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RELICT INVERTEBRATES IN LACUSTRINE HABITATS: LIFE HISTORY OF *PALLASEOPSIS QUADRISPINOSA* (SARS, 1867) (AMPHIPODA: GAMMARIDAE) IN A DEEP MESOTROPHIC LAKE

ABSTRACT: Three crustacean species of postglacial origin are found in lakes of northern Poland. One of them is *Pallaseopsis quadrispinosa* which inhabits deep, oligotrophic and mesotrophic lakes. The deepest lake in Poland (area 3.11 km², max. depth 108.5 m) and on the entire Central European Plain is Lake Hańcza, an α -mesotrophic lake of unique character. A study of *P. quadrispinosa* in this lake was carried out between April–October in 2000. Samples were collected at ten sites, to a depth of 16 m, using a tow net. In April, this amphipod crustacean was observed at depths of between 1–12 m with maximal density at 4–6 m (800 individuals per 100 m²). In May and July/August, the density was reduced and this organism was found mainly between 6–12 m. In October, *P. quadrispinosa* was distributed between 1–6 m, with a maximal density of 1400 individuals per 100 m² at 2–4 m. Seasonal changes in density at various depths and the spatial heterogeneity of the occurrence of this amphipod indicate migration, probably related to changes in the water temperature and the reproductive cycle. Breeding of *P. quadrispinosa* was observed throughout the study period, with reproductive peaks in the early spring and autumn. The average number of eggs carried by ovigerous females ranged from 12 to 64, and was significantly correlated with the size of the individual. Newborn juveniles were spatially isolated from the adults as they tended to accumulate at the shallower bottom depth. The sampled material revealed the presence of two subpopulations

of *P. quadrispinosa*. Environmental conditions, especially the consistently high level of dissolved oxygen, reproduction, apparently long life-span and occurrence in all parts of the lake indicate that the *P. quadrispinosa* population in Lake Hańcza is stable and in good condition.

KEY WORDS: relict glacial crustacean, life cycle, seasonal migrations, Lake Hańcza

1. INTRODUCTION

A few animal species of postglacial origin – mainly crustaceans and fishes – are found in water bodies of northern Europe. These species prefer deep oligotrophic or mesotrophic lakes with high oxygen levels in the profundal zone (all are cryophilic). Lakes of this type are quite rare, especially on the Central European Plain. The eutrophication of many lakes has led to the extinction of crustaceans and fishes of postglacial origin.

Three crustacean species of postglacial origin are found in the lakes of northern Poland (Samter 1905, Żmudziński 1990). One of these, *Pallaseopsis quadrispinosa* (Sars, 1867) (= *Pallasiola quadrispinosa*, *Pallasea quadrispinosa*, *Pallasiella quadrispinosa*) is also found in fresh waters in Germany, Scandinavia, the other Baltic countries, Rus-

sian Karelia, and even in the most brackish waters of the Baltic Sea (Hill 1988). This amphipod spread into the Baltic area at the end of the Pleistocene, after the formation of the Baltic Sea (Segerstråle 1976). In European fresh waters it was reported for the first time in 1900 in Lake Medü in Germany (Segerstråle 1957), and in Lake Wigry in Poland (Demel 1923).

The available data concerning *P. quadrispinosa* are usually limited to the confirmation of its presence in particular water bodies. The biology of *P. quadrispinosa* was described in detail by Hill (1988) and Wilga (1996). This amphipod prefers deep, oligo- and mesotrophic water bodies, and according to some reports (Thienemann 1928, Hill *et al.* 1990, Wilga 1996) inhabits not only the profundal zone, but also the sublittoral and littoral zones. Thienemann (1928) and Valle (1936) classified this species as epibenthic, and stressed that it might occasionally migrate vertically within the water column. According to Thienemann (1928), *P. quadrispinosa* is a cryophilic species, but its presence is mainly limited by dissolved oxygen level, with thermal conditions playing a secondary role. The life cycle of *P. quadrispinosa* takes 1–2 years (Hill 1988), and the timing of the breeding season may differ between separate water bodies (Samter and Weltner 1904, Ekman 1920, Mathinsen 1953, Hill 1988).

Since *P. quadrispinosa* is very rare and endangered in Poland, the need to protect this species is often stressed (Żmudziński 1990, 1995, Wilga 1996, Szlauer and Szlauer 1997). According to Jażdżewski and Konopacka (1995), this amphipod is, or was, present in 52 lakes in Poland. According to Żmudziński (1995), it inhabited 53 lakes within the present Polish borders at the beginning of the 20th century, but now it occurs in only 34 (Suwalskie Lakeland, Masurian Lakeland and Pomeranian Lakeland – north Poland). This species clearly prefers lakes with a maximum depth of > 60 m, surface area of > 10 km², volume of > 1 km³ and Secchi disk depth of > 5 m; the minimum water transparency in which *P. quadrispinosa* has been found is 2.5 m (Żmudziński 1990). Extinction of this species is probably related to increasing trophic state, and deterioration of oxygen conditions. In such water bodies,

P. quadrispinosa is initially restricted to shallow waters where it is able to find sufficient oxygen, but under such conditions, the population density decreases and complete extinction follows.

