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EFFECTS OF ENVIRONMENTAL FACTORS ON THE OCCURRENCE OF THE HARPACTICOIDA IN THE ZOOPLANKTON AND IN THE DIET OF THE SMELT *OSMERUS EPERLANUS* (L.) IN THE VISTULA LAGOON

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ABSTRACT

The composition of food consumed by larval and juvenile smelt (*Osmerus eparlanus*) in the Vistula Lagoon was analyzed taking into account changing environmental conditions. The fish and zooplankton were collected at two stages of research, at the end of May and at the beginning of June 2000. The meteorological conditions and physicochemical parameters of water were determined within a limited research area, where a dense network of 15 sampling sites was established. The digestive tracts of 2552 smelts with a standard body length (SL) of 10 to 34 mm were subjected to preparation. A qualitative and quantitative analysis of diet composition was performed within 5-mm fish body length classes, taking into consideration time- and space-variation, as well as changing environmental conditions, primarily wind strength and the depth of sampling sites. Particular attention was paid to the occurrence of a non-specific component in the diet of the pelagic smelt – copepods of the order Harpacticoida, found in bottom deposits. These organisms were present both in the zooplankton and in the food of smelt, and the intensity of their occurrence varied in time and space. The analysis revealed that the presence of the Harpacticoida in deep waters and in the diet of smelt was directly proportional to wind strength and inversely proportional to the depth of sampling sites.

Key words: depth, Harpacticoida, smelt (*Osmerus eperlanus*), turbulences, wind velocity.

INTRODUCTION

Planktonic crustaceans, including copepods (Copepoda), are major components of the food of some pelagic fish, e.g. the herring, as well as larvae and fry of the smelt (*Osmerus eperlanus*). The Harpacticoida are the smallest of all copepods, present in various environments, i.e. in freshwaters, seas (the majority of species), subpolar and tropical waters, as well as in caves and underground waters. The Harpacticoida can be usually found in bottom deposits and littoral zones, on aquatic plants and in the mud [22]. These copepods naturally occur in the benthic environment, but they are also a common zooplankton component in the waters of the Vistula Lagoon [2, 15, 35]. They are poor swimmers, so their presence in deep waters is a consequence of mechanical transportation of the surface layer of bottom deposits, due to intensive water turbulences caused by the wind.

The Harpacticoida can occur in the diet of fish that forage for prey in bottom deposits [1, 3, 7, 29, 46]. When these copepods appear in the depths, they can fall prey to pelagic fish, like the smelt.

The species composition of zooplankton in a given aquatic environment is the key factor affecting the diet of fish. However, many studies demonstrated that fish exhibit selective behavior, i.e. prey selectively on the zooplankton. The prey is chosen based on numerous factors, including: size of the organism [31] limited, especially at the earliest stages of development, by the dimensions of the predator's mouth [34, 45], energy value [16] related to digestion rate [44], as well as taxonomic preferences [51]. Some other traits of planktonic organisms that affect foraging behaviors of fish are: mobility (rate of moving) [23], pigmentation/color [38], smell [43].

In the feeding process, especially at the earliest life stages of fish, a significant role may be also played by a variety of abiotic factors, such as: temperature [27], access to light [26], transparency/turbidity [8], wave motion/turbulences [17]. High variation of these factors in an ecosystem over a short period of time may not only affect diet composition, but also reduce food intake [10].

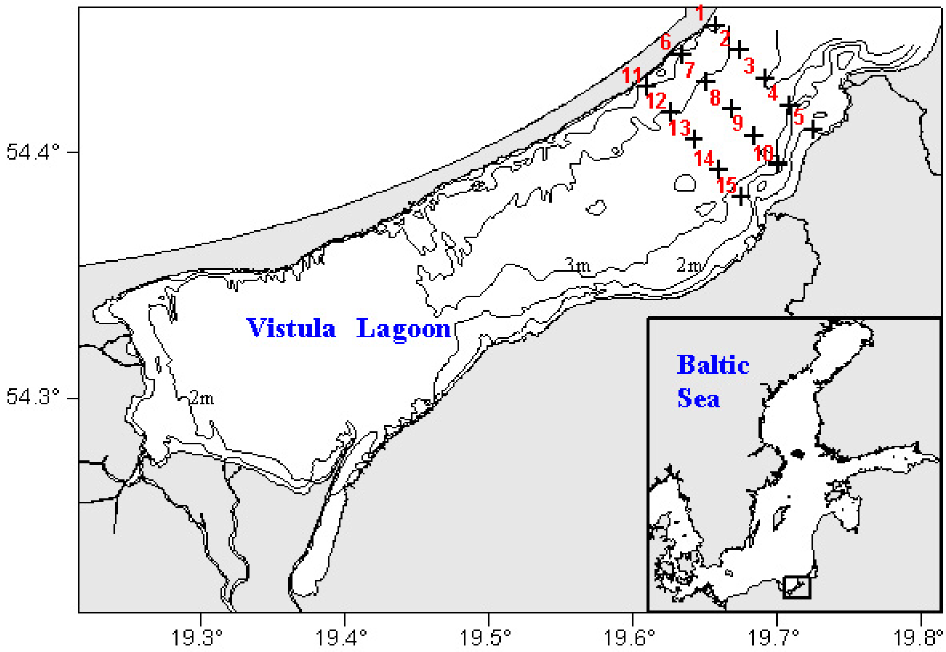
The Vistula Lagoon is an estuarine water body, subject to strong continental and marine influences, characterized by rapid changes in environmental conditions. The factor that produces the strongest effect on this ecosystem is wind. Wind direction and velocity decide about heat exchange, salinity, undulation, ice cover formation and many other hydro-meteorological phenomena [50]. The wind, and especially wave motion, may have a stimulating or inhibitory effect on the abundance of nutrients available to juvenile fish [12, 13]. In shallow water bodies, like the Vistula Lagoon (the mean and maximum depth of the Polish part of the Vistula Lagoon is 2.4 and 5.1 m respectively), wind-induced water mixing to the bottom makes the current carry away the surface layer of bottom deposits, together with bottom-dwelling organisms, which then remain broadly distributed throughout the water column in the form of suspension. One of the consequences of this process is an increase in water turbidity and worse visibility, which makes it difficult for predators to localize their prey [5, 32, 36]. On the other hand, this provides an opportunity for pelagic fish to enrich their diet with non-specific components unavailable to them under normal circumstances, since they can be found in bottom deposits only.

