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MORPHOMETRICS, FECUNDITY, DENSITY, AND FEEDING INTENSITY OF THE SPINYCHEEK CRAYFISH, *ORCONECTES LIMOSUS* (RAF.) IN NATURAL CONDITIONS

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ABSTRACT. The subject of the study was three populations of spinycheek crayfish, *Orconectes limosus* (Raf.) from lakes Staw Płociczno, Dgał Wielki, and Hańcza. The aspects of the spinycheek crayfish studied were the morphometric characters of females and males, individual absolute fecundity, sex ratio, size structure, density, biomass, and feeding intensity in an annual cycle. It was determined that the body proportions of males in forms I and II differed significantly, while the body proportions of female spinycheek crayfish were similar to those of form II males but different from the body proportions of form I males. The crayfish investigated in the current study had a lower individual absolute fecundity than did spinycheek crayfish of the same body weights from other Polish basins. The crayfish daily food ration exhibited a very strong relationship with the stomach fullness index and water temperature. The empirical formula of this relationship (ln Rd P = 0.397 + 0.094 t + 0.614 ln If) permitted estimating the daily food ration. The crayfish fed most intensely from the May to October period, during which they consumed in excess of 80% of their annual ration. The primary dietary component of the spinycheek crayfish was plant matter. Annually, the crayfish population consumed barely 0.27% of the wet weight of the aquatic vegetation in its range of occurrence.

Key words: SPINYCHEEK CRAYFISH, MORPHOMETRIC CHARACTERS, FECUNDITY, DENSITY, FEEDING INTENSITY

1. INTRODUCTION

1.1. PRESENTATION OF THE STUDY ISSUES

Four crayfish species occur in Polish waters: two native species, the noble crayfish, *Astacus astacus* (L.), and the narrow-clawed crayfish, *Astacus leptodactylus* Esch., and two North American species, the signal crayfish, *Pacifastacus leniusculus* Dana, and the spinycheek crayfish, *Orconectes limosus* (Raf.) (Kulmatycki 1935, Kossakowski 1973, Jażdżewski and Konopacka 1993, 1995, Strużyński and Śmietana 1998, 1999).

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The most common of the four species is the spinycheek crayfish, which occurs throughout the country and is very abundant in some aquatic basins (Jażdżewski and Konopacka 1993, 1995, Strużyński and Śmietana 1998, 1999, Ďuriš 1999, Mastyński 1999, Krzywosz 2001). Thanks to its high environmental tolerance, fecundity, and tendency to migrate, its area of occurrence is constantly expanding (Mastyński 1999, Krzywosz 2001). The spinycheek crayfish usually occupies new habitats permanently and the co-occurrence of the spinycheek crayfish with indigenous crayfish usually leads to the elimination of the latter (Kulmatycki 1935, 1936, Leńkowa 1962, Kossakowski 1966, Strużyński 1994, Białokoz et al.1996, Strużyński and Śmietana 1998, Mastyński 1999, Schulz and Smietana 2001, Gherardi et al. 2002). Despite its widespread and abundant occurrence, little is known about the morphology, biology, or environmental role of this species.

1.2. CRAYFISH OCCURRENCE IN EUROPEAN WATERS

The spinycheek crayfish is a relatively new species to European fauna. It was brought to the continent from Pennsylvania in 1890 by Max von dem Borne, a German breeder (Lehmann and Quiel 1927, Kulmatycki 1935, Gajewski and Terlecki 1956, Leńkowa 1962, Kossakowski 1966). This species was introduced with the aim of replacing the indigenous species (the noble and narrow-clawed crayfish) that had been decimated by the epizootic crayfish plague caused by the fungus *Aphanomyces astaci* Schikora. The epizooic crayfish plague broke out in western Europe in the mid nineteenth century and in subsequent years spread to nearly all of Europe. Fresh outbreaks of plague are observed to the present day (Leńkowa 1962, Alderman et al. 1990, Białokoz et al. 1996, Alderman 1997). This disease has nearly eliminated populations of indigenous crayfish. The spinycheek crayfish was not able to compensate for the loss of indigenous species since the size it attained was not attractive to the consumer. Thus, other larger species that better suited market demand began to be introduced. In 1960 two new species were brought to Europe, the signal and the *Orconectes virilis* (Hagen) crayfish (Kossakowski 1966, Brink 1983), followed in subsequent years by other crayfish originating from various continents. Currently, the inland waters of Europe are inhabited by ten alien crayfish species, *Pacifastacus leniusculus* Dana, *Procambarus clarkii* (Girard), *Procambarus* sp., *Orconectes limosus* (Raf.), *Orconectes immunis* (Hagen), *Orconectes virilis* (Hagen), *Orconectes rusticus* (Girard), *Cherax destructor* Clark, *Cherax* *quadricarinatus* (von Martens), and *Cherax tenuimanus* (Smith), and five native species, *Astacus astacus* (L.), *Astacus leptodactylus* Esch., *Astacus pachypus* Radke, *Austropotamobius pallipes* (Lereboullet) and *Austropotamobius torrentium* (Schrank) (Holdich 2002, Souty-Grosset et al. 2006).

The spinycheek crayfish is a widespread species in Europe. It inhabits 20 European countries and is continuously expanding its range of occurrence (Kossakowski 1956, 1973, Leńkowa 1962, Westman and Westman 1992, Payne 1997, Strużyński and Śmietana 1998, 1999, Hamr 2002, Holdich 2002, Kozák et al. 2004, Petrusek et al. 2006, Puky and Schád 2006, Souty-Grosset et al. 2006). It has also settled in all types of stagnant and running waters, with the exception of typically mountainous waters. It is capable of tolerating highly polluted waters and those altered or created by humans such as ports and canals or even heated waters. It also lacks any specific requirements with regard to bottom type. It lives in areas that are quite shallow and as well as those that are as deep as 80 m (Leńkowa 1962, Kossakowski 1966, Białokoz et al. 1996, Śmietana and Strużyński 1999).

1.3. CURRENT KNOWLEDGE OF SPINYCHEEK CRAYFISH BIOLOGY

The spinycheek crayfish has only rarely been the subject of study, which is why detailed species descriptions based on representative samples are very few. The first mention in the Polish literature of the spinycheek crayfish was not until 1935 (Kulmatycki 1935), which was after the species had inhabited Polish territory for nearly fifty years. Prior to this, the first European papers had appeared focusing mainly on the morphometrics of the spinycheek crayfish (Seligo 1895, Lehmann and Quiel 1927). Pieplow (1938) published a detailed and wide-ranging paper in which it was concluded, among other things, that the distinguishing character of the spinycheek crayfish males was the build of the first pair of pleopods, that occur in two morphological forms (I and II). Kossakowski (1966) emphasized that this character distinguished the male spinycheek crayfish from the males of the remaining crayfish species occurring in Poland. This author described precisely the differences between the two forms of males. The first pair of pleopods of form I males have a lamella that is rolled into itself thus forming a channel that ends in “whiskers” (Fig. 1A). This pleopod modification permits the males to deposit sperm into the female spermatheca during mating. In form II males (Fig. 1B), the first pair of pleopods do not have whiskers, and

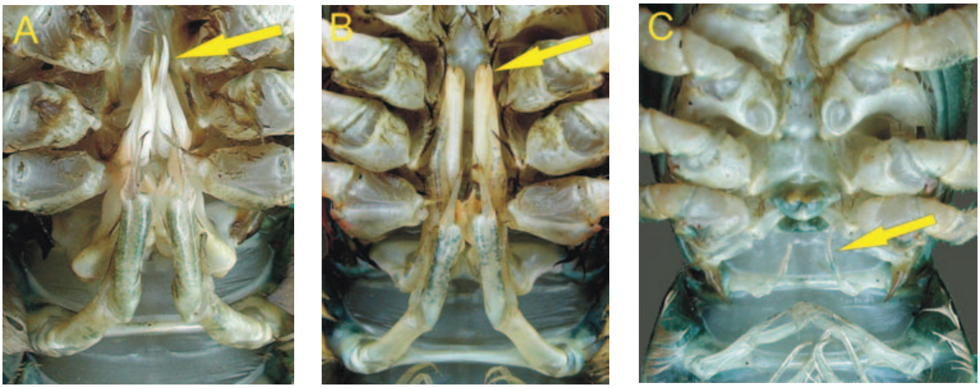

Fig. 1. First pair of pleopods in the spinycheek crayfish. A – form I male spinycheek crayfish. B – form II male spinycheek crayfish. C – female spinycheek crayfish.

the lamellae do not form channels that permit the delivery of sperm to the female. As is noted in other females of the various crayfish species occurring in Poland, the female spinycheek crayfish have the first pair of pleopods only in rudimentary form (Fig. 1C) (Pieplow 1938, Kossakowski 1966).

Juvenile, sexually immature males only occur as form II, while mature males occur in both forms. Mature males occur as form II during the summer following the spring moult, and as form I during the rest of the year (Pieplow 1938, Kossakowski 1966). Due to an extended moulting period, both forms of adult males are noted in the summer. In their histological studies of male gonads, Chybowski and Juchno (2002) confirmed that at the beginning of July in addition to differences in the build of the first pair of pleopods, there are also differences between the histological pictures of gonads from form I and II males. In July, but also in September and October, there were more abundant quantities of sperm in the gonads of form I males than in those of form II males.

In his comparison of spinycheek crayfish males of both forms, Pieplow (1938) also drew attention to the fact that at the same body length, form I males are heavier and their chelipeds are larger. Kossakowski (1962) and Chybowski (2000) have also conducted studies of morphometric characters of these two male forms, but they were not compared.

Spinycheek crayfish fecundity has only been described in a few basins (Stypińska 1972, 1973, 1978, Orzechowski 1984, Schulz and Smietana 2001). It was determined that the fecundity of the spinycheek crayfish was higher than that of both the noble and narrow-clawed crayfish (Leńkowa 1962, Kossakowski 1966, Stypińska 1973, Schulz and Smietana 2001).

The density of spinycheek crayfish in natural basins is generally several tens of kilograms per hectare of inhabited area. In the lakes of the Mazurian and Suwałki districts density ranged from 29 to 58 kg ha^{-1} (Krzywosz et al. 1995). Extremely high spinycheek crayfish density was confirmed only in the Koronowski Reservoir by Orzechowski (1984), according to whom density ranged from 60 to as much as 3100 kg ha^{-1}.

Although crayfish are omnivorous animals, their diet is clearly dominated by plant matter (Pieplow 1938, Kossakowski 1966, Anwand 1993, MacIsaac 1994, Anwand and Valentin 1996, Reynolds and O'Keeffe 2005), and their consumption of aquatic vegetation can have a significant impact on these plants (Chambers et al. 1990, Dubois et al. 1999). Studies of crayfish feeding intensity are usually conducted experimentally under laboratory conditions for particular types of food. Studies such as these were conducted for the noble crayfish by Hessen and Skurdal (1988), Söderbäck et al. (1988), and Henttonen and Lindqvist (1995), for the signal crayfish by Tamkeviciene (1985), for the crayfish *Orconectes virilis* by Brown et al. (1990) and Roth et al. (2006), and for the spinycheek crayfish by Simon and Garnier-Laplace (2005) and Staszak and Szaniawska (2006). Tcherkashina (1977), in her pond studies of the food consumption of the crayfish species *Astacus leptodactylus cubanicus*, has been the only researcher to perform a study under conditions similar to natural ones. No works on spinycheek crayfish food consumption under natural conditions were found in the available literature.

1.4. AIM OF THE PRESENT WORK

The aim of the study performed was to determine the morphometric characters of the spinycheek crayfish and its individual and population variation based on a reliable sample size. An additional aim was to investigate the population structure of the spinycheek crayfish and population indexes including the sex ratio and body size, individual absolute fecundity, abundance, and density. Special emphasis was placed upon determining the as yet unknown feeding intensity of the spinycheek crayfish in an annual cycle under natural conditions using five study methods. Simultaneously, these methods were evaluated for their applicability in estimating crayfish food consumption. The type of food consumed was determined, as well as the stomach fullness index, food evacuation period, and the daily, periodic and annual food rations. In order to evaluate the impact the spinycheek crayfish has on plant abundance, the species structure, biomass, and distribution of aquatic vegetation were also studied.

2. STUDY AREA

Studies were conducted in three lakes in northeastern Poland, Staw Płociczno, Dgał Wielki, and Hańcza, which differed with regard to both morphometrics and trophic status.

