ENVIRONMENTAL PREFERENCES OF *CRANGON CRANGON* (LINNAEUS, 1758), *PALAEMON ADSPERSUS* RATHKE, 1837, AND *PALAEMON ELEGANS* RATHKE, 1837 IN THE LITTORAL ZONE OF THE GULF OF GDAŃSK

BY

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ABSTRACT

This study concerns the environmental requirements of the shrimp, *Crangon crangon*, and the prawns, *Palaemon adspersus* and *Palaemon elegans*, which occur in the Gulf of Gdańsk. Specimens were sampled from the 0.5-1.0 m and 5.0-10.0 m depth layers in the southwestern part of the Gulf, near the seaside resort of Sopot, in 2002-2003. The dominant species was *C. crangon*, the largest concentrations of which were recorded at 5.0-10.0 m. Seasonal changes were observed in the composition of the population of these three species during the year. *P. elegans*, a relative newcomer to the Polish zone of the Baltic Sea, has occupied a vacant ecological niche (the 0.5-1.0 m depth zone) and in doing so, has avoided competition with the native *C. crangon*. In the littoral zone (0.5-1.0 m) off Sopot, and also off Hel and Gdynia, *P. elegans* occurred together with *P. adspersus*. The diverse requirements of these three species with respect to biotic (e.g., food) and abiotic factors (e.g., substrate, dissolved oxygen) enable them to coexist in the waters of the Gulf of Gdańsk.

RÉSUMÉ

Cette étude concerne les exigences environnementales des crevettes *Crangon crangon*, *Palaemon adspersus* et *Palaemon elegans*, qui sont présentes dans le golfe de Gdańsk. Les spécimens ont été récoltés à 0,5-1,0 m et 5,0-10,0 m de profondeur dans la partie sud-ouest du golfe, près de la station balnéaire de Sopot, en 2002-2003. L'espèce dominante était *C. crangon*, dont les effectifs les plus élevés ont été trouvés à la profondeur de 5,0-10,0 m. Des variations saisonnières ont été observées dans la composition de la population de ces trois espèces au cours de l'année. Présent depuis peu dans la zone polonaise de la mer Baltique, *P. elegans* a occupé une niche écologique vacante (la zone de profondeur 0,5-1,0 m) et a ainsi évité la compétition avec l'espèce autochtone *C. crangon*. Dans la zone littorale (0,5-1,0 m) au large de Sopot, et également au large de Hel et Gdynia, *P. elegans* est présent avec *P. adspersus*. Les exigences différentes de ces trois espèces par rapport aux facteurs biotiques (nourriture) et abiotiques (nature du fond, oxygène dissous) leur permettent de coexister dans les eaux du golfe de Gdańsk.

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INTRODUCTION

Crangon crangon (Linnaeus, 1758), *Palaemon adspersus* Rathke, 1837, and *Palaemon elegans* Rathke, 1837 all occur in the littoral zone of the Polish Baltic coast (Demel, 1935; Żmudziński, 1967; Łomniewski et al., 1975; Jażdżewski & Konopacka, 1995). *P. elegans* is a species new to the Polish part of the Baltic, its presence in the Gulf of Gdańsk having first been reported in 2002-2003 (Janas et al., 2004).

All three species are marine, euryhaline, and eurythermal (Berglund, 1980; Ramirez de Isla Hermandez & Taylor, 1985; Köhn & Gosselck, 1989; Barnes, 1994; Jażdżewski & Konopacka, 1995). Preferring highly productive estuaries with strong tidal movements of brackish water masses (Tiews, 1970), the brown shrimp, *C. crangon* inhabits shallow sandy and sandy-muddy sea beds (Smaldon, 1979; Barnes, 1994; Jażdżewski & Konopacka, 1995). *P. adspersus* is a shallow-water prawn found at depths of 0-6 m, often in estuarine conditions (Smaldon, 1979; Hayward & Ryland, 1996). In summer, it principally inhabits coastal underwater meadows of vascular plants like *Zostera* sp., *Ruppia* sp., or *Potamogeton* sp. (Köhn & Gosselck, 1989; Jażdżewski & Konopacka, 1995). *P. elegans* is characteristic of open habitats (Barnes, 1994), usually in the tidal zone, on sandy bottoms covered with macroalgae or seagrasses (chiefly *Zostera marina*), bare sandy sea beds, the brown algae belt, and stony bottoms (Berglund, 1980; Berglund & Bengtsson, 1981; Dalla Via, 1985; Hayward & Ryland, 1996). It occurs in large numbers in ports and fishing harbours.