P. quadrispinosa was observed for the first time in Lake Hańcza by Lityński (Koźmiński 1932). According to Jażdżewski and Konopacka (1995), this species might have migrated from Lake Wigry (area of 21.7 km², maximum depth of 73 m, also mesotrophic) situated downstream along the Czarna Hańcza River (see below) due to its ability to move upstream (Samter and Weltner 1904, Ekman 1915, 1920, 1940). It probably inhabited Lake Hańcza soon after the glacial retreat and has been living there for several thousand years under favorable environmental conditions: low trophic status and high oxygen level.

The aim of the present study was to determine the condition of the ancient population of *P. quadrispinosa* (distribution, density, size structure, sex ratio, fecundity and life cycle) inhabiting Lake Hańcza, a permanently α -mesotrophic and unique lake which is the deepest on the Central European Plain.

2. STUDY AREA

Lake Hańcza is located within the Suwalskie Lakeland (NE Poland). It extends from 54°14'38.86" N to 54°17'00.12" N, and from 22°47'44.66" E to 22°49'32.67" E. The area of the lake is 3.114 km² and its volume 120 × 10⁶ m³ (Hillbricht-Ilkowska and Wiśniewski 1993). It is the deepest lake on the entire Central European Plain, with a maximum depth of 108.5 m (unpublished reading – 113.5 m) and mean depth of 38.7 m. It is a holomictic and dimictic water body (Szczepański 1961). The Czarna Hańcza River, a tributary of the Neman River, flows through the lake. Along the shoreline, boulders of various sizes form a stony littoral (litho-littoral) zone, which is quite rare in lowland lakes. Common reed [*Phragmites australis* (Trin. ex. Steudel)] is not abundant and underwater meadows of *Chara* spp. rim the lake from a depth of 0.5–1.0 m to 6.0 m.

Mixing may take place at temperatures below 4°C (Stangenberg 1936, Szczepański 1961), and during winter stag-

nation the bottom water temperature may fall to 0.9°C (Kozmiński and Wiszniewski 1935). During the late spring/early summer, a thermocline develops at a depth of 8–15 m (Szczepański 1961, Cydzik *et al.* 2000), and it may exhibit a sharp thermal gradient (Kozmiński 1932) with a decrease in temperature of up to 5.2°C between 7 and 8 m. In the autumn, the thermocline descends from 8 m to below 20 m (Szczepański 1961). The epilimnetic dissolved oxygen level recorded in August 1991 exceeded 100%, while in the thermocline (8–12 m) and in the hypolimnion it was decreased slightly, reaching 80% in the latter, which is similar to values obtained in 1996 and 1997 (Cydzik *et al.* 2000). According to Cydzik *et al.* (2000), in summer the temperature in the deepest parts of the lake was 4.2°C, while the oxygen concen-

tration was 9.6 mg O₂ L⁻¹, which is in agreement with the results of earlier studies. Lake Hańcza is mainly classed as an α -mesotrophic lake, but it is sometimes referred to as oligotrophic. An examination of water transparency data collected between 1935 and 1985 suggested that eutrophication had not occurred (Hillbricht-Ilkowska and Wiśniewski 1993).

The fauna of Lake Hańcza is noteworthy (Kołodziejczyk 2007); the leeches (Koperski 2003) and molluscs (Kołodziejczyk 1994, 1999) have received most attention. These include two postglacial relicts, the leech *Theromyzon maculosum* (Rathe, 1862) and the snail *Marstoniopsis sholtzi* (Schmidt, 1856), plus the rare snail *Myxas glutinosa* (O.F. Müller, 1774) and an abundant population of the zebra mussel, *Dreissena polymorpha* (Pallas, 1771). Lake Hańcza is one of two lakes of the South Baltic basin in which the Siberian sculpin, *Cottus poecilopus*, a postglacial relict fish, occurs (Heckel, 1836) (Kotusz *et al.* 2004).

Lake Hańcza is the largest lake in the Suwalski Landscape Park, and in 1963 it was designated a landscape-water reserve. Since 1974 this lake has been on the UNESCO Aqua Project list.

3. METHODS

Investigations were carried out from April to October 2000. Water temperature and dissolved oxygen level in the water near (approx. 5 cm above) the lake bottom down to a depth of 25 m were measured at two sampling sites using a YSI 57 dissolved oxygen meter. Water transparency was evaluated using a Secchi disc.

Samples of *P. quadrispinosa* were collected using a modification of the procedures of Hill (1988), Żmudziński (1990, 1995) and Wilga (1996). A tow net of 20 × 50 cm inlet area, and 1mm mesh size, with a terminal net trap of 50 mm mesh size was used. The net, equipped with runners to support it about 5 cm above the lake bottom, was towed behind a boat for 50 m (surface area of one sample = 25 m²). One sample (drag) was collected at each depth. This sampling method can only be regarded as semi-quantitative (Hill 1988). The samples were washed on a benthic sieve of 1mm mesh size, amphipod