The aim of the present study was to determine the environmental factors that affect the composition of the food of larval and juvenile smelt in the Vistula Lagoon, by verifying the hypothesis that the occurrence of bottom-dwelling copepods of the order Harpacticoida in the diet of pelagic smelt is related to the impact of wind on this shallow water body.

MATERIALS AND METHODS

Samples of zooplankton and ichthyoplankton were collected in the Vistula Lagoon between May 17 and May 24, and between May 30 and June 06, 2000 (14 days), to observe the effects of environmental factors, mainly increasing water temperature and changing hydro-meteorological conditions, on the growth rate and feeding ecology of smelt larvae and fry. The biological materials were collected once a day at 15 sampling stations situated in three rows, five in each, perpendicular to the axis of the Vistula Lagoon (Fig. 1). At the sampling stations where zooplankton and ichthyoplankton samples were taken, temperature was measured and recorded with a CTD probe, salinity was estimated as a function of depth and water transparency was determined using a Secchi disk. Wind velocity and direction were measured manually at each of the sampling stations.

Fig. 1. Distribution of the sampling stations for ichthyoplankton and zooplankton sample collection in the Vistula Lagoon



Ichthyoplankton were captured with a rectangular neustonic trawl with an effective mouth opening area of 2 m^2, equipped with a 500 µm mesh plankton net and a flow-meter to determine the volume of filtered water and ichthyoplankton density per unit volume (100 m^3). Ichthyoplankton samples were preserved in 10% formalin buffered with borax to pH 8-9, and divided into subsamples. Zooplankton samples were collected with a pump, in 40 l of water, and filtered through a 40 µm gauze. Then the concentrated samples were preserved in 4% formalin.

Smelt larvae and fry were separated from the ichthyoplankton subsample containing various fish species [47]. All larval and juvenile smelt were counted to determine their density (individuals·100 m^{-3}). The body lengths of smelt (standard length – SL) were determined exact to 0.5 mm for about 50 individuals collected at each station, or for all individuals if their number was lower than 50. A total of **4675** individuals were measured, which enabled to assign them to the following 5-mm body length classes: **10-14, 15-19, 20-24, 25-29, 30-34 mm**. 10 individuals of each class were taken for analysis of the contents of their dige-stive tracts. Prior to analysis the fish were dried on filter paper and weighed exact to 0.001 g. The digestive tracts of smelt were subjected to preparation under a magnifying glass, and all zooplankton organisms were identified to the lowest taxonomic unit (LTU) in the Sedgwick-Rafter plankton counting chamber, under a microscope. A total of **2552** digestive tracts of smelt were subjected to preparation.

The biomass of consumed food was calculated by the Standard Weight (SW) method [24] and the Individual Body Volume (IBV) method [24]. Food samples were prepared as described by Bottrell et al. [9], Culver et al. [11] and Vijverberg and Frank [48]. A detailed analysis of zooplankton samples was performed as recommended by HELCOM [4].

In order to determine time- and space-variation in the quantity and quality of food consumed by smelt, and to select major food components, the relative importance of food component a was calculated (RI_a), [19]:

$$RI_a = 100\, AI_a / \sum_{i=1}^{n} AI_i, \quad AI_a = F_a + N_a + V_a,$$

where:

F – occurrence frequency of a food component [6], N – percentage of a food component in the total number of food components, V – percentage of a food component in the total food volume (biomass), n – number of food components. The relative importance of food components was calculated for particular samples, days and sampling sites. The percentage of a given food component in the total food biomass and in the total numbers of food components was determined for all fish in a sample.