An interesting question is whether *C. crangon*, *P. adspersus,* and *P. elegans* are able to coexist in the waters of the Gulf of Gdańsk. The literature suggests that their ecological demands are sufficiently diverse for this to be the case. A whole range of papers describes and analyses these requirements in the Baltic Sea (e.g., Żmudziński, 1961; Jażdżewski, 1971; Motycka, 1973; Boddeke, 1975; Wiktor, 1980; Wiktor et al., 1980; Berglund, 1980, 1981, 1984; Baden & Pihl, 1984), but not one tackles the problem of their coexistence. By no means exhausting the topic, the present study is a first attempt at characterizing the relationships between them. A further aim is to obtain more data on the part played by the newcomer (*P. elegans*) in its new environment.

MATERIALS AND METHODS

The study sites were located in the southwestern part of the Gulf of Gdańsk, off the seaside resort of Sopot (54°27′N 18°35′E). The prawns and shrimp were caught from depths of 0.5-1.0 m and 5.0-10.0 m between 11:00 and 13:00 hrs.

Samples were collected at each station once a month in July, September, and December 2002, and throughout 2003, except January, February, and August, at a depth of 0.5-1.0 m, and in July, and September 2002, and January, April, and July 2003, at a depth of 5.0-10.0 m. The animals from the 5.0-10.0 m layer were captured with a bottom drag net (66 × 33 cm; 5 mm mesh) trawled for a distance of 100 m. The samples from 0.5-1.0 m were caught with a 1 × 2 m trawl (6 mm mesh) hauled over a distance of 100 m. The type of bottom, water temperature (°C) and salinity (psu) were measured at both stations at the same time as the shrimp and prawn samples were collected. The animals were stored in a 4% formalin solution.

The shrimps were identified according to Holthuis (1987). Length was measured from the tip of the rostrum to the end of the telson to an accuracy of 1 mm. The wet weight of each specimen was determined to 0.001 g. Sex was determined by the size and shape of the endopodite of the first pleopod, which is almost invisible to the naked eye in males, and by the presence (males) or absence (females) of the male appendage (appendix masculina) (Balss, 1926; Lloyd & Yonge, 1947). Sex determination is accurate for animals longer than 20 mm. The number of ovigerous females was counted. The weight-to-length (W/L) ratio between individuals was determined using Lagler's formula, where a = proportionality constant or intercept, and b = exponent.

RESULTS

The seabed at these sampling stations is bare and sandy. The salinity at both sites was approximately the same (6.4 to 6.7 psu at 0.5-1.0 m and 6.8 to 7.0 psu at 5.0-10.0 m). Only the water temperature varied: from 0.3°C in February 2003 to 23.2°C in July 2003.

With respect to both numbers and biomass, the dominant species of the three under study was *Crangon crangon*: 82% (758 specimens) of all the specimens collected. The proportions of the other two species were much smaller: *Palaemon elegans* with 16% (144 specimens) and *Palaemon adspersus* with 2% (18). Most *C. crangon* were taken from the 5.0-10.0 m layer. *P. elegans* dominated in the shallower waters, while *P. adspersus* was noted in very small numbers only in the 0.5-1.0 m layer. Biomass was proportional to numbers (fig. 1).

The numbers of *C. crangon* varied during the year. Since the 0.5-1.0 m depth layer is situated off a bathing beach, not many organisms of any kind are found there. At this depth, the largest numbers of *C. crangon* were recorded in spring and autumn, while its largest concentrations in deeper waters were noted in late autumn and in winter (fig. 2). During the warmest months *C. crangon* was absent from the 0.5-1.0 m depth layer, but *P. elegans* and *P. adspersus* were present there