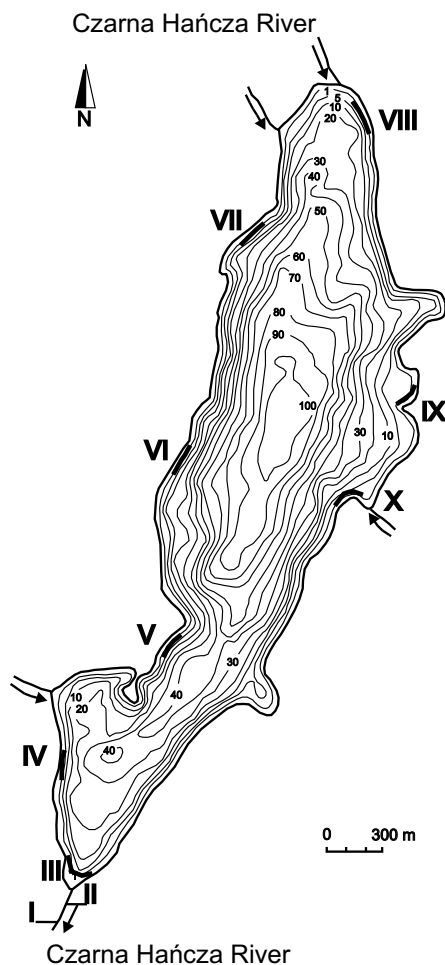


Fig. 1. Sampling sites in the littoral zone of Lake Hańcza (III–X) and the Czarna Hańcza River (I–II).

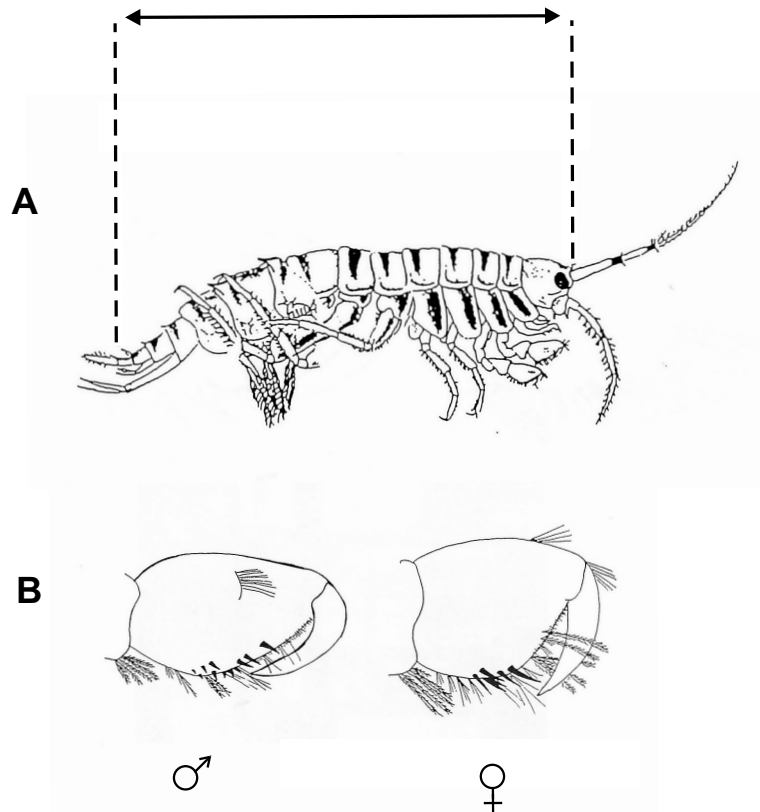


Fig. 2. *Pallaseopsis quadrispinosa*: A – length measurement; B – sex determination from the morphology of the first pair of gnathopods (acc. to Wilga 1969, altered).

crustaceans were identified and preserved in 70% methanol.

According to Wilga (1996), *P. quadrispinosa* is abundant in the littoral zone from late autumn until spring, while in summer it migrates to the deeper parts of the lake. Therefore, to evaluate its horizontal distribution in the lake, samples were taken from a depth of 2–4 m at eight sites in April, immediately after the melting of the ice cover, and also in October (Fig. 1). In addition, samples were taken from the Czarna Hańcza River and its outflow (sites I and II, Fig. 1) in July and August using a Surber drag sampler, with a 30 × 30 cm square inlet, placed on the bottom.

In April, May, late July/early August, and in October, the distribution of *P. quadrispinosa* at various depths, and the size and sex ratio were studied. At sites VI and X, samples were taken from depths of 1–2 m, 2–4 m, 4–6 m, 6–12 m, and 12–16 m.

The collected *P. quadrispinosa* individuals were measured with 1 mm accuracy – following the procedure of Chapelle (1995)

– from the base of the antenna to the end of the telson (Fig. 2). The sex was determined in accordance with Wilga (1996), based on differences in the structure of the 1st pair of gnathopods (Fig. 2). Where no differences in morphological structure of the gnathopods were observed, the individuals were classed as juveniles. The eggs in the breeding chambers of females were counted at 25× magnification.

4. RESULTS

The water temperature and dissolved oxygen concentration near the lake bottom down to a depth of 25 m were similar at the two sampling sites (Fig. 3). In April, immediately after melting of the ice cover, the temperature was 3.0°C at the surface (near the shore line), and progressing deeper it gradually fell down to 2.0°C (Fig. 3). In May, the temperature of the surface water was increased to 15.0°C, and a thermocline developed at a depth of 5–12 m. In late July/early August, the water

temperature was 15.0–16.0°C from the surface down to 6 m, while at a depth of 10–15 m it decreased to 5.0–6.0°C. In October, a temperature of 7.5°C was recorded down to a depth of 10 m, and an indistinct thermocline occurred at 14–16 m. The dissolved oxygen concentration near the lake bottom (Fig. 3) in April ranged from 11.0 to 15.0 mg O₂ L⁻¹, from the shore line to a depth of 25 m. In May, the dissolved oxygen concentration at all depths was 10.0 mg O₂ L⁻¹, in late July/early August, a value of 7.0–8.0 mg O₂ L⁻¹ was recorded, and in October it ranged from 9.5 mg O₂ L⁻¹ near the shore line to 5.0 mg O₂ L⁻¹ at a depth of 25 m at site X. The Secchi disc depth ranged from 9.5 m in April to 5.5 m in June.