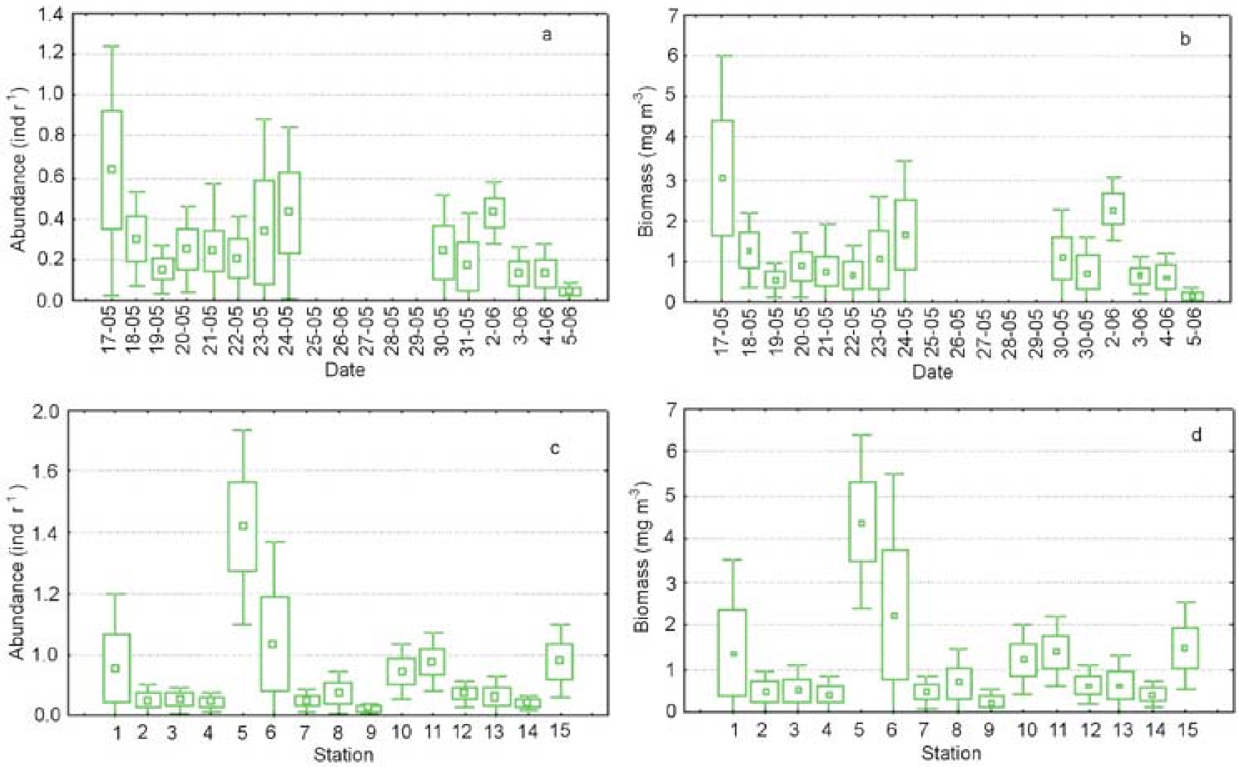
The results of the study, in the form of measurable indices, were analyzed statistically. The statistical significance of relationships between the numbers of copepods of the order Harpacticoida in the diet of larval and juvenile smelt and environmental factors were compared using coefficients of correlation. The significance of differences between the relative importance (RI) of this food component, representing its percentage in the total number of food components and food biomass, as well as the occurrence frequency of the Harpacticoida in the digestive tracts of smelt at two stages of research, was verified by the Mann-Whitney U test. The effects of wind strength and the depth of a sampling site on the occurrence of the Harpacticoida in deep waters (an in fish food) were determined by multiple regression analysis. All statistical analyses follow Sokal and Rohlf [41], and Zar [49], and were performed using Statistica PL. 6.0 software.

RESULTS

Harpacticoida in the environment and in the food of smelt

The occurrence of benthic organisms in the zooplankton is usually a consequence of some factor stimulating changes in the normal living conditions. That is why the results of the present study were analyzed from the perspective of circumstances under which bottom-dwelling copepods of the order Harpacticoida become a component of the zooplankton. The numbers and biomass of the Harpacticoida in deep waters of the Vistula Lagoon varied in time, but revealed daily fluctuations rather than general trends or noticeable differences between two experimental periods (Figs. 2a,b). This could indicate the lack of correlations between fluctuations in these parameters and seasonality, as in the case of typical zooplankton components (Copepoda, Cladocera, Rotatoria). In fact the poorly swimming copepods appeared in the pelagial zone as a result of mechanical transportation, activated by an instantaneous, strong effect of some external factor. Figures 2c, d show that an increased occurrence of the Harpacticoida in the zooplankton was recorded within limited areas, i.e. at sampling sites in the littoral and shallow (below 3 m) zone. At the first stage of research such a situation was observed at both Lagoon shores (stations 1, 5, 6, 10, 11, 15), and at the second stage – in the south-eastern part of the investigation area only (stations 5 and 10).

