Polish brackish coastal waters are much higher than those of *P. adspersus.* Indeed, the resources of *P. elegans* are some of the highest ever found among the nektobenthic crustaceans of this region and constitute a rich source of food for the predators foraging there. *P. elegans*, a new link in the food web, has increased the flow of energy from producers and consumers to consumers at higher trophic levels and at the same time from the benthic to the pelagic zone of the Baltic Sea.

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