2.1. LAKE STAW PŁOCICZNO

Lake Staw Płociczno (54°01.28' N, 22°59.20' E), with a water surface area of 22.1 ha, is located at an altitude of 136.3 m above sea level in the Nemen River drainage basin (Table 1). The lake's basin extends from the south to the north with a distinct shallow bay at its northeastern edge. The lake's shoreline is not highly developed, its bottom is not highly differentiated, and the sides of the basin slope gently. Generally, the bottom is of a hard substrate, and only in the bay it is muddy. During the summer period, there is clear thermal stratification. The lake is a lake eutrophic and is classified as a bream lake. The spinycheek crayfish occurs abundantly in Lake Staw Płociczno and has done so for more than twenty years.

TABLE 1

Morphometric parameters of the lakes (data from IFI Olsztyn, Poland). L – length of shoreline, S – lake surface area

Parameter	Staw Płociczno	Dgał Wielki	Hańcza
Surface area (ha)	22.1	94.5	311.4
Maximum depth (m)	14.2	17.6	108.5
Mean depth (m)	3.0	5.3	38.7
Maximum length (m)	1360.0	1300.0	4525.0
Maximum width (m)	255.0	1125.0	1175.0
Shoreline development ($L/2\sqrt{\pi S}$)	2.0	1.5	1.9
Lake water volume (thous. m^3)	671.0	4996.0	120364.1
Range of submerged vegetation (m)	7.0	5.0	5.0

Emerged vegetation is very poor, and it grows in an interrupted and thin band along the shoreline. Slightly more vegetation is encountered on the northwestern edge of the lake, where common reed, *Phragmites australi*s (Cav.) Trin. ex Steud dominate and are accompanied by water horsetail, *Equisetum limosum* L., common sweet flag, *Acorus calamus* L., and sedges, *Carex* spp. Generally, submerged vegetation covers the lake bottom to a depth of 5 m or in some locations to 7 m. The dominant among the submerged vegetation is stonewort, *Chara* spp., which comprises in excess of 67% of the total vegetation biomass.

2.2. LAKE DGAŁ WIELKI

Lake Dgał Wielki (54°06.5’ N, 21°47.6’ E) with a water surface area of 94.5 ha, is situated at an altitude of 120.1 m above sea level in the Pregola River drainage basin (Table 1). The lake is oval shaped with little development along its shoreline. The lake bottom is diverse, and the sides of the lake basin generally slope gently. The lake bottom in the shallow areas near the shore is hard, and only the bays are very muddy. With one permanent inflow and two outflows, this water body is a flow-through lake. Clear thermal stratification occurs in lake during the summer period. Lake Dgał Wielki is a lake eutrophic lake that is classified as a bream type lake, and the spinycheek crayfish has occurred in it for about fifteen years.

Emerged vegetation is not abundant and grows in a interrupted, thin band along the shoreline. A slightly larger quantity of vegetation is noted in the southeastern part of the lake. The dominant plant is the common reed. Submerged vegetation covers the bottom to a maximum depth of 5 m. The decided dominant is the stonewart, which comprises nearly 90% of the total plant biomass.

2.3. LAKE HAŃCZA

Lake Hańcza (54°15.8’ N, 22°48.7’ E) is located at an altitude of 227.3 m above sea level in the Nemen River drainage basin. The surface area of the lake is 311.4 ha (Table 1). Extending sharply from the north to the south, Lake Hańcza is the deepest Polish lake with a maximum depth of 108.5 m. The shoreline is not highly developed, and the sides of the lake basin are very steep. The lake bottom is highly diversified and is covered with stones, gravel, and sand. Only in the bays and in the vicinity of the inflow and outflow is the bottom muddy. The Czarna Hańcza River flows through the lake. Lake Hańcza is a mesotrophic lake and is classified as a vendace type lake. The spinycheek crayfish has occurred in this lake for over twenty years.

Emerged vegetation is not abundant, and submerged macrophytes occur most frequently in mats, and only in the vicinities of the outflow and inflow does the vegetation grow in bands. The dominant among emerged vegetation is the common reed. Submerged vegetation, mostly of the genus Chara, occurs more frequently than does emerged vegetation. Submerged vegetation occurs on the lake bottom to a depth of 5 m.

3. MATERIALS AND METHODS

The subject of the study was three populations of spinycheek crayfish from lakes Staw Płociczno, Dgał Wielki, and Hańcza. The study materials were collected during the 1999-2003 period.

3.1. ESTIMATION OF THE SUBMERGED VEGETATION BIOMASS

Estimating the biomass of submerged plants and with floating leaves occurring in Lake Staw Płociczno was conducted on 30 July 2000. Eight transects were designated along which plant samples were collected with Bernatowicz grabs with surface areas of 0.16 m^2 (Bernatowicz 1960) to depths that limited the area occurrence of the vegetation (Fig. 2). From 10 to 15 samples were collected along each transect. The species structure of submerged plant assemblages and those with floating leaves were determined with the anchor method (Królikowska 1997). The phytosociological description of the vegetation that occurred was based on the classification system by Podbielkowski and Tomaszewicz (1986).

3.2. STUDY RANGE

The morphometric characters of the spinycheek crayfish were determined based on the measurements of 4317 individuals from lakes Staw Płociczno, Dgał Wielki, and Hańcza (Table 2). Absolute fecundity was examined in 249 females from lakes Staw Płociczno and Dgał Wielki. The size structure and sex ratio of the catchable part of spinycheek crayfish population in Lake Staw Płociczno was estimated by examining the size distribution and sex ratio of 1283 specimens during one year. The abundance

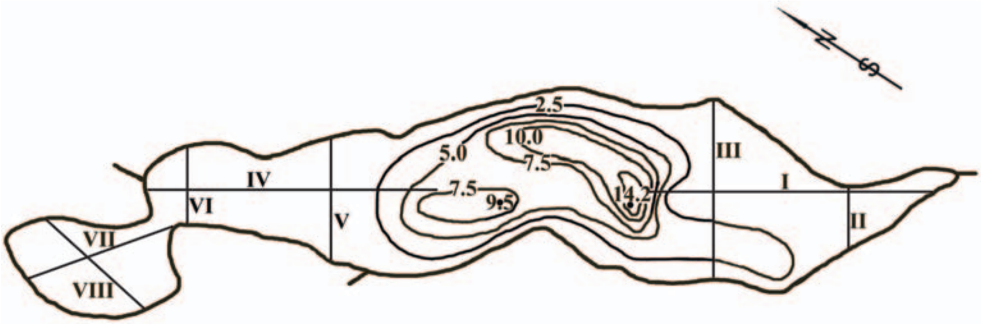

Fig. 2. Vegetation sampling sites in Lake Staw Płociczno. I-VIII designated transects along which samples were collected.

and biomass of spinycheek crayfish was estimated in Lake Staw Płociczno by tagging a total of 839 specimens and recapturing 647 specimens. The range of occurrence of the spinycheek crayfish in the lake was determined by capturing crayfish in traps deployed along deep transects. A total of 83 crayfish were caught for this aim. The spinycheek crayfish feeding intensity in Lake Staw Płociczno was determined by examining the stomach content of 1248 individuals (Table 2).

TABLE 2

Number of specimens used in the studies

	Lake			
Study type	Staw Płociczno	Dgał Wielki	Hańcza	Total
Morphometrics	2532	1494	291	4317
Size structure and sex ratio	1283			1283
Abundance and biomass	1486			1486
Fecundity	181	68		249
Range of occurrence	83			83
Feeding intensity	1248			1248

3.3. CATCH GEAR

Crayfish catches were made with seines, fyke net frames, or crayfish traps. The seines were comprised of two wings and a bunt. The overall length of the gear was about 20 m, with the wings comprising about 17.5 m and the bunt about 2.5 m. The height of the wings at the bunt was 1.5 m, and the mesh size throughout the seine was 5.5 mm. A single seine haul covered a surface area of about 900 m^2.

The fyke net frame was comprised of an antechamber, two chambers with bellies and a bunt. The antechamber was stretched over a wooden frame measuring 0.6 × 1.0 m. The chambers were stretched on seven hoops measuring 0.5 m in diameter in the first to 0.3 m in the last. The mesh size in the chambers was 20 mm, and in the bunt it was 5.5 mm. The fyke net frame was deployed in the water current outflow from Lake Staw Płociczno.

The crayfish traps were shaped cylindrically and measured 0.5 m in length and 0.25 m in diameter. They were constructed of netting material (5.5 mm mesh bar length) that was stretched over three hoops and secured with two stays. Bellies were placed at both ends, and the traps were baited with fresh fish.

The type of gear deployed depended on the catch location in the lake and the purpose for which the collected material would be used.

Lake Staw Płociczno crayfish were caught as follows:

– seine – to determine the morphometrics, population structure, fecundity, and feeding intensity;
– fyke net frame – to determine morphometric characters, population structure, and fecundity;
– crayfish traps – to determine morphometric characters and range of occurrence.

Lake Dgał Wielki crayfish were caught as follows:

– crayfish traps – to determine morphometric characters and fecundity.

Lake Hańcza crayfish were caught as follows:

– crayfish traps – to determine morphometric characters.

3.4. INVESTIGATIVE METHODS

3.4.1. CRAYFISH MEASUREMENTS

The crayfish specimens caught were weighed, measured, and sexed. The crayfish body wet weight (W) was determined by weighing the crayfish to the nearest 0.1 g. Eight crayfish body measurements were taken as proposed by Kossakowski (1962) (Fig. 3) as follows: total body length (TL) from the rostrum to the end of the abdomen; cephalothorax length (CL) from the rostrum to the abdomen; cephalothorax length to the cervical groove (CfL) from the rostrum to the cervical groove; cheliped length (ChL) from the tip to the connection with the next segment; the widest cephalothorax width (CW); width of the first abdominal segment (AW); width of the largest cheliped (ChW);

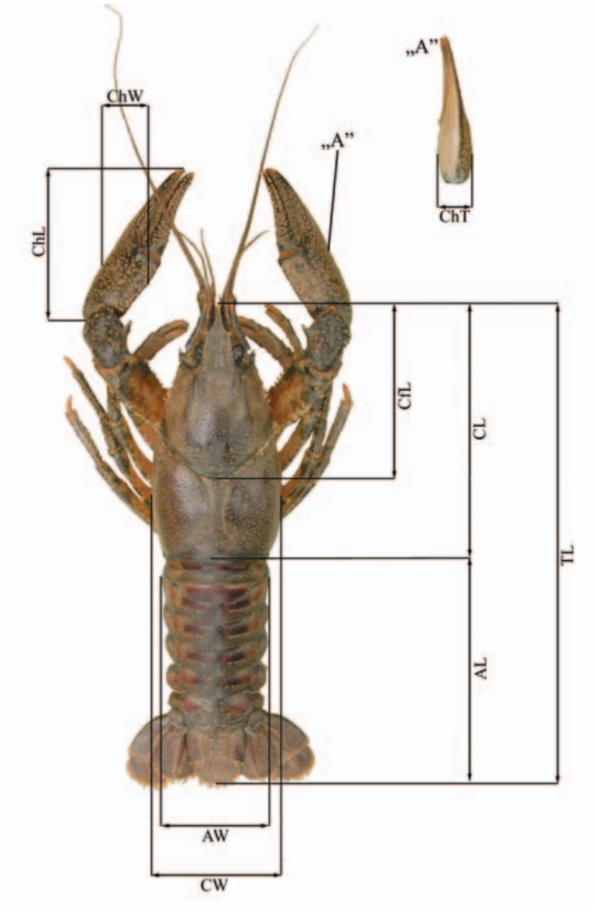

Fig. 3. Measurements performed on the studied crayfish. TL – total length (mm); AL – abdomen length (mm); CL – cephalothorax length (mm); CfL – cephalothorax length to the cervical groove (mm); ChL – cheliped length (mm); CW – the widest cephalothorax width (mm); AW – width of the first abdominal segment (mm); ChW – width of the largest cheliped (mm); ChT – thickness of the largest cheliped (mm).

thickness of the largest cheliped (ChT). Abdomen length (AL) was calculated by subtracting cephalothorax length (CL) from total length (TL). The measurements were made to the nearest 0.1 mm, with the exception of total length, which was measured to the nearest 1.0 mm.