Fig. 2 (a,b,c,d). Mean numbers and biomass of the Harpacticoida in the waters of the Vistula Lagoon on particular days and at particular stations. The symbols in the diagrams denote: small square – mean, rectangular – ± standard error, "whiskers" – ±0.95 confidence interval



The Harpacticoida appeared irregularly in the diet of juvenile smelt, and their abundance varied in time and space. Greater numbers and biomass of this component were observed in the second experimental period (May 30 – June 5), as compared with the first one (Figs. 3a,b). The Harpacticoida were consumed by the smelt primarily in the shallow, littoral zones, especially at the southern shore of the Vistula Lagoon: stations 5, 10, 15 (Figs. 3c,d). In the period of increased consumption of Harpacticoida (Figs. 3a,b) the population of young smelt was dominated by individuals whose body length was in a range of 22 – 27 mm. Probably the Harpacticoida are consumed most willingly by this group of fish (Fig. 4a). The distribution of Harpacticoida in the digestive tracts of fish divided into SL classes, and the significance of differences in the body size of smelt, are presented in Fig. 4b and Table 1.

Fig. 3 (a,b,c,d). Mean numbers and biomass (individuals and µg·digestive tract^{-1}) of the Harpacticoida in the diet of smelt on particular days and at particular stations. The symbols in the diagrams denote: small square – mean, rectangular – ± standard error, "whiskers" – ±0.95 confidence interval

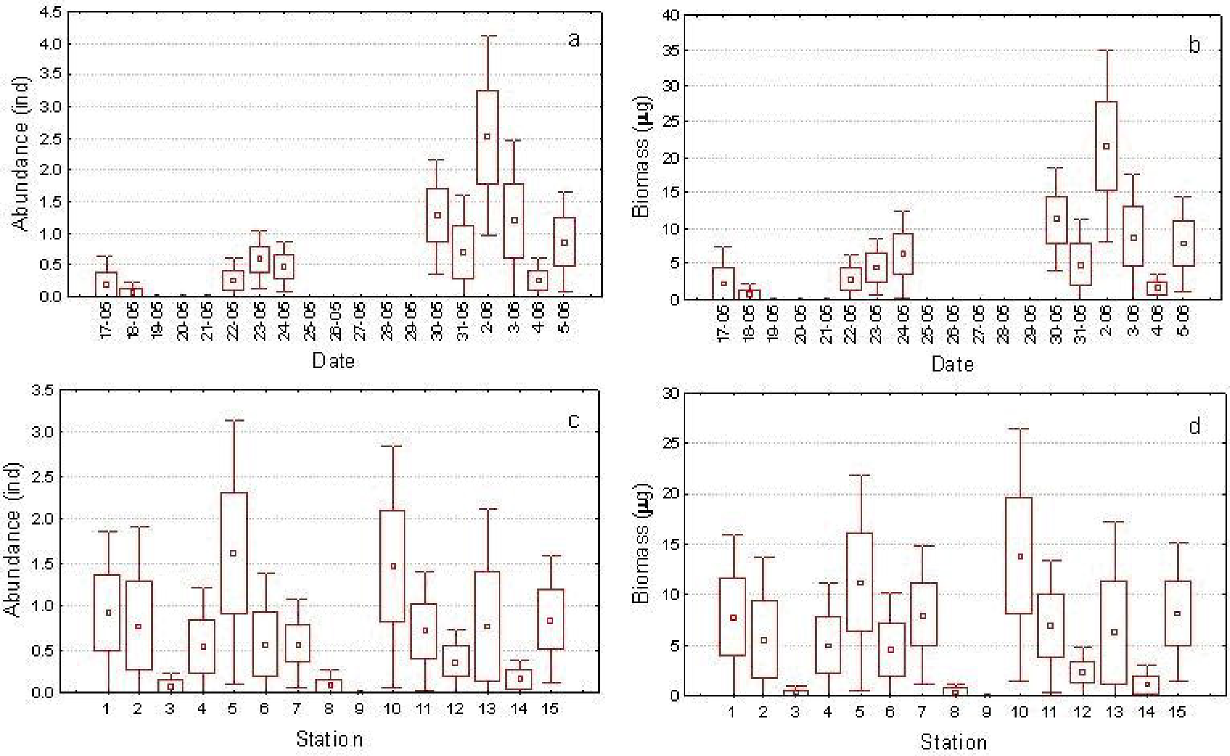
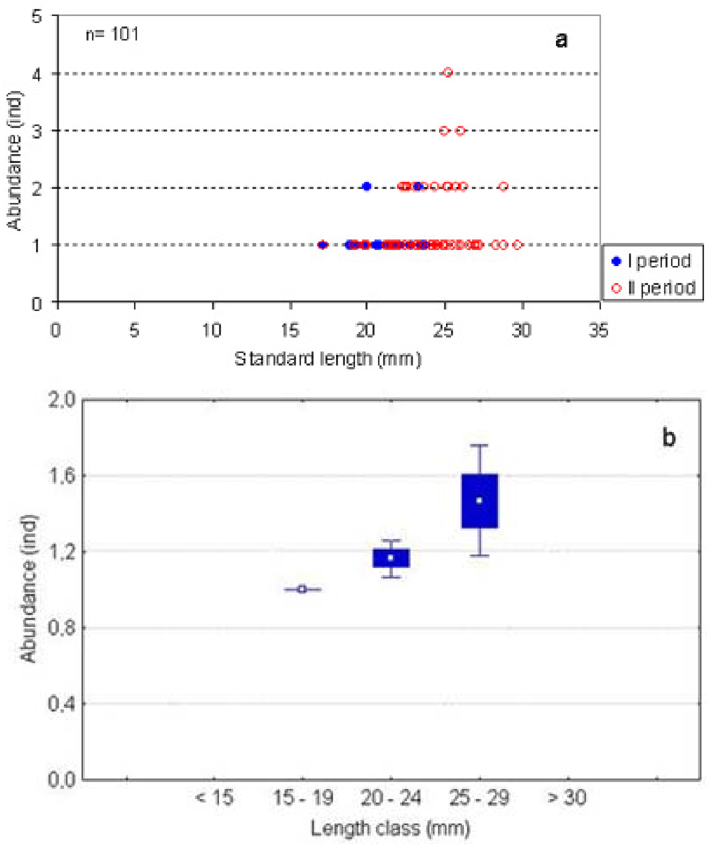