At a depth of 2–4 m, the density of *P. quadrispinosa* in April ranged from 0 (sampling sites III and X) to 108 ind. × 100 m⁻² (site VI). *P. quadrispinosa* was most numerous at sites V, VI and VII, situated in the mid-western part of the lake (Fig. 4), while in the eastern and southern parts it was scarce, with

numbers of up to 12 ind. × 100 m⁻². In October, the density of this amphipod ranged from 0 at site IV to 1120 ind. × 100m⁻² at site X, located in the middle part of the eastern shore. *P. quadrispinosa* was less numerous in the north-eastern, and north-western parts of the lake, while at the sites situated in the southern, and south-western parts its density was only 4 and 8 ind. × 100 m⁻². At all sites, the density of *P. quadrispinosa* varied over time (Fig. 4), most dramatically at site X. In the southern part of the lake, *P. quadrispinosa* occurred sporadically or was absent, and it was never found in samples from the Czarna Hańcza River (sampling sites I and II).

A similar pattern of changes in *P. quadrispinosa* density with depth was observed at the two investigated sites (Fig. 5). The differences between the sampling sites were greatest in April. At site VI this amphipod was observed at depths from 2–4 m to 6–12 m, but in sampling site X it was recorded primarily at 4–6 m (816 ind. m⁻²), and sporadically at 6–12 m. In May,

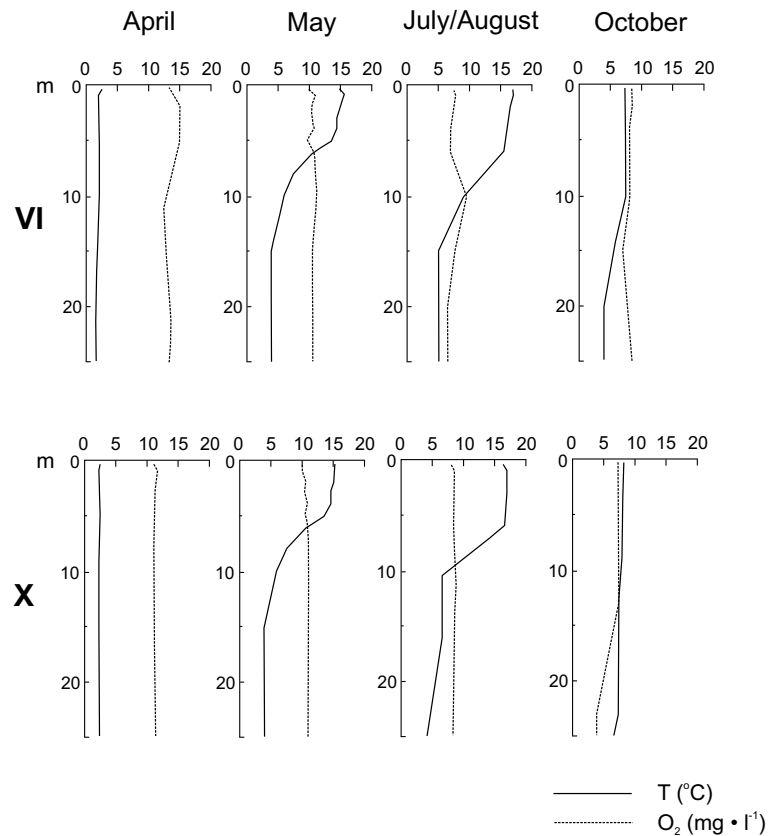


Fig. 3. Water temperature (°C) and dissolved oxygen level (mg O₂ L⁻¹) at different depths of Lake Hańcza (VI, X – sampling sites as in Fig. 1).