The results of these measurements were used to calculate the following proportions (Kossakowski 1962): total length to abdomen length (TL/AL); total length to cephalothorax length (TL/CL); total length to anterior cephalothorax length to the cervical groove (TL/CfL); total length to cheliped length (TL/ChL); total length to cephalothorax width (TL/CW); total length to cheliped width (TL/ChW), abdomen length to abdomen width (AL/AW); cephalothorax length to cephalothorax width (CL/CW); cheliped length to cheliped width (ChL/ChW); cheliped length to cheliped thickness (ChL/ChT).

3.4.2. EVALUATION OF POPULATION PARAMETERS

Crayfish absolute fecundity was determined with specimens caught in March and April, which are the months when the spinycheek crayfish female oocytes are at the greatest diameter and the peak of development (Juchno and Chybowski 2003). The crayfish caught were preserved in a 4% formalin solution. Absolute female crayfish fecundity was determined by counting all of the mature eggs in the gonads (Smart 1962, Prins 1968, Stypińska 1972, 1973, 1978, Orzechowski 1984).

The size structure and sex ratio of the catchable spinycheek crayfish population in Lake Staw Płociczno was evaluated throughout the year based on the size distribution of crayfish bodies (TL) and the sex ratio.

The abundance of the catchable part spinycheek crayfish population was determined with the Petersen method, based on results of tagging the animals and collecting returns at 15 stations (Fig. 4). The biomass of the catchable population was calculated by multiplying abundance by the mean crayfish body weight.

The range of occurrence of spinycheek crayfish in the lake was determined based on the effectiveness of catches with crayfish traps. The area inhabited by the crayfish was the area determined by the isobath of the deepest occurrence.

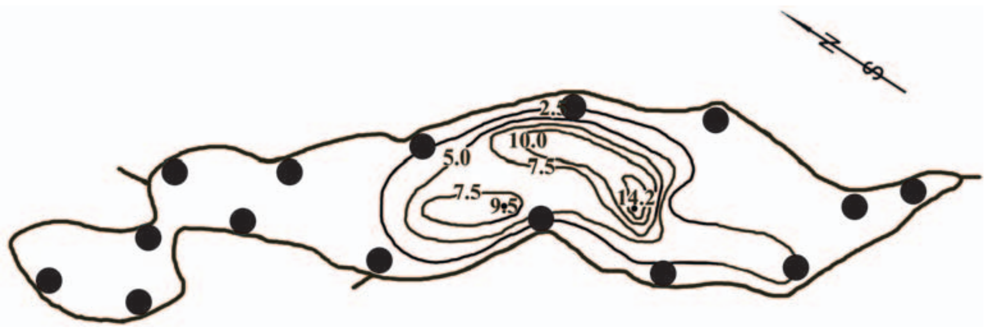

Fig. 4. Location of spinycheek crayfish catches in Lake Staw Płociczno during abundance determinations.

3.4.3. PROCEDURE FOR DETERMINING FEEDING INTENSITY

The index of stomach fullness (If) was calculated as the quotient of the weight of the stomach contents and body wet weight and expressed as per mille (‰) of body wet weight. Samples used to determine If were collected throughout twenty-four hour periods at intervals of four hours, except in March when samples were collected at eight-hour intervals. The number of samples ranged from 19 to 106 specimens.

Specimens used to determine the food evacuation time from the stomach (h) were caught in the lake at a set time (at midnight) monthly throughout the year. The number of samples ranged from 25 to 71 specimens. The crayfish caught were placed in basins supplied with filtered water from Lake Staw Płociczno. Subsamples of crayfish were collected at even time intervals and the mass of stomach contents was determined until the moment the stomachs had been completely evacuated. The food evacuation time from the stomach (h, hour) was designated as the zero point $(x_1 = \frac{-b - \sqrt{\Delta}}{2a}$ or $x_2 = \frac{-b + \sqrt{\Delta}}{2a}, \Delta = b_1^2 - 4b_0b_2)$ the second degree polynomial was calculated for the dependence of stomach fullness on gastric evacuation time ($If = b_0 + b_1h + b_2h^2$, where: If – mean monthly index of stomach fullness (‰ body wet weight), h – gastric evacuation time (hour), b_0 , b_1, b_2 – polynomial coefficients).

The daily food ration (Rd, ‰ body wet weight) was calculated simultaneously with four methods:

1. The Bajkov method (1935) using the formula:

$$Rd = 24 \text{ If } h^{-1}$$

where:

If – mean index of stomach fullness (‰ body wet weight),

h – gastric evacuation time (hour).

2. The Kogan method (1963) using the formula:

$$Rd = \sum_{i=1}^{n}(T_{i+1} - T_i)b + If_{i+1} - If_i$$

where:

If – periodical index of stomach fullness during subsequent sampling events (‰ body wet weight),

T – hour the i-th sample is collected,

b – coefficient expressing the maximum daily decrease in the fullness index (‰ body wet weight hour^{-1}).

3. The Thorpe method (1977) using the formula:

$$Ifr = 0.5\,(If_{i+1} + If_i)\,e^{-b(T_{i+1}-T_i)}$$

$$Rd = \sum_{i=1}^{n} 0.5\,(3If_{i+1} - If_i - 2Ifr)$$

where:

If – periodical index of stomach fullness during subsequent sampling events (‰ body wet weight),

T – hour the i-th sample is collected,

b – coefficient expressing the maximum daily decrease in the fullness index (ln ‰ body wet weight hour^{-1}),

e – basis for the natural logarithm.

4. The Elliott and Persson method (1978) using the formula:

$$Rd = \sum_{i=1}^{n} \frac{[If_{i+1} - If_i\,(e^{-b_1(T_{i+1}-T_i)})]\,b_1(T_{i+1} - T_i)}{1 - e^{-b_1(T_{i+1}-T_i)}}$$

where:

If – periodical index of stomach fullness during subsequent sampling events (‰ body wet weight),

T – hour the i-th sample is collected,

b – coefficient expressing the maximum daily decrease in the fullness index (ln ‰ body wet weight hour^{-1}),

e – basis for the natural logarithm.

The value of coefficient b, which was used to calculate the daily food ration in the Kogan, Thorpe and Elliot and Persson methods is presented in Table 3.

The daily food ration that is required for spinycheek crayfish survival was calculated with the Winberg method (1956). The following was assumed to calculate the daily food ration required for survival:

- 1 cm^3 oxygen equals 20 J (Mel’nichuk et al. 1978),
- caloric value of the crayfish body is 2880 J g^{-1} (estimated based on Cummins (1967)),

TABLE 3

The coefficients b used to calculate the daily food ration with three methods

Month	Kogan (1963) (‰ body wet weight h^{-1})	Thorpe (1978) (ln ‰ body wet weight h^{-1})	Elliott and Persson (1978) (ln ‰ body wet weight h^{-1})
March	0.295	0.306	0.004
April	0.707	0.168	0.016
May	2.313	0.287	0.129
June	1.405	0.136	0.192
July	1.672	0.120	0.141
August	1.510	0.186	0.144
September	2.624	0.208	0.097
October	0.742	0.054	0.051
November	0.967	0.109	0.031
December	1.367	0.233	0.024

- caloric value of crayfish food is 2090 J g^{-1} (estimated based on Cummins (1967)),
- 80% of the food energy is assimilated (Winberg 1956),
- active metabolism of crayfish under natural conditions is, similarly to fish, 1.5 fold higher than that calculated (Mel'nichuk et al. 1978).

The daily ration according to the Winberg method was calculated with the formula:

$$C = 1.25 (P + R)$$

where:

C – energy value of the food consumed by the crayfish (J),

P – energy value of the increase in crayfish weight (J),

R – energy value of overall metabolism (J),

R was calculated using the formula provided by Tcherkashina (1977):

$$r = 0.0005 W^{0.8347}$$

where:

r – respiration (crayfish oxygen consumption in cm^3 O_2 $hour^{-1}$),

W – mean crayfish body wet weight in mg.

The values of respiration (r) obtained were multiplied by tabularized temperature coefficients (Winberg 1956), which permitted determining the respiration values that occur at 20°C, in accordance with the Krogh curve.

The annual food consumption of crayfish was determined by summing the daily ration calculated with the various methods. For the periods between the days when samples were taken, the daily food ration was interpolated. The mean annual body weight increases of the crayfish in the catchable population was determined by calculating the weighted average of crayfish body weight increases separately for each year of crayfish life. In order to do this, it was assumed, following Pieplow (1938), that after the first year of life spinycheek crayfish, regardless of gender, attain a mean body length of 55 mm, after the second 72 mm; after the third 87 mm; and after the fourth 102 mm. The mean body weight (W, g) for these lengths was calculated based on the dependence between the body weight of crayfish from Lake Staw Płociczno and their total length:

$$W = 0.0000119954\ TL^{3.20779}\quad (R^2(\%) = 95.3,\ SE = 1.11,\ P < 0.0001).$$

The degree to which food is utilized for body growth (K_1) and the feeding coefficient (FC) were calculated from proportions of body weight increases and annual food consumption.

3.5. CALCULATIONS AND STATISTICAL ANALYSIS

Mean:

- body weight (W, g);
- total length (TL, mm);
- cephalothorax length (CL, mm);
- cheliped length (ChL, mm);
- crayfish body proportions (M) and variability coefficient of these proportions (V);
- number of eggs;

were calculated using descriptive statistics (Multiple-Variable Analysis, Summary Statistics). The differences between means were calculated with the least significant differences method or Fisher's LSD. The normality of the size structure of the crayfish caught with fyke net frames or crayfish traps was verified with the Chi^2 test. Differences between the size structure of crayfish caught with the fyke net frame and seines was calculated with the Kolmogorov-Smirnov test. Differences between daily ration values calculated with the Elliott and Persson method, and the predicted values were calculated with the t test method of paired comparisons.

Dependencies:

- body weight on total length and cephalothorax length;
- total body length on cephalothorax length;
- cheliped length on total length and cephalothorax length;
- absolute fecundity on body weight, total length and cephalothorax length;
- stomach fullness index on water temperature;
- food evacuation time on water temperature and stomach fullness index;
- daily food ration calculated with the Elliot and Persson method on water temperature and stomach fullness index;

were calculated using simple and multiple linear regression equations for variables that were transformed and untransformed to the natural logarithm (ln). A model that best fit the empirical data was chosen for further analysis. The statistical evaluation of model fit was based on standard error (SE), determination coefficient (R^2(%)), and the value of the probability coefficient (P).

Crayfish abundance was calculated with the formula by Petersen (Ricker 1975)

$$N = M\,C\,R^{-1}$$

where:

N = abundance of the catchable part of the crayfish population;

M – number of tagged crayfish;

C – number of crayfish caught;

R – number of tagged crayfish returns.

All of the calculations and statistical analysis in the present work were done using the Statgraphics Plus v. 4 software.

4. RESULTS

4.1. SUBMERGED VEGETATION SPECIES STRUCTURE AND BIOMASS IN LAKE STAW PŁOCICZNO

The occurrence of eighteen species of submerged vegetation was confirmed in Lake Staw Płociczno: *Chara tomentosa* L.; *Ch. aculeolata* Kütz.; *Ch. rudis* A. Br.; *Ch. hispida* L.; *Nitellopsis obtusa* (Desv.) I. Groves.; *Spirogyra* sp.; *Drepanocladus aduncus* (Hedw.) Moenk.; *Fontinalis antipyretica* L.; *Polygonum amphibium* L.; *Ranunculus circinatus* Sibth.; *Ceratophyllum demersum* L.; *Myriophyllum spicatum* L.; *M. verticillatum* L.; *Elodea canadensis* Rich.; *Potamogeton perfoliatus* L.; *P. pectinatus* L.; *P. compressus* L.; *P. mucronatus* L. These species formed three basic plant assemblages in the lake:

1. *Charetum tomentose* (Sauer 1937) Corillion 1957 – mossy stonewort assemblage. This assemblage formed extensive submerged meadows that extended to depths of even 7 m. The species comprising the assemblage included *Ch. tomentosa* and *Ch. rudis,* which were accompanied by clusters of *M. spicatum*, *M. verticilatum, R. circinatus, E. canadensis* and, less frequently, *F. antipyretica*, *P. mucronatus*, and *P. perfoliatus*;
2. *Charetum rudis* Dąmbska 1966 – common stonewort assemblage. This assemblage, with the species *Ch. rudis, Ch. tomentosa*, *M. spicatum*, *R. circinatus, E. canadensis, P. mucronatus,* and *P. perfoliatus,* occurred in a strip of submerged vegetation that was located at greater depths and in the part of the lake where the shoreline sloped steeply (central part of the lake);
3. *Nitellopidetum obtusae* (Sauer 1937) Dąmbska 1966 – this assemblage was typical of the southwestern part of the lake and was represented mainly by *N. obtusa, Ch. tomentosa*, and *Ch. aculeolata* as well as *M. spicatum*.