Fig. 4. Relationship between the abundance of food components denoted as the Harpacticoida and the body length of the predator – the smelt (SL, mm):
a) results for particular individuals, with a division into two stages of research,
b) results aggregated in arbitrarily adopted length classes. The symbols in diagram b denote: small square – mean, rectangular – ± standard error, "whiskers" – ±0.95 confidence interval



Harpacticoida did not constitute a major food component for fish. Their relative importance in the diet of juvenile smelt, similarly as the relative importance of some other, smaller organisms, i.e. nauplial stages of Copepoda, rotifers (Rotatoria) and the planktonic larva *Dreissena polymorpha* (veliger stage), was at a low level (RI = 1-19). This could indicate that the above zooplankton components in the Vistula Lagoon were not readily consumed by juvenile smelt. Due to their very small size and a low unit energy value, these copepods are consumed only under favorable conditions, determined in this study.

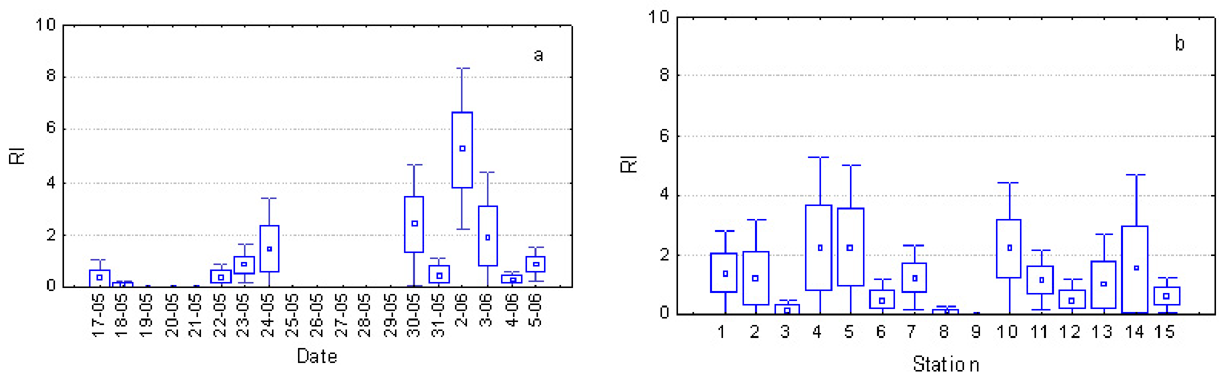
Table 1. Probability of the occurrence of the null hypothesis (H_0) that there are no differences in the numbers of copepods of the order Harpacticoida in the food of larval and juvenile smelt in the Vistula Lagoon between 5-mm fish body length classes

Harpacticoida			
Length class (mm)	15 – 19	20 – 24	25 – 29
15 – 19		0.4085	0.0391*
20 – 24	0.4085		0.0462*
25 – 29	0.0391*	0.0462*	

Values followed by * are statistically significant at P<0.05.

The Harpacticoida occurred more frequently and in greater numbers in the food of smelt captured at the second stage of research (May 30 – June 5), compared with the first stage (May 17 – May 24) – Fig. 5. The significance of differences between the relative importance (RI) of this food component, representing its percentage in the total number of food components and food biomass, as well as the occurrence frequency of the Harpacticoida in the digestive tracts of smelt at two stages of research, was verified by the Mann-Whitney U test at a probability level of P = 0.004 (P< 0.05).