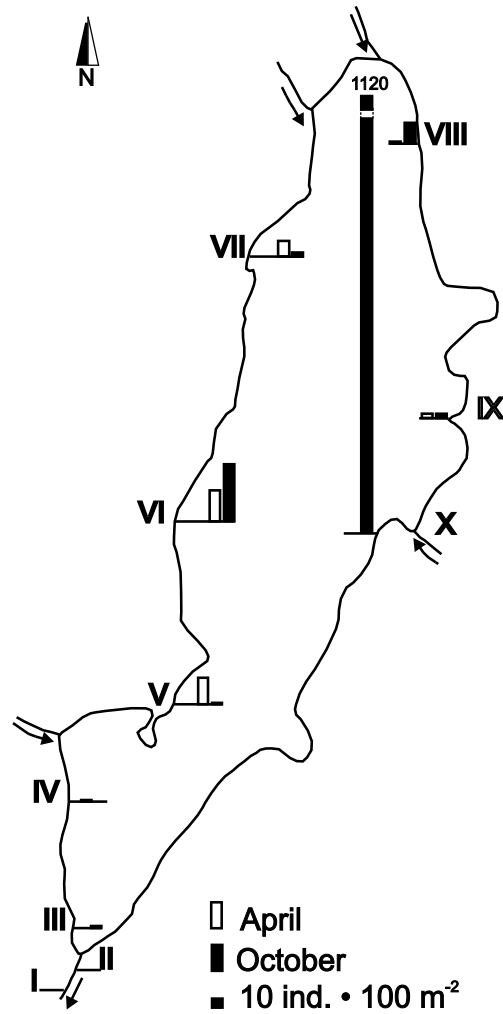


Fig. 4. Density of *Pallaseopsis quadrispinosa* at different sites in Lake Hańcza (depth 2–4 m) and in the Czarna Hańcza River.

P. quadrispinosa was scarce at a depth of 6–12 m at both sites, and was only sporadically found at 4–6 m (site VI) and 2–6 m (site X). In late July/early August this organism was abundant at 6–12 m with similar densities at both sites, while it was only sporadically found in shallower regions or deeper near the bottom. In October, *P. quadrispinosa* occurred from 1–2 m to 4–6 m at both sampling sites, with maximum density at 2–4 m, site X (1440 ind. \times 100 m⁻²).

At site VI in April (Fig. 6), juveniles predominated at a depth of 6–12 m, most being 1–4 mm long. They were sporadically accompanied by adults of body length 6–7 mm. Adults were more numerous at 2–4 m; females of body length from 5 to 14 mm – some of them ovigerous – and males of up

to 15 mm. *P. quadrispinosa* occurred sporadically between 4 and 6 m. In late July/early August, this amphipod was most numerous at 6–12 m. Here, juveniles, adult females, and occasional males of 5–10 mm body length were found, but ovigerous females were absent. Single individuals were also found in deeper water near the bottom. In October, females of 4–11 mm body length were the most abundant form at a depth of 2 to 6 m, and ovigerous individuals were found sporadically. Males and juveniles were very scarce and these attained body lengths of 8–15 mm and 5–6 mm, respectively.

At site X in April (Fig. 6), *P. quadrispinosa* were present mainly at 4–6 m, with females most numerous – some of which were ovig-

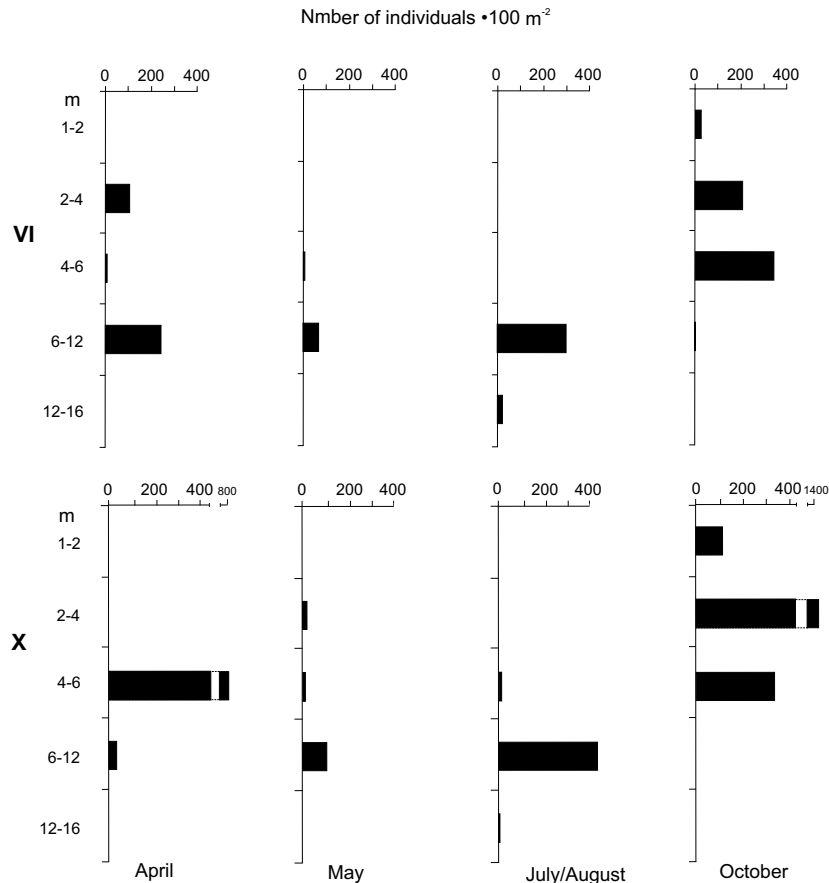


Fig. 5. Seasonal dynamics of *Pallaseopsis quadrispinosa* in Lake Hańcza at different depths (VI, X – sampling sites as in Fig. 1)

erous – and males scarce. In late July/early August, almost all of these amphipods were caught at the depth of 6–12 m. Small juveniles and females were the most abundant, while males were again scarce. In October, females of 6–13 mm predominated and were extremely numerous at 2–4 m, while males, ovigerous females, and juveniles were found sporadically, exclusively in the 1–2 and 4–6 m zones.