The plant assemblages intermingled with each other, and it was difficult to determine a clear border between their areas of occurrence. Nevertheless, the decided dominants were species from the family Characeae (*Ch. rudis, Ch. tomentosa*, *Ch. aculeolata*, *Ch. hispida*, *N. obtusa*), which was accompanied only by small mats of other submerged vegetation.

Submerged vegetation occurred normally at depths to 5 m, although in some locations they occurred as deep as 7 m. The area occupied by this vegetation was about 17 ha (approximately 78% of the lake area).

The wet weight of the submerged vegetation per m^2 was 6365.9 g (Table 4). The dominant among the vegetation was Characeae *(*67%). The combined vegetation biomass in Lake Staw Płociczno was approximately 1100 tons wet weight.

TABLE 4

Mean submerged vegetation biomass in Lake Staw Płociczno

Species	Wet biomass ($g\ m^{-2}$)
Chara sp.	2946.0
Nitellopsis obtusa	1323.1
Myriophyllum spicatum	560.3
Potamogeton pectinatus	463.9
Myriophyllum verticilatum	268.0
Spirogyra sp.	254.8
Ranunculus circinatus	129.4
Drepanocladus aduncus	128.4
Potamogeton perfoliatus	75.1
Elodea canadensis	68.8
Polygonum amphibium	59.9
Fontinalis antiperitica	59.9
Potamogeton mucronatus	28.3
Potamogeton compressus	trace
Ceratophyllum demersum	trace

4.2. MORPHOMETRIC CHARACTERS OF THREE SPINYCHEEK CRAYFISH POPULATIONS

Total length (TL) of female spinycheek crayfish ranged from 29.0 to 130.0 mm, cephalothorax length (CL) range was from 13.9 to 65.1 mm, cheliped length (ChL) was from 6.6 to 44.4 mm, and body weight (W) was from 0.5 to 63.2 g (Table 5). The means of female TL, CL, ChL, and W were higher in Lake Dgał Wielki (Fisher test, $P \leq 0.05$) than in females from lakes Hańcza and Staw Płociczno (Table 5).

The total length of form I male spinycheek crayfish was from 50.0 to 123.0 mm, cephalothorax length was from 25.4 to 62.3 mm, cheliped length was from 14.1 to 56.8 mm, and body weight was from 3.8 to 59.4 g (Table 5). As was the case with the females, form I males from Lake Dgał Wielki had higher means of total length,

TABLE 5

General characters of the measured spinycheek crayfish. W – body weight (g); TL – total length (mm); CL – cephalothorax length (mm); ChL – cheliped length (mm); ± – 95% confidence interval

		Lake Staw Płociczno		Lake Dgał Wielki		Lake Hańcza		All lakes	
	Parameter	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Females	TL	75.3 ± 0.5[a]	31.0-105.0	95.7 ± 1.7[d]	29.0-130.0	86.4 ± 2.8[c]	47.0-121.0	81.0 ± 0.7[b]	29.0-130
	CL	36.2 ± 0.3[a]	15.0-50.5	45.8 ± 0.8[c]	13.9-65.1	40.9 ± 1.4[b]	19.8-56.5	38.8 ± 0.3[b]	13.9-65.1
	ChL	19.8 ± 0.2[a]	6.6-29.3	27.4 ± 0.6[d]	6.6-44.4	24.4 ± 1.2[c]	9.4-36.3	22.0 ± 0.3[b]	6.6-44.4
	W	12.4 ± 0.2[a]	0.8-30.3	27.0 ± 1.2[d]	0.5-63.2	19.7 ± 1.8[c]	2.2-46.3	16.5 ± 0.5[b]	0.5-63.2
Males form I	TL	78.3 ± 0.5[a]	50.0-105.0	95.8 ± 0.6[c]	56.0-123.0	87.0 ± 1.3[b]	62.0-110.0	86.7 ± 0.5[b]	50.0-123.0
	CL	38.5 ± 0.3[a]	25.4-53.9	47.5 ± 0.3[c]	26.5-62.3	42.2 ± 0.7[b]	30.2-52.4	42.7 ± 0.3[b]	25.4-62.3
	ChL	29.1 ± 0.3[a]	14.1-47.9	38.5 ± 0.4[c]	16.6-56.8	34.4 ± 0.9[b]	14.7-49.3	33.7 ± 0.3[b]	14.1-56.8
	W	16.1 ± 0.3[a]	3.8-34.0	30.1 ± 0.5[c]	5.2-59.4	22.5 ± 1.0[b]	7.4-42.9	22.7 ± 0.4[b]	3.8-59.4
Males form II	TL	68.1 ± 1.9[a]	33.0-95.0	75.5 ± 5.0[b]	33.0-110.0			69.9 ± 1.9[a]	33.0-110.0
	CL	33.2 ± 0.9[a]	14.5-47.1	37.2 ± 2.6[b]	16.7-55.3			34.2 ± 1.0[a]	14.5-55.3
	ChL	20.9 ± 0.8[a]	5.6-36.0	24.6 ± 2.4[b]	8.5-41.8			21.8 ± 0.9[a]	5.6-41.8
	W	9.8 ± 0.7[a]	0.6-25.2	15.0 ± 2.5[c]	0.9-38.7			11.1 ± 0.9[b]	0.6-38.7

Values with a different letter index in the same row differ significantly statistically (Fisher test, $P \leq 0.05$)

cephalothorax length, cheliped length, and body weight than did form I males from lakes Hańcza and Staw Płociczno (Fisher test, $P \leq 0.05$) (Table 5).

Total length of form II spinycheek crayfish males ranged from 33.0 to 110.0 mm, cephalothorax length was from 14.5 to 55.3 mm, cheliped length was from 5.6 to 41.8 mm, and body weight ranged from 0.6 to 38.7 g (Table 5). The means of body length, cephalothorax length, cheliped length, and body weight of form II males from Lake Dgał Wielki were higher (Fisher test, $P \leq 0.05$) than those of males from Lake Staw Płociczno (Table 5).

The analysis of spinycheek crayfish body proportions (Table 6) indicated that at the same total length the female of the species had a longer abdomen (AL), a shorter cephalothorax (CL), a shorter anterior cephalothorax section (CfL), and shorter chelipeds (ChL) than did form I and II males. The female cheliped was thinner (ChW) than that of form I males, but wider (ChW) than the cheliped of form II males. At the same total length, form II spinycheek crayfish males had a longer abdomen (AL), a shorter cephalothorax (CL), a longer anterior cephalothorax segment (CfL), and shorter

TABLE 6

Mean proportion values (M) and variability coefficient values (V) of female and male spinycheek crayfish

Proportion	Lake Staw Płociczno						Lake Dgał Wielki						Lake Hańcza				Total					
			Males						Males						Males				Males			
	Females		form I		form II		Females		form I		form II		Females		form I		Females		form I		form II	
	n=1234		n = 1079		n=219		n=444		n=979		n=71		n=94		n=197		n=1772		n = 2255		n=290	
	M	V (%)	M	V (%)	M	V (%)	M	V (%)	M	V (%)	M	V (%)	M	V (%)	M	V (%)	M	V%	M	V%	M	V%
TL/AL	1.923^{c}	2.2	1.965^{f}	2.7	1.952^{de}	2.6	1.917^{b}	2.9	1.983^{h}	2.7	1.965^{efg}	3.9	1.900^{a}	2.9	1.943^{d}	3.1	1.920^{bc}	2.5	1.971^{g}	2.8	1.955^{e}	3.0
TL/CL	2.085^{f}	2.4	2.039^{c}	2.9	2.053^{d}	2.8	2.095^{g}	3.4	2.021^{a}	2.8	2.043^{bcd}	4.5	2.115^{h}	3.4	2.065^{e}	3.4	2.090^{fg}	2.8	2.033^{b}	3.0	2.050^{d}	3.3
TL/CfL	3.168^{c}	3.2	3.125^{b}	3.4	3.112^{ab}	3.4	3.193^{e}	3.6	3.099^{a}	3.4	3.112^{ab}	5.4	3.249^{f}	4.1	3.193^{e}	5.6	3.178^{d}	3.4	3.120^{b}	3.7	3.112^{ab}	4.0
TL/ChL	3.842^{h}	7.8	2.723^{c}	8.5	3.389^{e}	14.4	3.580^{f}	11.2	2.520^{a}	9.3	3.284^{d}	18.5	3.630^{f}	11.6	2.589^{b}	13.9	3.765^{g}	9.4	2.62^{b}	10.1	3.364^{de}	15.5
TL/CW	4.220^{ef}	3.6	4.077^{c}	3.5	4.306^{h}	5.0	4.199^{d}	3.9	3.994^{a}	3.4	4.211^{def}	6.2	4.252^{fg}	4.6	4.097^{c}	5.3	4.217^{e}	3.7	4.043^{c}	3.8	4.283^{gh}	5.4
TL/ChW	9.492^{g}	10.9	7.714^{c}	8.8	9.984^{i}	14.2	8.861^{e}	15.6	7.213^{a}	9.1	9.691^{gh}	20.4	8.577^{f}	13.2	7.159^{a}	12.5	9.285^{d}	12.7	7.448^{b}	9.9	9.912^{hi}	15.9
AL/AW	2.193^{a}	7.0	2.370^{c}	5.1	2.493^{f}	6.1	2.234^{b}	9.0	2.383^{d}	5.2	2.519^{f}	9.0	2.187^{a}	8.9	2.424^{e}	8.9	2.203^{a}	7.7	2.379^{d}	5.6	2.499^{f}	6.9
CL/CW	2.024^{e}	3.7	2.001^{c}	3.2	2.098^{g}	4.9	2.006^{c}	3.9	1.977^{a}	3.0	2.062^{f}	4.5	2.011^{cde}	4.4	1.984^{ab}	4.3	2.019^{d}	3.8	1.989^{b}	3.3	2.089^{g}	4.8
ChL/ChW	2.469^{b}	6.4	2.837^{d}	5.6	2.952^{f}	7.2	2.470^{b}	6.9	2.867^{e}	5.7	2.949^{f}	6.7	2.364^{a}	6.8	2.778^{c}	8.0	2.464^{b}	6.6	2.845^{d}	6.0	2.951^{f}	7.0
ChL/ChT	4.332^{c}	8.8	4.699^{f}	8.0	5.036^{h}	10.3	4.184^{a}	8.8	4.616^{d}	7.5	4.879^{g}	13.6	4.174^{a}	9.8	4.607^{de}	9.2	4.287^{b}	9.0	4.655^{e}	7.9	4.998^{h}	11.2

Values with a different letter index in the same row differ significantly statistically (Fisher test, $P \leq 0.05$)

(ChL), thinner (ChW), and narrower (ChT) chelipeds than did form I males. All of these differences were statistically significant (Fisher test, $P \leq 0.05$).

Most of the proportions studied exhibited high variability (Table 6). Among the analyzed proportions, only those of total length to abdomen length and to cephalothorax length (TL/AL and TL/CL) in females and form I males exhibited less than 3% variability, while the proportions of cheliped measurements (TL/ChL, TL/ChW, ChL/ChW, ChL/ChT) exhibited the highest variability, which even exceeded 10%. Variability in the proportions of form II males was decidedly larger than that in females and form I males (Table 6).