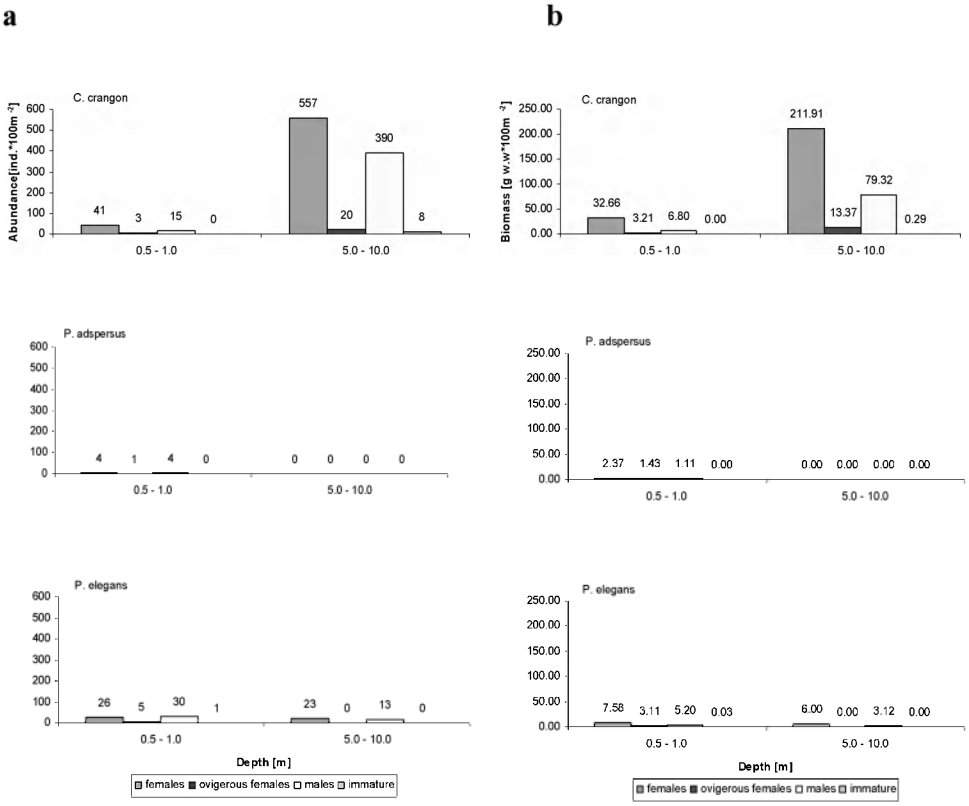

Fig. 1. Total year density (a) and biomass (b) per 100 m^2 of sea bed of females, ovigerous females, males, and immature individuals (in that very order from left to right) of *Crangon crangon* (Linnaeus, 1758), *Palaemon adspersus* Rathke, 1837, and *Palaemon elegans* Rathke, 1837 at depths of 0.5-1.0 m and 5.0-10.0 m.

(figs. 2 and 3). The latter species was noted only in summer in the shallowest waters of the Gulf, while the former was recorded throughout the study period, in various numbers, in both depth layers (fig. 3).

The mean body length decreased in the following order: *P. adspersus* 38.8 ± 9.7 mm; *P. elegans*, 32.0 ± 4.7 mm; *C. crangon*, 30.9 ± 6.7 mm. Females were longer than males in all three species, and ovigerous females were longer than non-ovigerous females (table I; figs. 4, 5, 6). Table II shows the differences in body weight between animals of different sex. Females are heavier than males and ovigerous females are heavier than non-ovigerous females. Individuals occurring at depths of 0.5-1.0 m were heavier than those from deeper waters (table II).

C. crangon specimens from shallow waters were longer (mean length ± SD = 37.6 mm ± 6.1 at 0.5-1.0 m, and 29.6 mm ± 6.1 at 5.0-10.0 m); the difference between the maximum length of males (42 mm) and females (53 mm) was 11 mm. Seasonal changes in length are observed in this species. In the 0.5-1.0 m depth