A summary of the results from each sampling site at all depths (Fig. 7) revealed that at site VI, in April, juvenile individuals comprised 65% of the population, females 20%, while ovigerous females and males represented 7.5% each. In late July/early August, the proportion of juveniles decreased slightly, and the percentage of females did not change, while that of males increased to 15% and no ovigerous females were found. In October, females comprised almost 65% of the popula-

tion, and ovigerous females 5%, whereas the proportion of males increased to 20% and that of juveniles fell considerably. At site X (Fig. 7) in April, ovigerous females predominated (45%), the proportion of non-breeding females and males were 34 and 19%, respectively, and juveniles comprised only 2% of the population. In the summer, the population structure at site X was similar to that observed at site VI. In October, non-breeding females predominated, ovigerous females were found sporadically (0.5%), while the percentage of males increased, and that of juveniles decreased significantly.

A positive correlation between body length and the number of eggs was identified (Fig. 8). The number of eggs per ovigerous female ranged from 12 to 64, and body length from 9 to 15 mm. The average number of eggs per ovigerous female was higher in April than in October, except in the largest females.

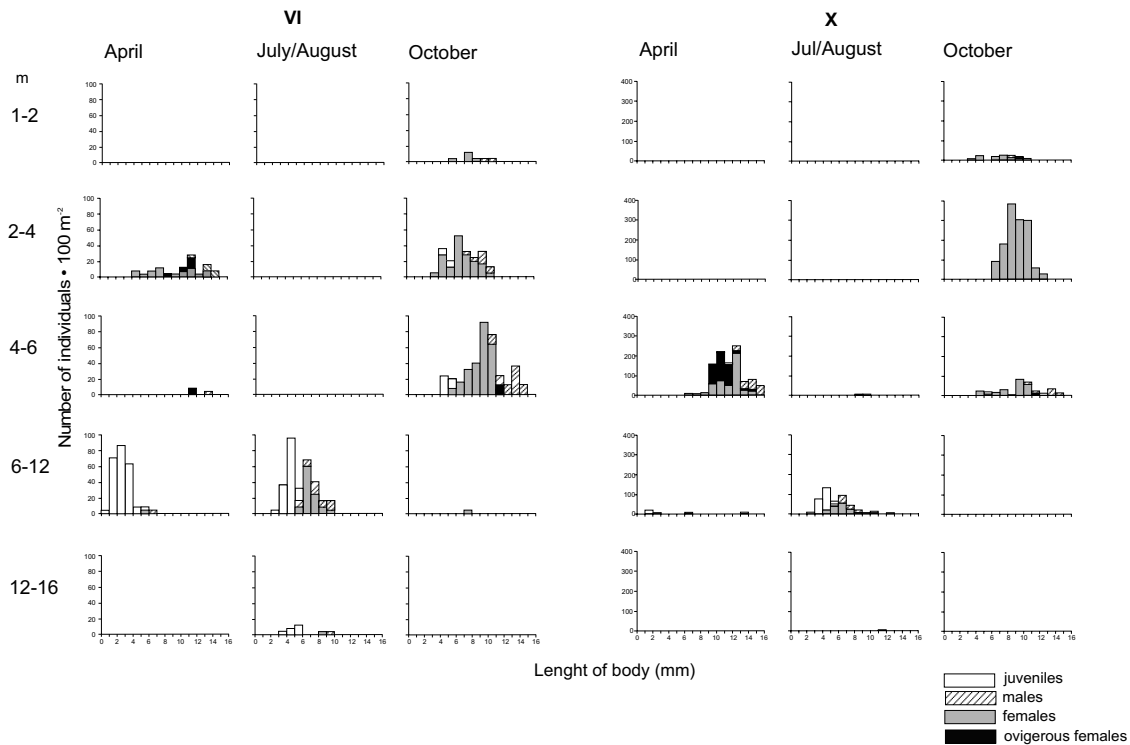


Fig. 6. Size structure and sex ratio of *Pallaseopsis quadrispinosa* in Lake Hańcza at different depths and in different months (VI, X – sampling sites as in Fig. 1; no data shown for May 2000, because of very low number of individuals caught).

5. DISCUSSION

The density of *P. quadrispinosa* per unit of lake bottom surface area found in the present study is an indicator of the real density of this amphipod, as the method of sampling is semi-quantitative (Hill 1988). Hill (1988) and Wilga (1996) collected material using the same method, but showed only the number of collected specimens.

In Lake Stora Öfsjön (area of 3.2 km², maximum depth of 30 m) (Sweden), Hill (1988) observed *P. quadrispinosa* at a depth of 4 m, while Prus (1992) found it at 30–60 m in Lake Wigry. In Lake Insko (area of 5.96 km², maximum depth of 32 m, location Inskie Lakeland, north-western Poland) (Wilga 1996) this amphipod was observed mainly in the sublittoral zone and in a deep part of the littoral zone only in winter, similar to the situation in Lake Stora Öfsjön. In Lake Hańcza, *P. quadrispinosa* was present not only in the profundal zone (Żmudziński 1995), but also in the whole littoral zone (Fig. 5). *Chara* spp. meadows occur at a depth of

1–6 m in this lake and it is likely that submerged macrophytes are used as shelters by this amphipod to reduce the predatory pressure of fish. *P. quadrispinosa* is consumed by fish (e.g. burbot, *Lota lota* (L.)), especially in the autumn and winter (Hill *et al.* 1990). In Lake Hańcza, both the burbot (unpublished observation) and the Siberian sculpin, *Cottus poecilopus* (Kotusz *et al.* 2004) are predators of *P. quadrispinosa*.