The dependency of body weight and total length in both females and males was very well demonstrated with multiplicative equations (Table 7), which also best explained the dependency of body weight and cephalothorax length (Table 8). There was a distinct, positive relationship between body length and cephalothorax length in spinycheek crayfish, which was well explained with linear regression equations (Table 9). Cheliped length exhibited a positive dependence on total length, which was well described by multiplicative equations (Table 10). The dependency of cheliped length and cephalothorax

TABLE 7

Parameters of the multiplicative regression equation ($W = b_0 TL^{b_1}$) that best explained the dependence of body weight (W, g) on total length (TL, mm) in spinycheek crayfish, n – number (specimens), b_0, b_1 – regression coefficientat with 95% confidence intervals, SE – standard error, R^2(%) – determination coefficient, $P < 0.0001$

Crayfish	Lake	n	b_0	b_1	SE	R^2(%)
Females	Staw Płociczno	1234	0.00002 ± 0.00000	3.08 ± 0.03	1.07	97.3
	Dgał Wielki	444	0.00001 ± 0.00000	3.17 ± 0.04	1.11	97.8
	Hańcza	94	0.00002 ± 0.00001	3.08 ± 0.13	1.11	96.1
	Total	1772	0.00002 ± 0.00000	3.09 ± 0.02	1.09	98.0
Males form I	Staw Płociczno	1079	0.00002 ± 0.00000	3.11 ± 0.04	1.08	94.8
	Dgał Wielki	979	0.00001 ± 0.00000	3.21 ± 0.05	1.08	94.7
	Hańcza	197	0.00003 ± 0.00002	3.00 ± 0.13	1.10	91.8
	Total	2255	0.00002 ± 0.00000	3.14 ± 0.02	1.08	96.9
Males form II	Staw Płociczno	219	0.00001 ± 0.00000	3.15 ± 0.05	1.09	98.6
	Dgał Wielki	71	0.00001 ± 0.00000	3.25 ± 0.08	1.11	98.9
	Total	290	0.00001 ± 0.00000	3.18 ± 0.04	1.10	98.7

length was most faithfully represented by multiplicative equations, as was the case with the dependencies of cheliped parameters with weight and length (Table 11).

TABLE 8

Parameters of the multiplicative regression equation ($W = b_0CL^{b_1}$) that best explained the dependence of body weight (W, g) on cephalothorax length (CL, mm) in spinycheek crayfish, n – number (specimens), b_0, b_1 – regression coefficient with 95% confidence intervals, SE – standard error, R^2(%) – determination coefficient, P < 0.0001

Crayfish	Lake	n	b_0	b_1	SE	R^2(%)
Females	Staw Płociczno	1234	0.0003 ± 0.0000	2.96 ± 0.03	1.09	96.3
	Dgał Wielki	444	0.0002 ± 0.0000	3.04 ± 0.04	1.11	97.8
	Hańcza	94	0.0005 ± 0.0002	2.84 ± 0.13	1.11	95.6
	Total	1772	0.0002 ± 0.0000	3.01 ± 0.02	1.10	97.6
Males form I	Staw Płociczno	1079	0.0004 ± 0.0001	2.90 ± 0.04	1.08	95.7
	Dgał Wielki	979	0.0004 ± 0.0001	2.90 ± 0.04	1.08	94.7
	Hańcza	197	0.0005 ± 0.0002	2.84 ± 0.12	1.10	92.0
	Total	2255	0.0003 ± 0.0000	2.94 ± 0.02	1.08	97.0
Males form II	Staw Płociczno	219	0.0002 ± 0.0000	3.07 ± 0.05	1.09	98.7
	Dgał Wielki	71	0.0002 ± 0.0001	3.02 ± 0.07	1.11	99.0
	Total	290	0.0002 ± 0.0000	3.04 ± 0.04	1.09	98.8

TABLE 9

Parameters of the linear regression equation ($TL = b_0 + b_1 CL$) that best explained the dependence of total length (TL, mm) on cephalothorax length (CL, mm) in spinycheek crayfish, n – number (specimens), parb_0, b_1 – regression coefficient with 95% confidence intervals, SE – standard error, R^2(%) – determination coefficient, P < 0.0001

Crayfish	Lake	n	b_0	b_1	SE	R^2(%)
Females	Staw Płociczno	1234	4.25 ± 0.74	1.97 ± 0.02	1.73	96.7
	Dgał Wielki	444	5.49 ± 1.42	1.97 ± 0.03	2.90	97.4
	Hańcza	94	6.26 ± 3.11	1.96 ± 0.07	2.49	96.7
	Total	1772	2.80 ± 0.54	2.01 ± 0.01	2.20	97.9
Males form I	Staw Płociczno	1079	7.93 ± 1.07	1.83 ± 0.03	2.07	94.0
	Dgał Wielki	979	11.85 ± 1.35	1.77 ± 0.03	2.29	93.9
	Hańcza	197	8.16 ± 3.57	1.87 ± 0.08	2.81	90.8
	Total	2255	7.13 ± 0.64	1.86 ± 0.01	2.13	96.4
Males form II	Staw Płociczno	219	2.81 ± 1.10	1.97 ± 0.03	1.71	98.5
	Dgał Wielki	71	5.57 ± 1.67	1.88 ± 0.04	2.01	99.1
	Total	290	4.18 ± 0.88	1.92 ± 0.03	1.82	98.8

TABLE 10

Parameters of the multiplicative regression equation ($ChL = b_0TL^{b_1}$) that best explained the dependence of cheliped length (ChL, mm) on total length (TL, mm) in spinycheek crayfish, n – number (specimens), b_0, b_1 – regression coefficient with 95% confidence intervals, SE – standard error, R^2(%) – determination coefficient, P < 0.0001

Crayfish	Lake	n	b_0	b_1	SE	R^2(%)
Females	Staw Płociczno	1234	0.08 ± 0.01	1.28 ± 0.03	1.07	88.1
	Dgał Wielki	444	0.06 ± 0.01	1.34 ± 0.03	1.08	94.3
	Hańcza	94	0.03 ± 0.01	1.49 ± 0.10	1.08	91.2
	Total	1772	0.07 ± 0.00	1.32 ± 0.02	1.07	93.2
Males form I	Staw Płociczno	1079	0.04 ± 0.01	1.50 ± 0.03	1.06	87.4
	Dgał Wielki	979	0.03 ± 0.00	1.59 ± 0.04	1.06	87.5
	Hańcza	197	0.02 ± 0.01	1.65 ± 0.13	1.11	75.0
	Total	2255	0.05 ± 0.00	1.48 ± 0.02	1.07	90.6
Males form II	Staw Płociczno	219	0.04 ± 0.01	1.46 ± 0.05	1.08	94.6
	Dgał Wielki	71	0.04 ± 0.01	1.50 ± 0.07	1.09	96.6
	Total	290	0.04 ± 0.01	1.47 ± 0.04	1.08	95.4

TABLE 11

Parameters of the multiplicative regression equation ($ChL = b_0CL^{b_1}$) that best explained the dependence of cheliped length (ChL, mm) on cephalothorax length (CL, mm) in spinycheek crayfish, n – number (specimens), b_0, b_1 – regression coefficient with 95% confidence intervals, SE – standard error, R^2(%) – determination coefficient, P < 0.0001

Crayfish	Lake	n	b_0	b_1	SE	R^2(%)
Females	Staw Płociczno	1234	0.24 ± 0.02	1.23 ± 0.03	1.07	87.8
	Dgał Wielki	444	0.20 ± 0.02	1.29 ± 0.03	1.08	94.3
	Hańcza	94	0.14 ± 0.04	1.39 ± 0.08	1.07	92.8
	Total	1772	0.20 ± 0.01	1.29 ± 0.02	1.07	93.0
Males form I	Staw Płociczno	1079	0.17 ± 0.02	1.41 ± 0.03	1.06	89.7
	Dgał Wielki	979	0.15 ± 0.02	1.44 ± 0.03	1.06	87.6
	Hańcza	197	0.09 ± 0.04	1.60 ± 0.12	1.10	78.7
	Total	2255	0.18 ± 0.01	1.39 ± 0.02	1.07	91.6
Males form II	Staw Płociczno	219	0.16 ± 0.03	1.39 ± 0.05	1.09	94.0
	Dgał Wielki	71	0.15 ± 0.03	1.40 ± 0.05	1.08	97.4
	Total	290	0.16 ± 0.02	1.39 ± 0.04	1.09	95.4

It must be noted that with all of these dependencies (body weight with total length and cephalothorax length, total length and cephalothorax length, cheliped length and total length and cephalothorax length) the equations obtained best fit the empirical data from form II males from Lake Dgał Wielki, while the poorest fit was for the form I males from Lake Hańcza (Table 7-11).

4.3. STRUCTURE AND INDEXES OF THE CATCHABLE SPINYCHEEK CRAYFISH POPULATION IN LAKE STAW PŁOCICZNO

4.3.1. SEX RATIO

In the summer season, females dominated among the spinycheek crayfish caught with the fyke net frame (Fig. 5), while form I males dominated among the males (Fig. 6). Form II males occurred in the catches only from June to September and in November and were most abundant in July (Fig. 6). Of the crayfish caught throughout the year with fyke net frames, 40.9% were females and 59.1% were males.

In the catches made with seines, there were slightly more females than males caught in summer and late fall (Fig. 7). Females dominated decisively only in June and July, while males did so in January, March, May and December (Fig. 7). As was the case with the males caught with the fyke net frame, form I males dominated in seine catches (Fig. 8). Form II males occurred in the catches from May to December. Similarly to the fyke net frame catches, the maximum occurrence of form II males in the seine catches was noted in July (see Fig. 6 and 8). Annually, a mean of 45.2% females and 54.8% males were caught with seines.

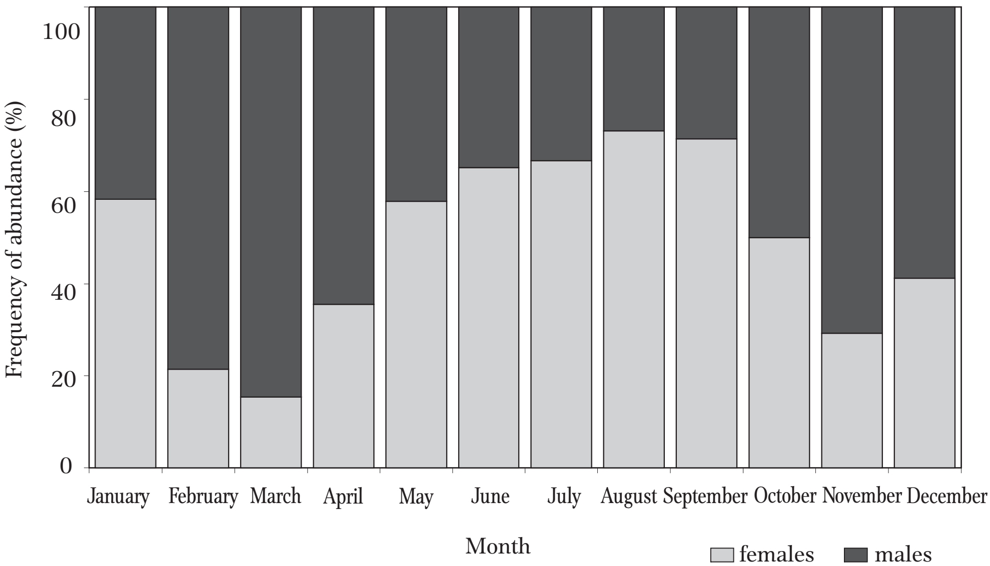

Fig. 5. Annual contribution of spinycheek crayfish females and males caught with fyke net frames in Lake Staw Płociczno.

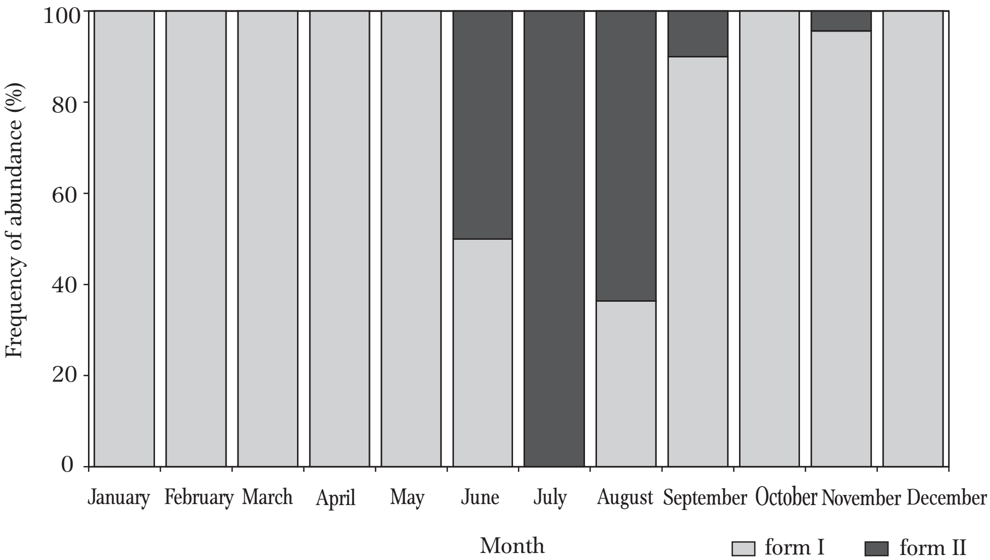

Fig. 6. Annual contribution of form I and II spinycheek crayfish males caught with fyke net frames in Lake Staw Płociczno.