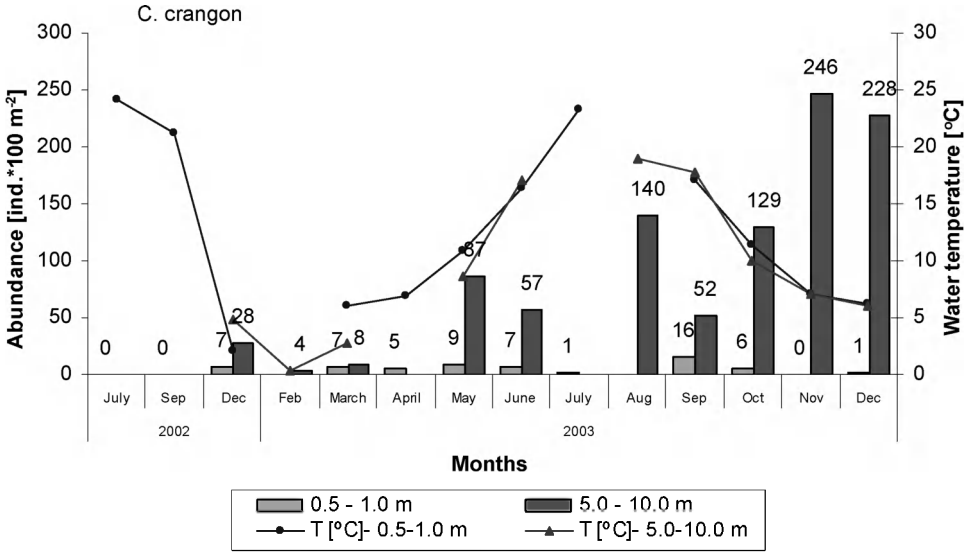

Fig. 2. The seasonal distribution of *Crangon crangon* (Linnaeus, 1758) and the seawater temperature at 0.5-1.0 m and 5.0-10.0 m (the figures above the columns denote the numbers of specimens per 100 m^2 of sea bed).

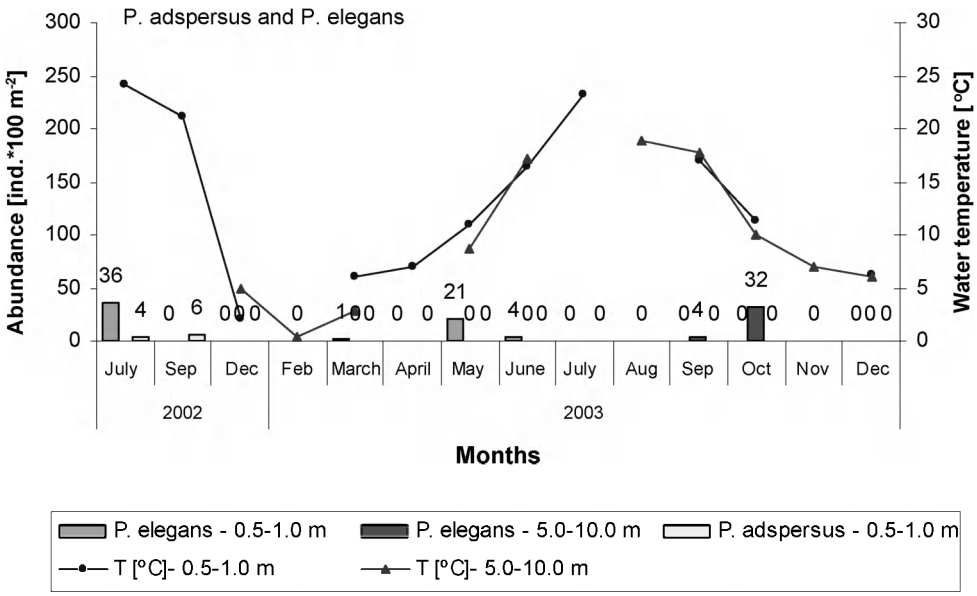

Fig. 3. The seasonal distribution of *Palaemon adspersus* Rathke, 1837 and *Palaemon elegans* Rathke, 1837, and the seawater temperature at 0.5-1.0 m and 5.0-10.0 m (the figures above the columns denote the numbers of specimens per 100 m^2 of sea bed).

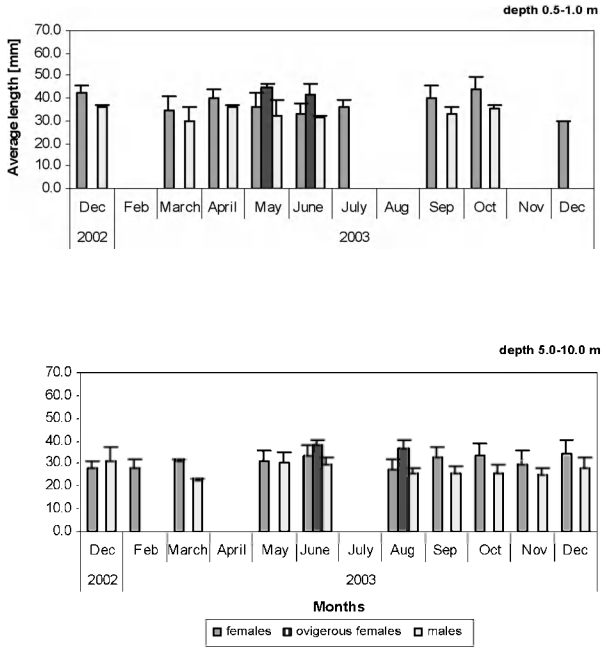

Fig. 4. The average monthly lengths (±SD) in males, females, and ovigerous females of *Crangon crangon* (Linnaeus, 1758) at depths of 0.5-1.0 m and 5.0-10.0 m.