The breeding period of *P. quadrispinosa* in Lake Hańcza started in October when a few ovigerous females appeared (Fig. 6). The peak of reproduction of this amphipod has previously been observed in winter (Mathinsen 1953, Hill 1988) or in spring (Wilga 1996). The abundance of the smallest individuals in April (Fig. 6) indicates that this process occurs primarily in the winter in Lake Hańcza.

The smallest breeding females had a body length of 9 mm, while most were 10–12 mm (Fig. 6, 8), which is similar to the situation found in Lake Insko (Wilga 1996). However, the maximum length of ovigerous females in Lake Hańcza (15 mm) was 2 mm greater than

that found in Lake Ińsko, which may indicate a longer lifespan. The maximum number of eggs per ovigerous female was also higher in Lake Hańcza than in Lake Ińsko (64 and 61, respectively). A strong positive correlation between female size and the number of eggs carried was identified in both October and April (Fig. 8). These values were higher in April, most probably because *P. quadrispinosa* is a postglacial relict and its reproduction rate is likely to be higher at lower temperatures. On the other hand, the shift of the reproductive season at site X (Fig. 7) suggests that breeding of *P. quadrispinosa* may take place over a wide thermal range with its life cycle controlled mainly by light, as proposed by Segerstråle (1970). In April, the youngest individuals were spatially isolated from the adults (Fig. 6). Such isolation has been observed before (Hill 1988), and was explained as a way to avoid cannibalism, although in this previous study juveniles occurred in shallower layers than the adults, which is the reverse of the situation found here. This separation disappeared later in the season (Fig. 6): the youngest individuals grew, and the largest disappeared, possibly as a result of dying after breeding (Hill 1988).

The observed differences in the distribution and density of *P. quadrispinosa* at various depths over the season might be related to the seasonal migrations reported previously by Hill (1988), and Żmudziński (1995). The measured concentrations of dissolved oxygen near the lake bottom were variable but never dropped below $6.5 \text{ mg O}_2 \text{ L}^{-1}$ (Fig. 3), and thus exceeded the minimum oxygen requirement of *P. quadrispinosa* of $4.0 \text{ mg O}_2 \text{ L}^{-1}$ (Thiennemann 1928). Seasonal migrations are more likely to have been related to thermal changes. In July/August, when the temperature in the littoral zone increased, *P. quadrispinosa* was most abundant at 6–12 m (Fig. 5), where the water temperature fell from 15 to 5°C (Fig. 3).

Seasonal migrations of *P. quadrispinosa* might also be related to their life cycle. This amphipod reproduced mainly during the cold period in the shallow water within a small area of the littoral zone. Therefore, it is possible that *P. quadrispinosa* performs seasonal migrations to reach a high density during breeding, especially given the finding that males were much less numerous than females (Fig. 7); at higher density the chances of encountering an individual of the opposite sex is increased.

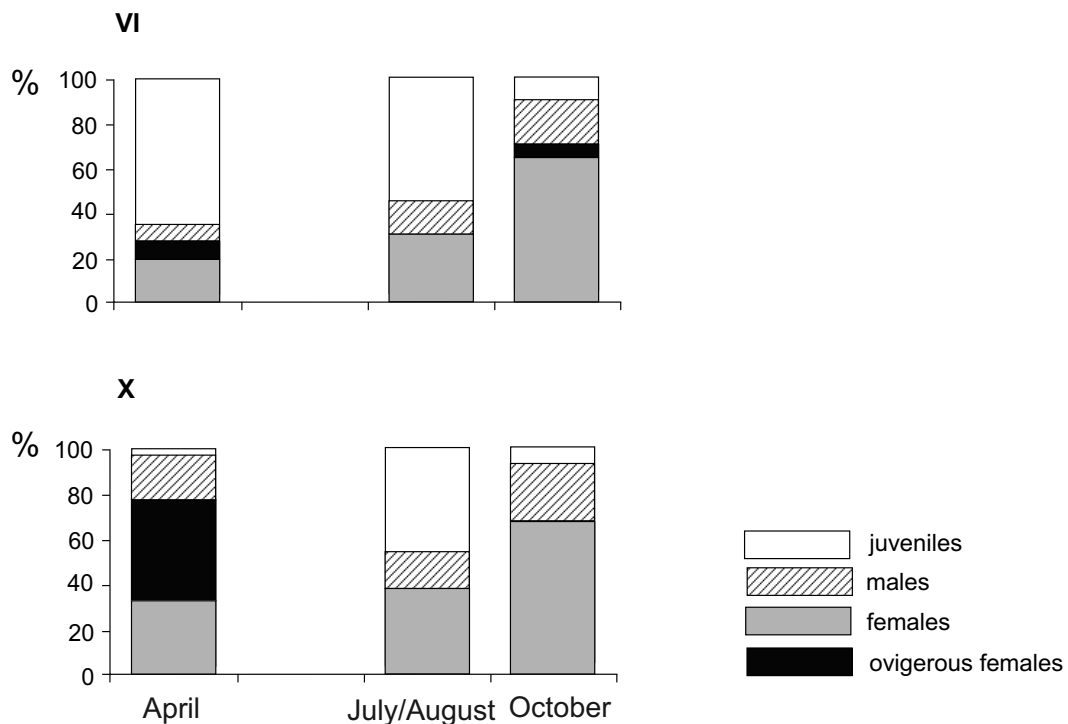


Fig. 7. Sex ratio of *Pallaseopsis quadrispinosa* in Lake Hańcza (VI, X – sampling sites as in Fig. 1; summary of data from all depths).