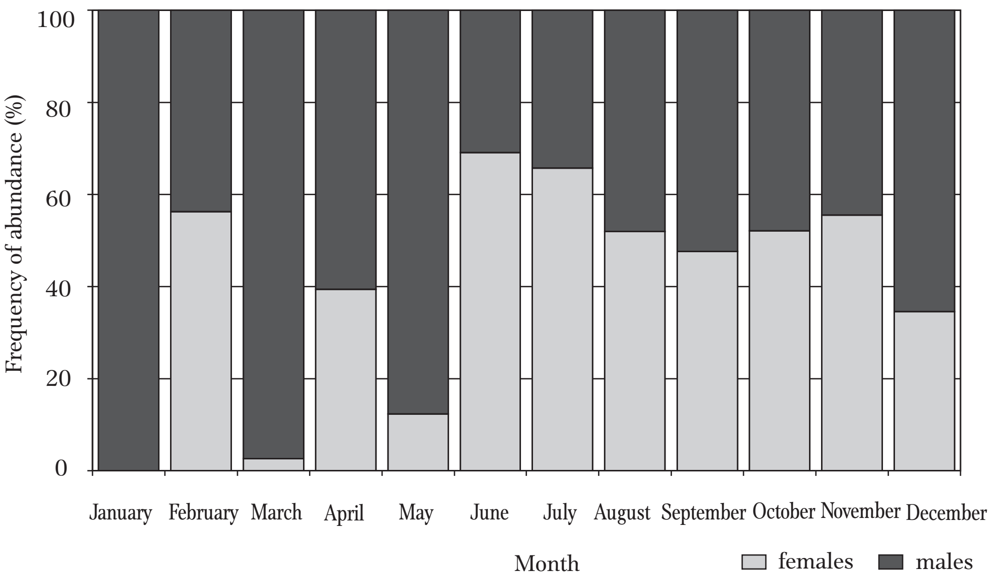

Fig. 7. Annual contribution of female and male spinycheek crayfish caught with seines in Lake Staw Płociczno.

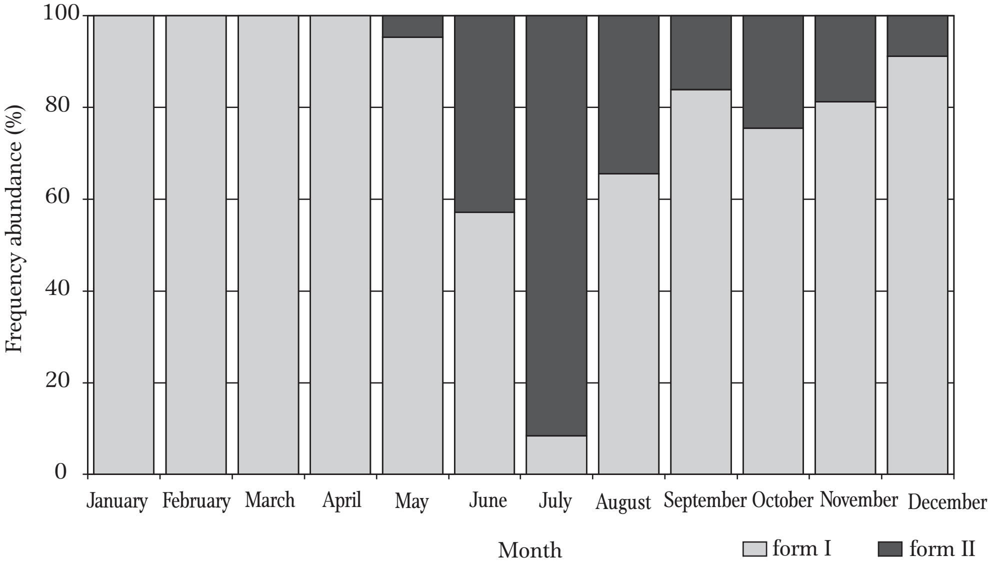

Fig. 8. Annual contribution of form I and II spinycheek crayfish males caught with seines in Lake Staw Płociczno.

4.3.2. SIZE STRUCTURE

The mean length of crayfish caught with the fyke net frame was 80.5 ± 0.6 mm and was significantly statistically higher (Fisher test, $P \leq 0.05$) than the mean length (75.2 ± 0.8 mm) of crayfish caught with seines. Throughout the year, the dominant crayfish in fyke net frame catches measured from 81 to 90 mm in total length (Fig. 9). The size distribution was close to normal distribution (Chi^2 test, $P = 0.02$). The size structure of the crayfish caught with seines was different. Crayfish ranging in total length from 71 to 80 mm dominated (Fig. 10). The size distribution structure was also close to the normal distribution (Chi^2 test, $P < 0.0001$). The difference in the size structure between the crayfish caught with the fyke nets and seines was statistically significant (Kolmogorov-Smirnov test, $P < 0.05$).

4.3.3 INDIVIDUAL ABSOLUTE FECUNDITY

The mean individual fecundity of female spinycheek crayfish from Lake Staw Płociczno was 247 eggs and was significantly statistically lower (Fisher test, $P \leq 0.05$) than the mean individual fecundity of females from Lake Dgał Wielki (499 eggs). The

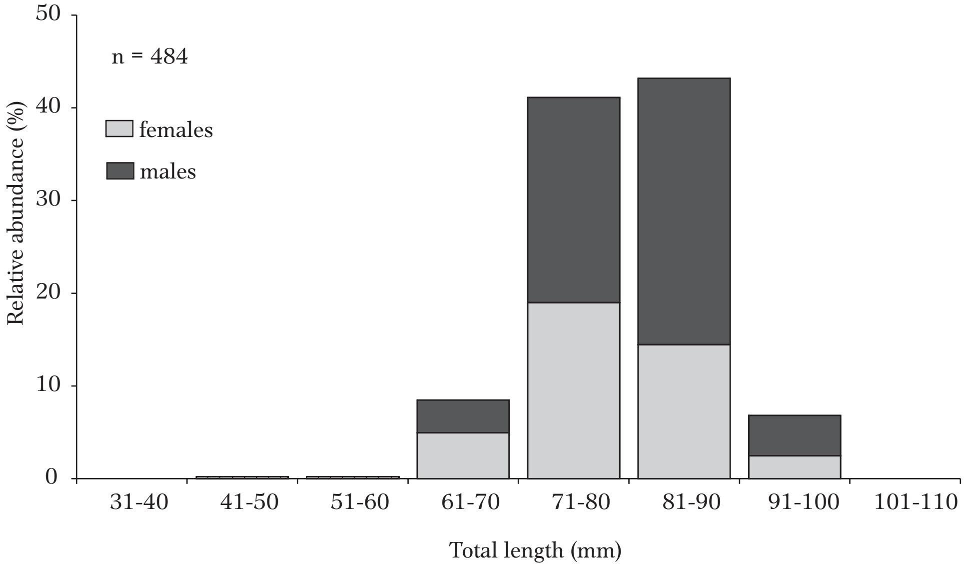

Fig. 9. Relative distribution (%) of the total length of female and male spinycheek crayfish caught with fyke net frames in Lake Staw Płociczno.

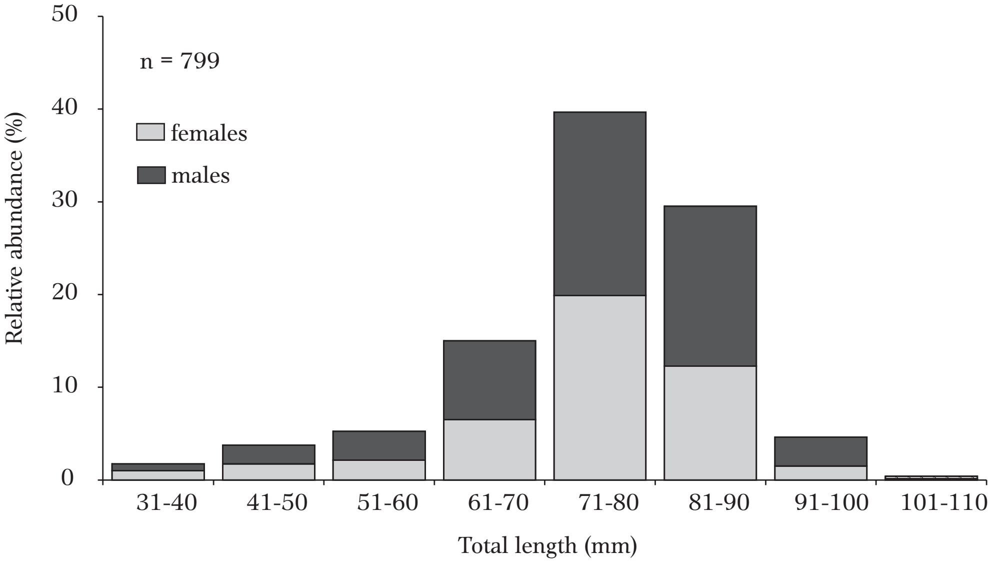

Fig. 10. Relative distribution (%) of the total length of female and male spinycheek crayfish caught with seines in Lake Staw Płociczno.

fecundity range was substantial (Table 12); in female spinycheek crayfish from Lake Staw Płociczno that weighed from 4.7 g to 23.4 g fecundity ranged from 56 to 431 eggs, and in females from Lake Dgał Wielki that weighed from 3.3 g to 56.0 g it was 138 to 926 eggs. The fecundity of females of a total length of up to 81mm from both lakes was not statistically significantly different; however, the fecundity of females with a total length exceeding 81 mm from Lake Dgał Wielki was statistically significantly higher than that of females from Lake Staw Płociczno (Table 12).

TABLE 12

Mean absolute fecundity (Fa, eggs female^{-1}) and its range in female spinycheek crayfish from lakes Staw Płociczno and Dgał Wielki, n – number (specimens), ± – confidence interval for the mean

Length class (mm)	Absolute fecundity					
	Staw Płociczno			Dgał Wielki		
	n	Mean (eggs)	Range (eggs)	n	Mean (eggs)	Range (eggs)
41-50				1	142	142-142
51-60	6	122 ± 68	56-212			
61-70	44	184 ± 15^a	86-310	3	194 ± 137^a	138-249
71-80	89	253 ± 11^a	105-407	2	323 ± 750^a	264-382
81-90	37	316 ± 21^a	196-431	6	385 ± 51^b	291-431
91-100	5	333 ± 95^a	229-413	18	463 ± 39^b	316-636
101-110				24	551 ± 48	340-861
111-120				13	595 ± 94	431-849
121-130				1	926	926-926

Values with different letter indices in the same row differ statistically significantly (Fisher test, $P \leq 0.05$)

Statistically significant dependencies were confirmed between absolute fecundity and body weight, total length, and cephalothorax length. All of these dependencies can be represented by multiplicative equations, and the dependency between fecundity and body weight was stronger than that between fecundity and both total length and cephalothorax length (Table 13, Fig. 11-13).