layer the larger animals were dominant in spring and autumn, the smaller ones in summer and winter. At the deep-water station, larger specimens were observed in summer, autumn, and winter. Ovigerous females were noted from mid-May to the end of August. Reproduction began in the shallower waters, but involved only the largest females in the population. In the succeeding months, ever smaller females matured (fig. 4). *P. adspersus* reached a maximum body length (rostrum — end of telson) of 38 mm (males) and 59 mm (females). Reproduction took place in summer, in females with a minimum body length of 40 mm (fig. 5). In *P. elegans*, mean body lengths at both depths were roughly the same (at 0.5-1.0 m, mean length ± SD = 32.0 mm ± 4.8; at 5.0-10.0 m = 31.6 mm ± 4.1). The difference between the maximum lengths in males (40 mm) and females (45 mm) was 5 mm. The largest specimens were recorded in March, the smallest ones in September. *P. elegans* females with eggs turned up at the shallower station in summer. Females reproduced when they achieved a body length of approximately 40 mm (fig. 6).

With respect to numbers and biomass, females dominated the populations of *C. crangon*, *P. adspersus*, and *P. elegans* (fig. 1), the respective figures being 62%, 56%, and 53% (figs. 7, 8, 9). The percentage of *C. crangon* females was higher at 0.5-1.0 m (75%) than at 5.0-10.0 m (60%). The sex ratio in this species was subject to seasonal variation: at the shallow-water station, males were present in

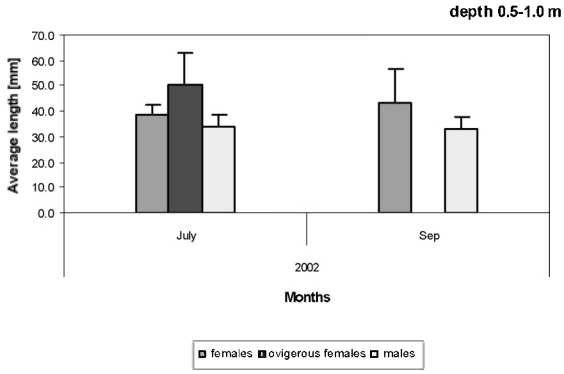

Fig. 5. The average monthly lengths (±SD) in males, females, and ovigerous females of *Palaemon adspersus* Rathke, 1837 at depth of 0.5-1.0 m.

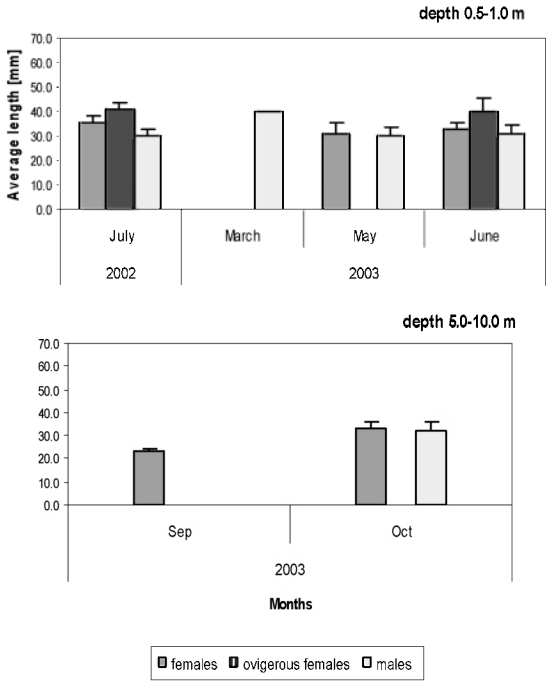

Fig. 6. The average monthly lengths (±SD) in males, females, and ovigerous females of *Palaemon elegans* Rathke, 1837 at depths of 0.5-1.0 m and 5.0-10.0 m.