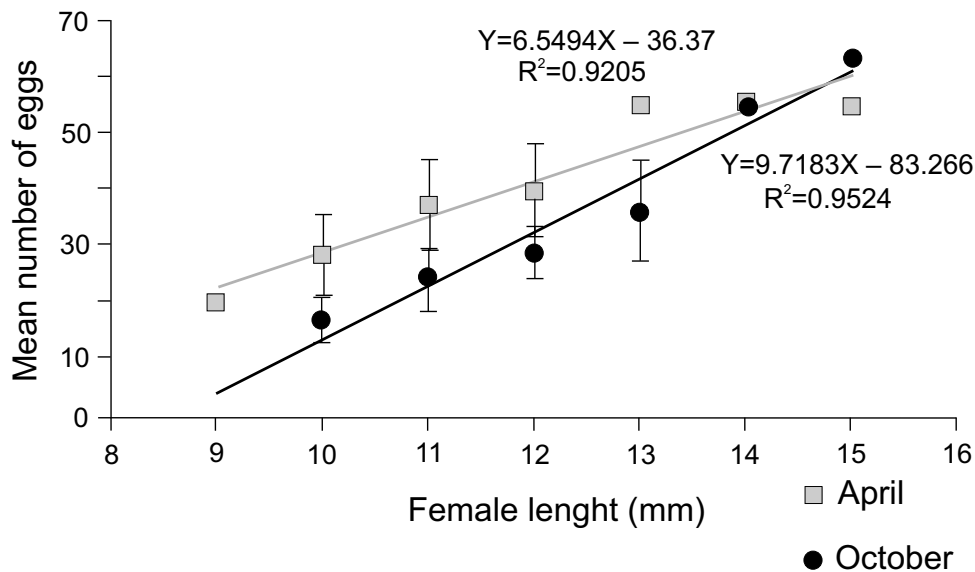


Fig. 8. Relationship between length of ovigerous *Pallaseopsis quadrispinosa* females and the number of eggs carried in Lake Hańcza in April and October 2000 (summary of data from sampling sites VI and X).

The considerable horizontal diversity of *P. quadrispinosa* density in the littoral zone of Lake Hańcza (Fig. 4) might have resulted from the extremely steep slope of the lake bottom; in very steep regions the colonizable surface is reduced. Variation in the slope may have also influenced the rate of amphipod migration. The difference in the density of the *P. quadrispinosa* population between the western (sampling station VI) and eastern (sampling station X) shore and the shift in its life cycle (Fig. 7) may have resulted from the different distances the animals had to cover during their migration along the lake bottom to reach the same depth.

In Lake Hańcza, *P. quadrispinosa* were found from the shoreline to a depth of 12 m, but between 12–16 m they were only sporadically detected (Fig. 5), or in the north and south parts of this lake, or in the Czarna Hańcza River (Fig. 4). This might indicate that Lake Hańcza is inhabited by two, at least partially isolated, subpopulations of this amphipod living near the western and eastern shores. Spatial isolation might explain some differences in certain population characteristics observed in the samples collected in various parts (stations VI and X) of the lake.

Dissolved oxygen concentrations measured in Lake Hańcza were found to be stable and sufficient for *P. quadrispinosa* to flourish. This lake is protected, which reduces the chances of pollution. In addition, compared with other relict crustaceans, *P. quadrispinosa* is less sensitive to the effects of pollution (Särkkä *et al.* 1990). In Lake Hańcza, *P. quadrispinosa* has high fertility, probably a long lifespan and inhabits all zones: littoral, sublittoral, and, after Żmudziński (1995), profundal. Two different subpopulations of this species probably occur in this lake. All of the above indicate that the *P. quadrispinosa* population in Lake Hańcza is stable and in good condition.

A serious potential threat to *P. quadrispinosa* in Lake Hańcza is a new, invasive species: the Ponto-Caspian amphipod *Pontogammarus robustoides* (G.O. Sars, 1894), which has become widespread in some Lithuanian lakes (Gumuliauskaite and Arbačiauskas 2008) and in some water bodies of the Great Masurian Lakes (Jażdżewska and Jażdżewski 2008) near the Suwalskie Lakeland. In the Great Masurian Lakes, a second invasive amphipod, the Ponto-Caspian invader, *Dikerogammarus haemobaphes* (Eichwald,

1841) first appeared in 2001 and has been recorded in 5 lakes in this area (Jażdżewski 2003). Furthermore, an invasive snail species, the New Zealand mud snail, *Potamopyrgus antipodarum* (J.E. Gray, 1843) was first noted in Lake Hańcza in 2000 (unpublished observation). These findings indicate that despite its relative isolation from adjacent water bodies, the unique ecosystem of Lake Hańcza may be exposed to the potentially negative impact of invasive species.

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