TABLE 13

Parameters of the multiplicative regression equation ($Fa = b_0 x^{b_1}$) that best described the dependence of absolute fecundity (Fa, eggs female^{-1}) on body weight (W, g), total length (TL, mm) and cephalothorax length (CL, mm), n – number (specimens), b_0, b_1 – regression coefficient with 95% confidence intervals, SE – standard error, R^2(%) – determination coefficient, P < 0.0001

y - x	Lake	n	b_0	b_1	SE	R^2(%)
Fa – W	Staw Płociczno	181	37.56 ± 8.91	0.74 ± 0.09	1.25	57.4
	Dgał Wielki	68	61.73 ± 19.80	0.61 ± 0.09	1.21	71.9
Fa – TL	Staw Płociczno	181	0.01 ± 0.02	2.29 ± 0.32	1.26	52.5
	Dgał Wielki	68	0.08 ± 0.17	1.88 ± 0.32	1.23	67.9
Fa – CL	Staw Płociczno	181	0.13 ± 0.16	2.10 ± 0.30	1.26	51.8
	Dgał Wielki	68	0.51 ± 0.75	1.77 ± 0.30	1.23	67.1

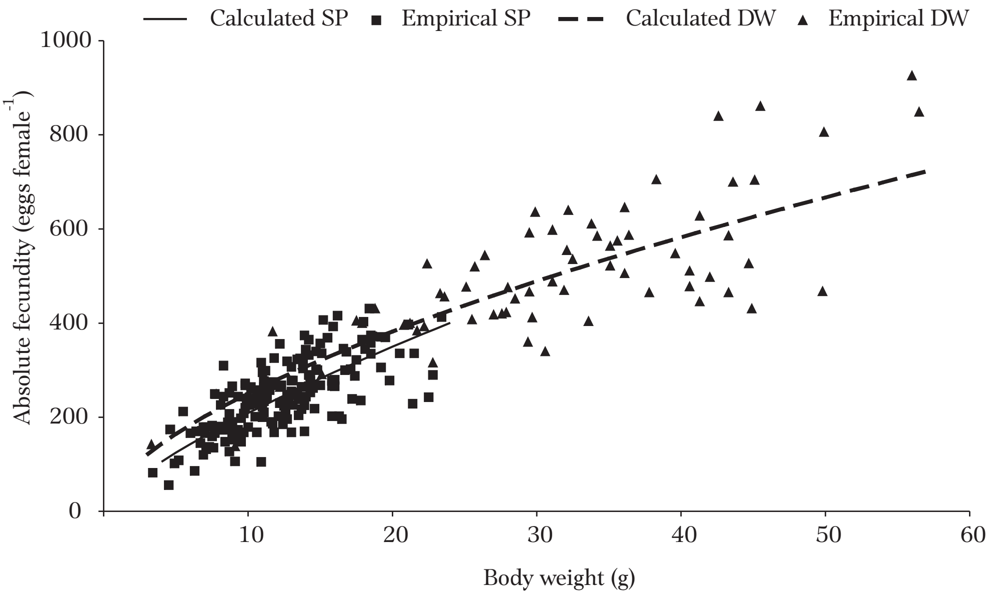

Fig. 11. Relationship between individual absolute fecundity and body weight of spinycheek crayfish females from lakes Staw Płociczno (SP) and Dgał Wielki (DW).

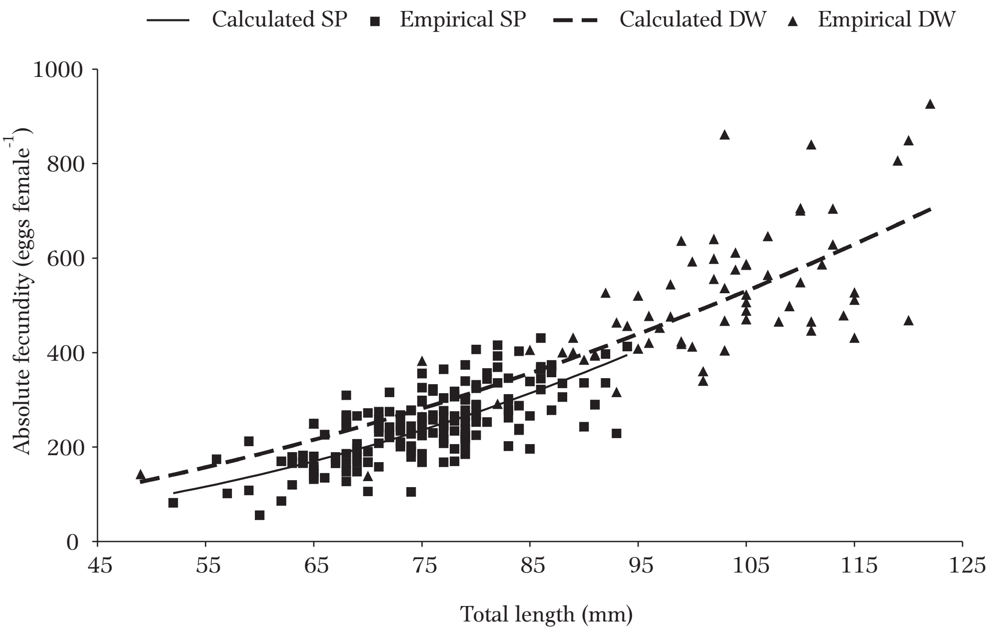

Fig. 12. Relationship between individual absolute fecundity and total length of spinycheek crayfish females from lakes Staw Płociczno (SP) and Dgał Wielki (DW).

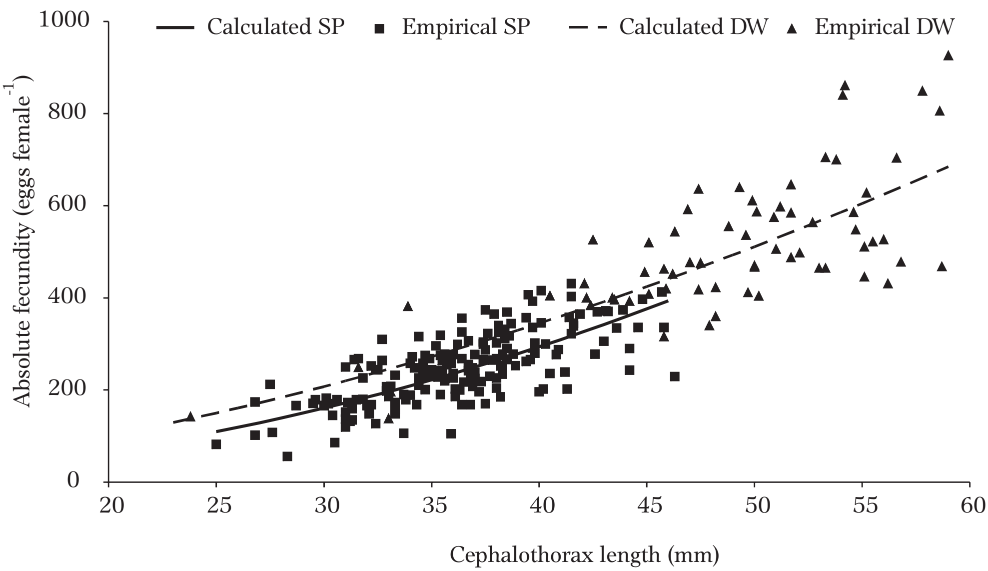

Fig. 13. Relationship between individual absolute fecundity and total cephalothorax length of spinycheek crayfish females from lakes Staw Płociczno (SP) and Dgał Wielki (DW).

4.3.4. ABUNDANCE AND BIOMASS OF THE CATCHABLE PART OF SPINYCHEEK CRAYFISH IN LAKE STAW PŁOCICZNO

A total of 839 crayfish specimens were caught and tagged at the designated sampling sites. A total of 647 crayfish were caught subsequently, including 14 tagged specimens. The abundance of the catchable part of the spinycheek crayfish population calculated with the Petersen method from Lake Staw Płociczno was 37935 specimens. The biomass of this segment of the population calculated as the quotient of the abundance and the mean weight of one specimen from the catchable population (12.0 g), was 455 kg wet weight. The range of occurrence of the spinycheek crayfish in Lake Staw Płociczno reached a depth of 3.0 m, and the area inhabited by the crayfish was approximately 14.1 ha. The density of the catchable population, calculated as the quotient of the abundance and the area inhabited by the crayfish was 2690 individuals ha^{-1} or 32.3 kg ha^{-1} (3.2 g m^{-2}).

4.4. SPINYCHEEK CRAYFISH FEEDING INTENSITY

The stomach fullness index was highly variable in both annual (Table 14) and daily (Fig. 14) cycles. Throughout the year, the highest mean stomach fullness index was noted in July (11.4‰ body wet weight) at the highest water temperature, while the lowest was in March (1.5‰ body wet weight) when the lowest water temperature was recorded during the study period. The highest daily stomach fullness index was generally noted at night (Fig. 14).

TABLE 14

Water temperature (°C), mean stomach fullness index (If, ‰ body wet weight), and gastric evacuation period (h)

Month	t	If	h
March	3.2	1.5	393.6
April	8.8	3.8	170.0
May	16.0	6.8	28.5
June	19.0	9.3	18.9
July	19.8	11.4	15.7
August	18.0	7.0	23.2
September	17.0	9.6	37.8
October	9.4	11.2	67.0
November	7.2	7.9	102.3
December	5.8	5.7	120.1

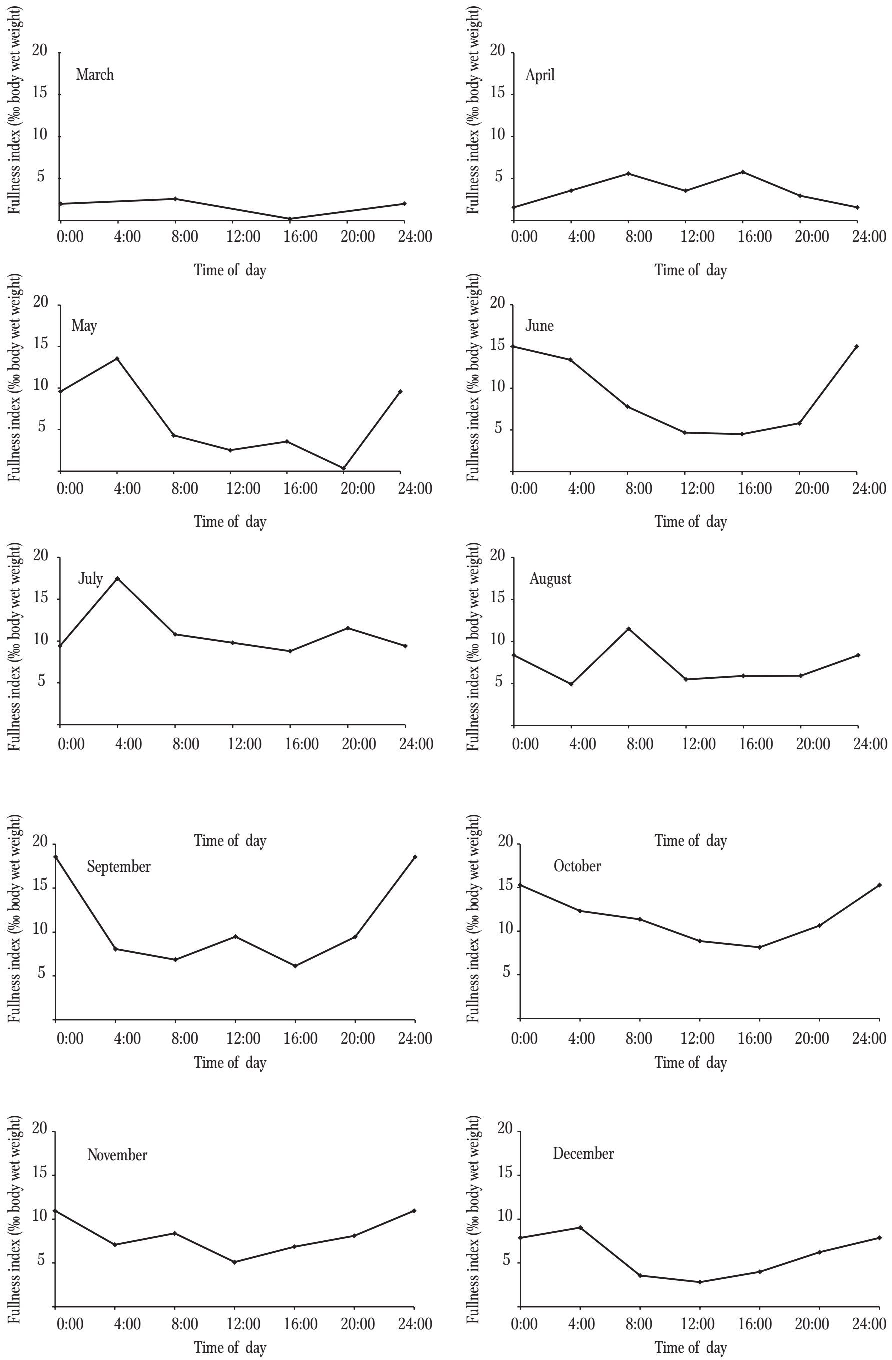

Fig. 14. Seasonal variation in the daily fluctuations of the mean stomach fullness indexes (If) of spinycheek crayfish from Lake Staw Płociczno.