larger numbers in spring and autumn, but there were fewer of them in summer and winter. At the deep-water station, the sex ratio was roughly the same throughout the year (fig. 7). In the case of *P. elegans*, the sex ratio with respect to water depth was the reverse of that in *C. crangon*. At 0.5-1.0 m the ratio was almost 1 : 1

TABLE I

Average lengths (±SD) of males, non-ovigerous females, and ovigerous females of *Crangon crangon* (Linnaeus, 1758), *Palaemon adspersus* Rathke, 1837, and *Palaemon elegans* Rathke, 1837 at depths of 0.5-1.0 m and 5.0-10.0 m

Species	Length (mm) Depth (m)	Males		Non-ovigerous females		Ovigerous females	
		average	±SD	average	±SD	average	±SD
C. crangon	0.5-1.0	33.3	4.4	38.7	6.0	42.0	4.3
	5.0-10.0	26.7	4.3	31.6	6.1	37.0	3.8
P adspersus	0.5-1.0	33.3	4.1	41.5	10.5	50.0	12.7
P elegans	0.5-1.0	30.1	3.4	32.8	4.3	40.5	3.3
	5.0-10.0	31.9	3.9	31.5	4.3	–	–

TABLE II

Average wet weight (±SD) of males, non-ovigerous females, and ovigerous females of *Crangon crangon* (Linnaeus, 1758), *Palaemon adspersus* Rathke, 1837, and *Palaemon elegans* Rathke, 1837 at depths of 0.5-1.0 m and 5.0-10.0 m

Species	Weight (g) Depth (m)	Males		Non-ovigerous females		Ovigerous females	
		average	±SD	average	±SD	average	±SD
C. crangon	0.5-1.0	0.469	0.202	0.806	0.384	1.069	0.276
	5.0-10.0	0.204	0.119	0.381	0.218	0.679	0.128
P adspersus	0.5-1.0	0.278	0.118	0.592	0.381	1.434	1.309
P elegans	0.5-1.0	0.176	0.083	0.297	0.107	0.623	0.175
	5.0-10.0	0.257	0.100	0.264	0.110	–	–

(females, 51%; males, 49%), but in deeper waters, females were decidedly more frequent than males (65%) (fig. 9).

The correlations between body length and body weight in *C. crangon*, *P. elegans*, and *P. adspersus* specimens were found to be exponential, and can be expressed by the following formulae:

Crangon crangon:

Depth 0.5-1.0 m: $W = 0.000004\ L^{3.3069}$ $R^2 = 0.9478$

Depth 5.0-10.0 m: $W = 0.000006\ L^{3.1449}$ $R^2 = 0.9137$

Palaemon adspersus:

Depth 0.5-1.0 m: $W = 0.000004\ L^{3.1673}$ $R^2 = 0.9352$

Palaemon elegans:

Depth 0.5-1.0 m: $W = 0.000002\ L^{3.3621}$ $R^2 = 0.8144$

Depth 5.0-10.0 m: $W = 0.000006\ L^{3.0740}$ $R^2 = 0.8973$

The weight of the shrimp and of these prawns increases in parallel with their body dimensions.

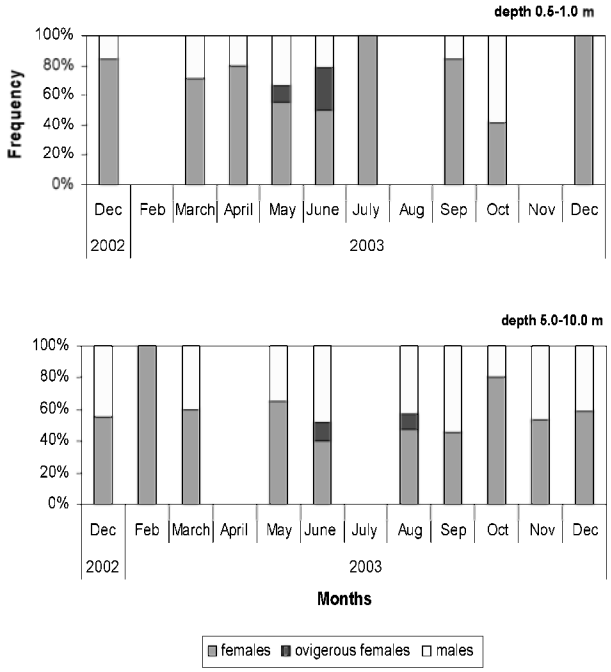

Fig. 7. The sex structure in the population of *Crangon crangon* (Linnaeus, 1758) at 0.5-1.0 m and 5.0-10.0 m.