Fig. 5. Time- (a) and space- (b) variation of the relative importance of the Harpacticoida as a component of fish diet over the experimental period. The symbols in the diagrams denote: small square – mean, rectangular – ± standard error, "whiskers" – ±0.95 confidence interval



Effects of environmental factors on the occurrence of the Harpacticoida in the zooplankton and in the diet of smelt

The varied abundance of Harpacticoida in the diet of smelt was a direct consequence of the availability of these copepods in deep waters. It was weakly, though significantly, correlated with Harpacticoida densities in the environment (r = 0.15, P<0.05), (Fig. 6), and strongly correlated with the environmental factors that decided about the presence of these organisms in the zooplankton: the depth of a sampling site (r = -0.24, P<0.05) and wind strength (r = 0.26, P<0.05) (Figs. 7, 8). A qualitative analysis showed that the Harpacticoida were more abundant in the zooplankton at shallower sampling sites than at those located in deeper waters (r = -0.42, P<0.05). This is a preliminary observation only, since these differences could result from local variations in the abundance of Harpacticoida in bottom deposits, which was not the subject of this study. However, it provided the basis for a complex analysis of the effects of the depth of a sampling site and wind strength (the key factor) on the presence of the Harpacticoida in the zooplankton in the ecosystem of the Vistula Lagoon. A multiple regression test confirmed the significance of these variables, which explained the variation in the numbers of the Harpacticoida in deep waters in 20% (Table 2). The probability of the occurrence of the Harpacticoida in the zooplankton was directly proportional to wing strength and inversely proportional to the depth of a sampling site (Fig. 9). Under identical wind conditions, the probability of the occurrence of the Harpacticoida in the vicinity of a station located in shallow waters (<2 m) was by 20 to 40% higher than the probability of their occurrence near a sampling site at a depth of >3.5 m. These differences, distinct at wind velocity of $>8\ m \cdot s^{-1}$, were gradually eliminated with an increase in wind strength.

Fig. 6. Relationship between the numbers of the Harpacticoida in the food and environment of the Vistula Lagoon – significantly correlated values, directly proportional at P < 0.05

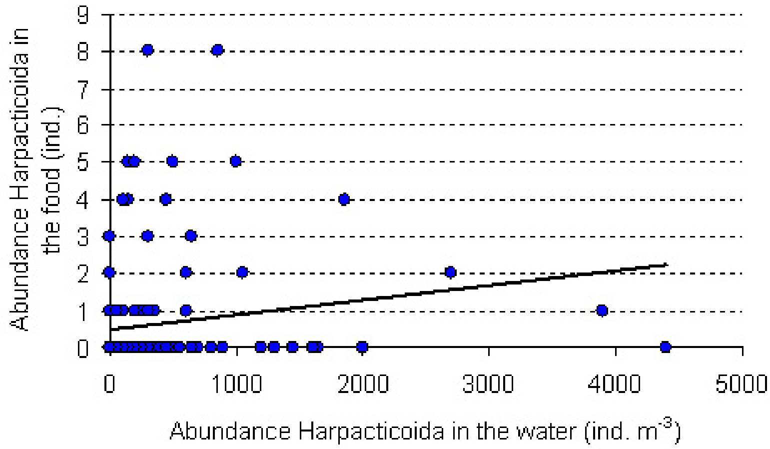


Fig. 7. Relationship between the numbers of the Harpacticoida in the food and the depth of a sampling site – significantly correlated values, inversely proportional at P<0.05

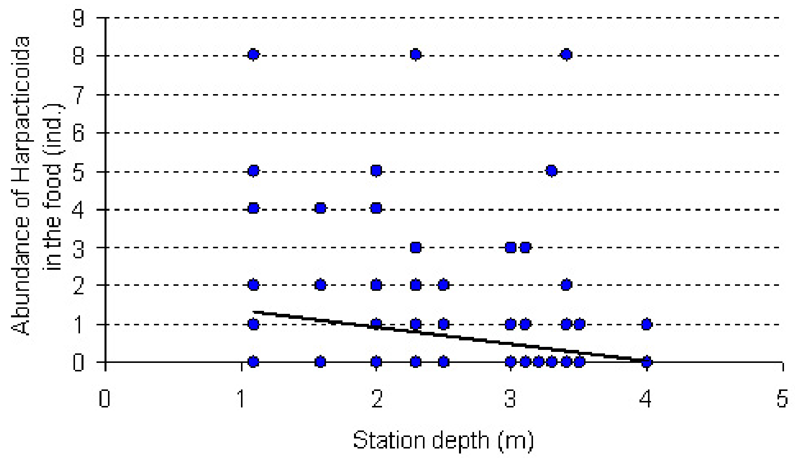


Fig. 8. Relationship between the numbers of the Harpacticoida in the food and wind velocity – significantly correlated values, directly proportional at P<0.05

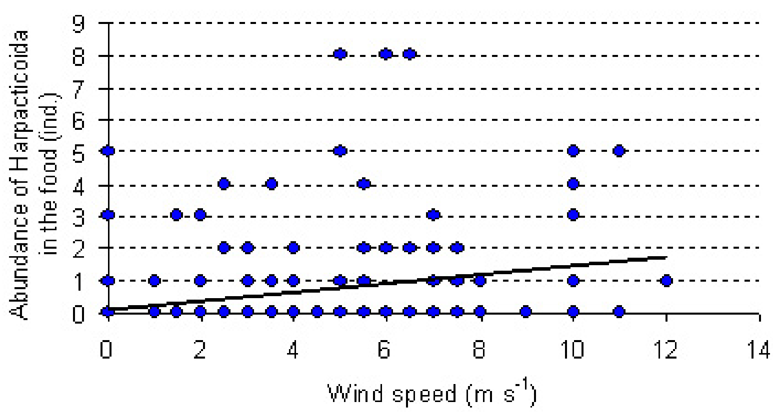


Fig. 9. Probability of Harpacticoida occurrence in the deep waters, depending on wind strength and the depth of a sampling site

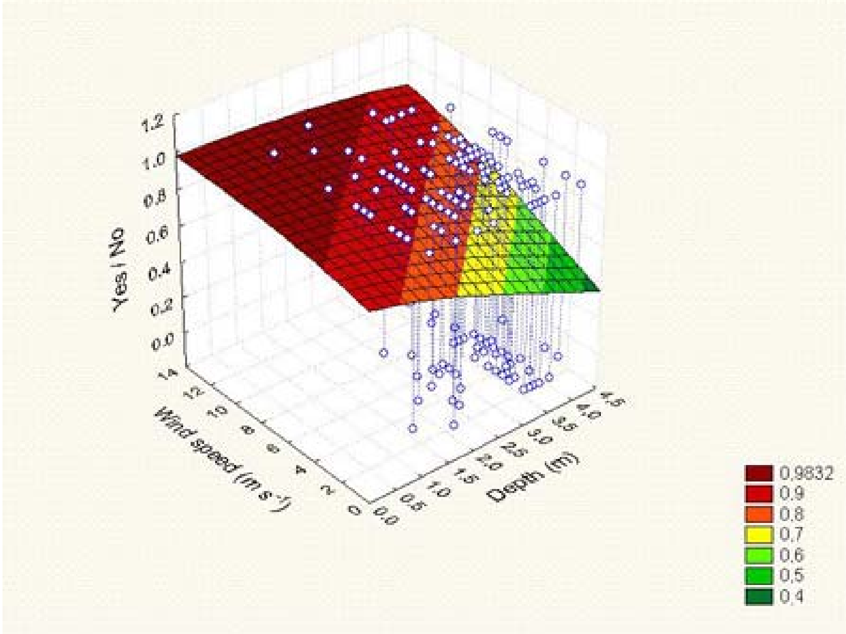


Table 2. Significance of partial correlations obtained as a result of multiple regression analysis for the effects of the depth of a sampling site and wind strength (independent variables) on the numbers of the Harpacticoida in the environment (dependent variable). The calculations were performed for 198 cases (samples)

Parameters	Depth (m)	Wind ($m \cdot s^{-1}$)
Abundance of Harpacticoida in the environment	-300.72**	27.74*

** P<0.00001, * P<0.05.

DISCUSSION

The presence of benthic organisms, such as the Harpacticoida, in the diet of smelt is related to the fact that this predator preys on bottom-dwelling organisms [3, 29, 46]. Studies on the food composition of juvenile fish of various species in some lakes near Węgorzewo [29] revealed the occurrence of the Harpacticoida in the diet of fish that had direct contact with the bottom, like the roach (*Rutilus rutilus*), tench (*Tinca tinca*) or ten-spined stickleback (*Pungitius pungitius*). Numerous authors who examined the diet of flat fish [1, 3, 7] reported that the Harpacticoida were major food components of juvenile sole (*Solea solea*), dab (*Limanda limanda*), plaice (*Pleuronectes platessa*) and flouder (*Platichtys flesus*). However, when the Harpacticoida appear in the depths, they fall prey also to pelagic fish, like the smelt.

The Harpacticoida were present in the diet of young smelt over the entire experimental period, but they were not counted among the main ingredients, isolated most often from the digestive tracts. At the second stage of research (May 30 – June 6) these copepods were more common and more abundant in the diet of smelt, as compared with the first experimental period (May 17 – May 24). These differences were confirmed by high levels of the relative importance (RI) of food components. The numbers of the Harpacticoida in the food corresponded to their densities in the ecosystem, which was also related to the location of a sampling site. Much higher densities of the Harpacticoida were recorded at sampling sites in shallow, littoral waters (below 2 m), compared with those situated in deeper waters, along the axis of the Vistula Lagoon.

The correlation between the numbers of Harpacticoida in the zooplankton of the Vistula Lagoon and the area of sample collection was also reported by other authors [2, 15]. According to Adamkiewicz-Chojnacka [2], the fact that one of Harpacticoida species was present in deep waters and absent in benthic samples taken at the same place, resulted most probably from the transportation of these organisms by water currents. Drzycimski and Różańska [15] studied the zooplankton of the Vistula Lagoon with no reference to the abundance of the Harpacticoida in bottom deposits. They observed greater numbers and a higher percentage of these copepods in the taxonomic composition of zooplankton samples at sampling sites located close to the shore (in the south-eastern part of this water body), as compared with stations situated centrally (along the axis of the lagoon), which corresponds to our results.