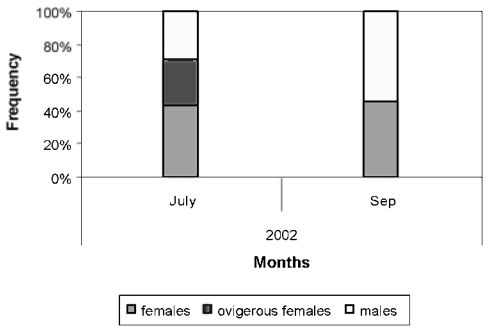

Fig. 8. The sex structure in the population of *Palaemon adspersus* Rathke, 1837 at 0.5-1.0 m.

DISCUSSION

The shrimp, *Crangon crangon*, and the prawns, *Palaemon adspersus* and *Palaemon elegans* were investigated in the Gulf of Gdańsk in 2002-2003. At depths of 0.5-1.0 m and 5.0-10.0 m, the bottom is sandy, which is the natural habitat of *C. crangon* (cf. Smaldon, 1979; Barnes, 1994; Jażdżewski & Konopacka, 1995); hence the large numbers of this species at these depths. The offshore underwater

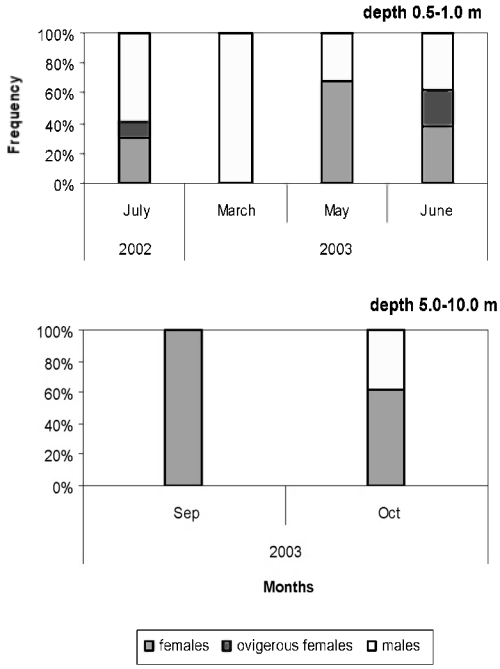

Fig. 9. The sex structure in the population of *Palaemon elegans* Rathke, 1837 at 0.5-1.0 m and 5.0-10.0 m.

meadows of vascular plants (not the sandy eulittoral) are the habitat preferred by *P. adspersus* (cf. Köhn & Gosselck, 1989; Jażdżewski & Konopacka, 1995). This is probably the reason for the small numbers of this species on the sandy bottom. *P. adspersus* could have reached the study area from the algae-coated piles of the nearby pier, a distance of c. 100 m, or from the patches of surviving underwater meadows (c. 2000 m). The presence of this prawn species only in summer (July, August, and early September) in the 0.5-1.0 m depth layer may be caused by its seasonal migration pattern: the offshore, autumn movement towards deeper waters, where this prawn spends the winter, and the onshore, spring movements (in April, or May at the latest) towards the warmer, coastal waters (Żmudziński, 1961; Hagerman & Østrup, 1980; Barnes, 1994). *P. elegans* was present in small numbers on the sandy bottom in both depth layers investigated, but the whole year round. Berglund & Bengtsson (1981) examined the causes for the absence of *P. adspersus* and the presence of *P. elegans* on bare sandy bottoms. When *P. adspersus* occurs on a sandy bottom it becomes visible, and because it is large and not very nimble, it is quickly picked up by predators. In addition, it obtains its food from the bottom vegetation. *P. elegans* in contrast, itself a predator, is much livelier, and is better able to escape from those animals that in turn prey on it. That is why the smaller *P. elegans* turns up in a variety of environments, including sandy

bottoms, whereas the larger *P. adspersus* occurs almost exclusively in eelgrass beds (Berglund, 1980).

The distribution of *C. crangon* and *P. elegans* with respect to depth is uneven. The largest numbers of the former were recorded at 5.0-10.0 m depth, a result also obtained by Wiktor et al. (1980) in the Gulf of Gdańsk. The probable reason for the small concentration of *C. crangon* in the eulittoral zone (0.5-1.0 m) is the instability of the environmental conditions (temperature, dissolved oxygen content, salinity) due to the constant movement of the water masses, and the influence of the inflowing streams, which reduce the salinity and carry pollutants (Report on the state of the environment..., 2002), not to mention the direct effect of all the various activities that people undertake on beaches. The oxygen requirements of *C. crangon* are known to be very high (Hagerman & Szaniawska, 1986; Attrill et al., 1999; Attrill & Power, 2000), and when the oxygen concentration falls below 20%, these crustaceans quickly move away from such hypoxic waters to normoxic ones. Over a short period of time, the amount of dissolved oxygen in the 0.5-1.0 m layer can vary from hypoxia to oversaturation. Concentrations of *P. elegans* were larger at 0.5-1.0 m depth than at 5.0-10.0 m. It seems that this species, a recent addition to the Gulf of Gdańsk's fauna, has occupied a vacant ecological niche, thereby avoiding competition with the native *C. crangon*. Furthermore, the broad tolerance of *P. elegans* to changes in temperature, salinity, and dissolved oxygen content has enabled it to survive in the unstable conditions of the eulittoral zone (0.5-1.0 m) (Berglund, 1980). In the North Sea, *P. elegans* occurs in intertidal rock pools, where it is regularly exposed to the oxygen deficiencies typical of that kind of habitat. It is thus well adapted to withstand hypoxia (Taylor & Spicer, 1988).

C. crangon is present in the Gulf of Gdańsk the whole year round, but its numbers and total biomass are subject to seasonal variations (Motycka, 1973; Wiktor et al., 1980; Łapińska & Szaniawska, 2005). It performs seasonal migrations (Tiews, 1970; Boddeke, 1975; Attrill & Power, 2000; Hostess, 2000): offshore in autumn and onshore in spring, depending on various factors, both biotic (reproduction) and abiotic (availability of food, temperature, salinity, dissolved oxygen). In the Gulf of Gdańsk it usually overwinters at depths of 20-40 m, whereas in summer it accumulates in large numbers in warm shallow waters, often at depths from 0.2 to 5.0 m (Żmudziński & Ostrowski, 1990). With the onset of the reproductive period, the females move off to deeper waters (Boddeke, 1976; Gelin et al., 2001). The seasonal migration pattern in *P. elegans* is similar: offshore in autumn, and back to shallower waters in spring (Kobyakova & Dolgopol'skaya, 1969). This explains the presence of this species in spring and summer at depths of 0.5-1.0 m and in autumn at 5.0-10.0 m.

Because *C. crangon* undertakes seasonal migrations, one comes across specimens with different body lengths at different times of the year (Lloyd & Yonge,

1947; Motycka, 1973; Jeffery & Revill, 2002). In the present study, the percentage of large specimens at depths of 0.5-1.0 m is highest (body length = c. 37-40 mm) in early spring and in autumn. In summer (May, June, July) the proportion of smaller individuals increases (c. 30-35 mm in length). With smaller specimens returning to shallower waters, the mean size of the population at depths of 0.5-1.0 m in late spring and early summer was smaller (by c. 5 mm). During the summer reproductive period, that year's newly-hatched young extend the population, which implies a reduction in the mean body length of this shrimp. In late autumn, the larger animals are the first to leave for deeper waters. Havinga (1930), Lloyd & Yonge (1947), and Motycka (1973) all noted higher proportions of males in deeper waters. Variations in the percentages of females in deeper waters may be due to migrations undertaken during the reproductive period.

The status of *P. elegans* with respect to the native shrimp and prawn species does not appear to be that of an invader, which often reduces the habitat size and population numbers of native species. In the littoral zone off Sopot, and also off Hel and Gdynia, *P. elegans* occurred together with *P. adspersus*. In Swedish waters, these prawns are usually found on a sandy bottom covered with *Zostera marina* (L.): *P. adspersus* lives on the plants growing on the bottom, while *P. elegans* lives on sea beds covered with *Z. marina* (cf. Berglund, 1980; Barnes, 1994). The average size difference between these two prawn species was found to be large enough to allow coexistence (Berglund, 1981). Presumably, *P. elegans*, which arrived in our waters from the North Sea, will soon become a permanent element in the macrozoobenthos of the Polish zone of the Baltic Sea.

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