It seems that increased consumption of the Harpacticoida by fish with body lengths in a range of SL = 20-29 mm resulted from the somatic growth of the predator, i.e. availability of the prey, to a slight degree only. These copepods were classified as small or medium-sized (depending on the developmental stage), in comparison with the size of particles consumed most willingly, i.e. further developmental stages, copepodit and adult *Eurytemora* sp. and *Acanthocyclops* sp. [21]. It follows that although the maximum size of food particles available to the smelt increased along with an increase in the body length of this predator (as in the case of the big cladoceran *Leptodora kindii*), medium-sized organisms were consumed most readily, irrespective of the body length class represented by smelt. Similar results were obtained by other authors [20, 34], also in the case of other fish species. It seems that the absence of the Harpacticoida in the diet of the smallest smelt (SL = 10-14 mm) did not result from problems with catching and swallowing the prey, but from much lower densities of these copepods in the zooplankton at the first stage of studies. In the second experimental period the densities of the Harpacticoida in deep waters were much greater, but this fact had no effect on an increase in the consumption of this component by the largest smelt (SL > 30 mm).

The Harpacticoida are bottom-dwelling copepods and poor swimmers (due to short antennae) [22], which makes it easy for larval fish to catch them, so they should theoretically be a common component of fish diet. On the other hand, the Harpacticoida are relatively small, and their energy value is low [42], which discourages smelt from consumption.

The occurrence of the Harpacticoida in the diet of juvenile smelt resulted from the effects of abiotic environmental factors in the Vistula Lagoon. The results of this study indicate close correlations between wind strength, the depth of a sampling site, research area and the presence of the Harpacticoida in the zooplankton and in the food of smelt. The probability of the occurrence of these copepods in the zooplankton was proportional to an increase in wind strength, accompanied by an increase in undulation intensity (turbulence), which made the current carry away the surface layer of bottom deposits, together with bottom-dwelling organisms, which then remained distributed throughout the water column, and to the water depth at a sampling site. However, the correlation between the densities of the Harpacticoida in the environment and in the food of fish, at a given sampling site, was low. This could be related to the lack of data on the abundance of these organisms in bottom deposits, as well as to the inhibitory effect of strong winds (above $7 \text{ m} \cdot \text{s}^{-1}$) on the foraging behavior of fish. The greatest number of this kind of particles in the diet of smelt was observed at an average wind velocity of 4 to $7 \text{ m} \cdot \text{s}^{-1}$.

Therefore, the wind, depending on its strength, may have a stimulating or suppressing effect on the abundance of nutrients available to juvenile fish. The positive influence of turbulence on increased consumption and somatic growth of fish may involve an improvement in nutrient availability through a considerable increase in the densities of planktonic crustaceans, thus increasing the probability of the predator (larval smelt and herring) meeting the prey [18, 28], or an improvement in the swimming ability of the predator, in comparison with the still water conditions [37]. Other authors [40] did not demonstrate differences in the patterns of foraging behavior of smelt (*Osmerus mordax*) coming from two estuarine regions of the St. Lawrence River, differing in terms of turbulence.

The mechanical effect of wind strength, causing moderate, desirable turbulences, on larval and juvenile fish, enables to reduce metabolic costs. Larvae carried away by waves may decrease the swimming activity of fish, creating favorable conditions for meeting the prey and allowing the predator to save energy for somatic growth [30]. The negative effect of very strong winds was demonstrated in studies on the anchovy [10] and cisco [25]. Such winds cause intensive wave motion, which decreases the densities of food components both during the storm and afterwards, and constitute a stress factor which often completely suppresses food intake by larva fish.

Wind-induced undulation or turbulence is followed by water mixing to the bottom. In deep water bodies it may even lead to destratification, stimulating – together with thermal changes – circulation, which oxygenates deeper water layers, thus improving physicochemical and foraging conditions [33, 39]. In shallow water bodies, like the Vistula Lagoon, wave motion activated by the wind is followed by an increase in turbidity, which is a consequence of high concentrations of organic and mineral suspended particles (high primary production levels). Turbidity reduces sunlight penetration and visibility, and hinders the development of young fish [14, 36]. The prey is localized visually, so predator success is highly dependent upon water transparency [5]. This shows that a certain level of turbulence, increasing water turbidity but not deteriorating visibility, is a desirable factor that has a beneficial effect on the nutrition of larval and juvenile fish, as well as on their growth rate [17].

CONCLUSION

In conclusion it may be stated that the occurrence of bottom-dwelling copepods of the order Harpacticoida in the diet of juvenile smelt was not affected by the limited availability of this component resulting from the somatic development of fish. The greatest effect was exerted by environmental factors: instantaneous wind velocity causing water mass motion, as well as bottom features, the thickness of bottom deposits and their colonization by the Harpacticoida.

The analysis revealed that the presence of the Harpacticoida in deep waters and in the diet of smelt was directly proportional to wind strength and inversely proportional to the depth of sampling sites.

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