The mean stomach fullness index exhibited a statistically significant ($P = 0.01$) positive dependency with water temperature. This dependency was best explained by the multiplicative equations:

$$If = 1.064\ t^{0.7638}$$

where:

If – mean stomach fullness index (‰ body wet weight),

t – water temperature (°C).

This equation has fairly high standard error ($SE = 1.52$) and a relatively low determination coefficient ($R^2(\%) = 58.4$), which means that using it to estimate the stomach fullness index would be too imprecise.

The gastric evacuation time fluctuated from 15.7 h in July to 393.6 h in March and was the longest at the lowest water temperature and the shortest at the highest temperature (Table 14). There was a negative statistically significant dependency between evacuation time and water temperature. This dependency was best described by the exponential equation:

$$h = 450.1 \times 0.848^{t}$$

where:

h – stomach content evacuation time (h),

t – water temperature (°C).

The equation is well fitted to the empirical data ($SE = 1.38$, $R^2(\%) = 91.6$, $P < 0.0001$) and might be used to estimate evacuation time. No statistically significant dependency was confirmed between evacuation time and stomach fullness, nor was improvement in fit to the empirical data noted when analyzing the combined impact of water temperature and stomach fullness index on evacuation time.

The daily food ration exhibited high fluctuation throughout the year (Table 15); great variability was also noted depending on the calculation method applied. The lowest daily food ration during the year was noted in March while the highest was in summer (Table 15). The daily food ration required for crayfish sustenance, calculated with the method Winberg was at its minimum in March and maximum in summer. The highest daily ration was calculated with the Kogan method, while the lowest was obtained with the Bajkov method. The remaining methods produced results that were very similar (Table 15).

TABLE 15

Daily food ration calculated with five methods: Bajkov (1935), Kogan (1963), Thorpe (1977), Elliott and Persson (1978), Winberg (1956), (‰ body wet weight)

Month	Bajkov	Kogan	Thorpe	Elliott and Persson	Winberg
March	0.1	7.1	5.5	2.5	0.8
April	0.5	17.0	12.2	7.0	10.7
May	5.7	55.5	28.2	24.7	30.9
June	11.4	33.7	23.1	39.3	40.7
July	17.4	40.1	27.2	38.4	44.5
August	7.2	36.2	23.7	25.6	39.2
September	6.1	63.0	36.1	28.5	34.7
October	4.0	17.8	13.7	14.1	12.1
November	1.9	22.6	18.0	10.9	9.1
December	1.1	32.8	21.9	8.5	7.4

Regardless of the calculation method, the daily food ration exhibited a positive statistically significant dependency with the stomach fullness index and water temperature. The closest dependency was noted for the results calculated with the Elliott and Persson method.

The dependency of the daily food ration and the stomach fullness index calculated with the Elliott and Persson method was best described with the following multiplicative equations:

$$RdP = 1.483\ If^{\ 1.238}$$

where:

RdP – predicted daily food ration (‰ body wet weight),

If – mean stomach fullness index (‰ body wet weight).

This equation was highly statistically significant ($P = 0.0013$, $SE = 1.60$, $R^2(\%) = 74.5$), which indicates that it can be used to make approximate predictions of the daily ration.

The dependency between the daily ration and water temperature calculated with the Elliott and Persson method was best described with the multiplicative equations:

$$RdP = 0.567\ t^{\ 1.383}$$

where:

RdP – predicted daily food ration (‰ body wet weight),

t – water temperature (°C).

This dependency is stronger (SE = 1.27, R^2(%) = 93.2, P < 0.0001) than that of the daily ration and stomach fullness index. The equation that represents this dependency can be used to predict the crayfish daily food ration with substantial precision.

The combined dependency of stomach fullness index and water temperature with the daily food ration is very strong (SE = 0.11, R^2(%) = 98.7, P < 0.0001). The following equation best explained this:

$$\ln RdP = 0.397 + 0.094\,t + 0.614 \ln If$$

where:
RdP – predicted daily food ration (‰ body wet weight),
If – mean stomach fullness index (‰ body wet weight),
t – water temperature (°C).

The daily food ration predicted with this equation was very near to the observed ration (Fig. 15), and no statistically significant differences were noted between them (t-test, α = 0.01, P = 0.98), which means that this equation can be applied to calculate the daily food ration.

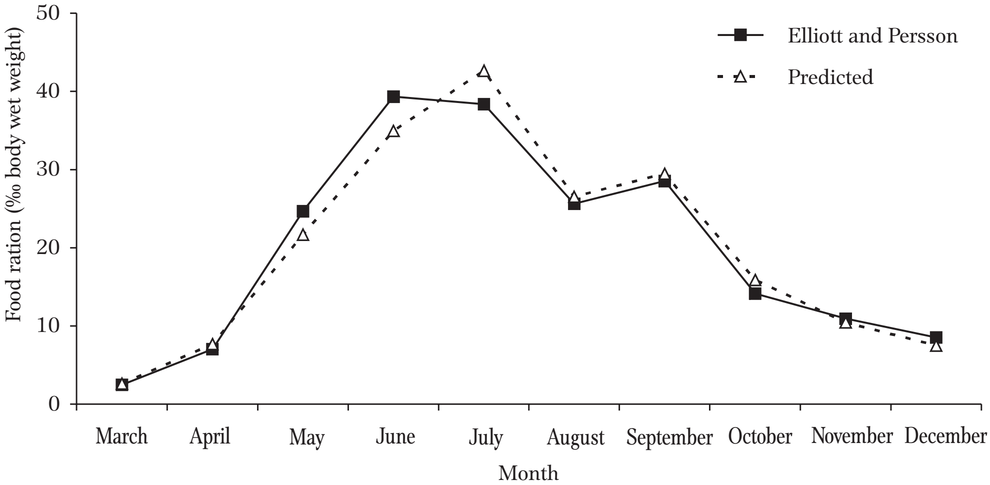

Fig. 15. Annual variability of food ration of spinycheek crayfish calculated with the Elliott and Persson (1978) method.

It was estimated that the annual food consumption by spinycheek crayfish fluctuated from 173.2‰ body wet weight to 1117.1‰ body wet weight depending on the estimation method applied (Table 16). The lowest annual food consumption was estimated with the Bajkov method, while the highest was determined with the Kogan method. The annual food consumption predicted with the equation ln RdP = 0.397 + 0.094 t + 0.614 ln If was nearly identical with the consumption estimated empirically using the Elliott and Persson method (Table 16).

TABLE 16

Monthly and annual food consumption calculated with five methods: Bajkov (1935), Kogan (1963), Thorpe (1977), Elliott and Persson (1978), Winberg (1956) and predicted monthly rations calculated with the regression equation (ln RdP = 0.397 + 0.094 t + 0.614ln If) in percentages (%) and grams (g) of body wet weight. W – mean body weight in g

Month	W	Bajkov		Kogan		Thorpe		Elliott and Persson		Winberg		Predicted	
	(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)	(g)
January	14.0	2.1	0.3	66.7	9.3	45.6	6.4	18.2	2.5	14.0	2.0	16.6	2.3
February	12.1	1.0	0.1	38.6	4.7	27.3	3.3	11.3	1.4	7.1	0.9	10.9	1.3
March	11.6	0.6	0.1	30.2	3.5	22.5	2.6	11.1	1.3	9.5	1.1	11.8	1.4
April	16.2	4.6	0.8	72.5	11.7	45.2	7.3	30.9	5.0	42.6	6.9	30.6	5.0
May	13.8	19.0	2.6	149.9	20.7	80.1	11.0	78.3	10.8	94.4	13.0	69.5	9.6
June	13.7	36.6	5.0	110.2	15.1	73.1	10.0	113.9	15.6	122.1	16.7	106.4	14.6
July	12.5	46.7	5.8	120.9	15.1	81.5	10.2	111.1	13.9	133.9	16.7	120.9	15.1
August	13.1	25.1	3.3	125.9	16.5	80.3	10.5	84.9	11.1	121.1	15.9	88.9	11.6
September	11.8	17.4	2.1	158.7	18.7	93.5	11.0	77.2	9.1	92.8	11.0	80.4	9.5
October	11.8	11.9	1.4	73.5	8.7	52.7	6.2	47.0	5.5	43.6	5.1	50.8	6.0
November	12.6	5.0	0.6	78.4	9.9	57.9	7.3	30.4	3.8	25.7	3.2	28.5	3.6
December	15.2	3.1	0.5	91.5	13.9	61.6	9.4	24.1	3.7	20.4	3.1	21.3	3.2
Annual ration		173.2	22.6	1117.1	147.8	721.1	95.3	638.4	83.8	727.1	95.6	636.4	83.2

During the year, the crayfish fed most intensively from May to October, when they consumed in excess of 80% of the annual feed ration estimated with the Bajkov, Elliott and Persson, and Winberg methods and in excess of 60% of the annual ration estimated with the Kogan and Thorpe methods.

The crayfish that were studied throughout the year fed on mixed feed with a decided preference for plant matter (Table 17). The share of plant food varied throughout the year and ranged from 54.6% in April to 96.1% in July. The mean weight of the share of plant matter was 84.8%, while that of animal matter was 15.2%.

TABLE 17

Mean weight share of food types (%)

Month	Food type: plant	animal
March	81.8	18.2
April	54.6	45.4
May	85.1	14.9
June	92.8	7.2
July	96.1	3.9
August	95.2	4.8
September	84.1	15.9
October	89.8	10.2
November	79.9	20.1
December	69.7	30.3

The annual food consumption of the catchable segment of the spinycheek crayfish population in Lake Staw Płociczno calculated with the Elliott and Persson method was 2904.7 kg food (20.6 g m^{-2}), including 2463.2 kg of plant matter (17.5 g m^{-2}) and 441.5 kg of animal matter (3.1 g m^{-2}). The spinycheek crayfish consumed throughout the year 0.27% of the total plant biomass found in the area they inhabited.

The mean effectiveness of the utilization of food matter for body weight gain (K_1) ranged from 5.7% to 37.7% depending on the calculation method applied (Table 18). The figure obtained with the Bajkov method was the highest, while that obtained with the Kogan method was the lowest. The feeding coefficient (FC) (for body wet weight) is the inverse of coefficient K_1, and was, thus, the lowest when estimated with the Bajkov method (2.7), and the highest with the Kogan method (17.4) (Table 18).

TABLE 18

Effectiveness of utilizing food for body weight gain (K_1) and the feeding coefficient (FC)

	K_1 Wet weight (%)	K_1 Energy (%)	Feeding coefficient (FC)
Bajkov	37.7	27.3	2.7
Kogan	5.7	4.2	17.4
Thorpe	8.9	6.5	11.2
Elliott and Persson	10.1	7.4	9.9
Winberg	8.9	6.4	11.2
Predicted	10.2	7.4	9.8

5. DISCUSSION

5.1. SPINYCHEEK CRAYFISH MORPHOMETRIC CHARACTERS

The body sizes attained by the crayfish determine their commercial and utilization values. The larger the crayfish is the more valuable it is. In comparison with other crayfish species inhabiting Polish waters, the spinycheek crayfish is small. According to Kossakowski (1966) and Mastyński (1999), the total length of spinycheek crayfish does not usually exceed 100 mm, although specimens of this species do sometimes attain larger sizes. Kulmatycki (1936), caught a specimen measuring 122 mm in length in Lake Juno, while Krzywosz et al. (1995) caught crayfish measuring 120 mm in Mazurian and Suwałki waters. Leńkowa (1962) caught even larger specimens of spinycheek crayfish, and the largest specimen measured by her was 128 mm in length. The majority of spinycheek crayfish in the studied lakes did not differ substantially from the values above, although there was substantial variation. The crayfish in Lake Staw Płociczno were the smallest with a maximum length not exceeding 105 mm. In Lake Hańcza, the crayfish were larger at a maximum length of 121 mm, while the maximum length of spinycheek crayfish in Lake Dgał Wielki was as long as 130 mm. Such large spinycheek crayfish had not been noted previously in Polish waters. Nevertheless, the largest spinycheek crayfish are much smaller than noble, narrow-clawed or signal crayfish, which often attain total lengths exceeding 150 mm (Leńkowa 1962, Kossakowski 1966, Strużyński 1994, Westman and Savolainen 2002, Souty-Grosset et al. 2006).

The existing data indicate that the size of spinycheek crayfish within a particular habitat is related to the period in which they have inhabited the basin and the composition of its ichthyofauna. Studies conducted in Mazurian and Suwałki lakes indicate that in the first year following initial inhabitation crayfish attained larger sizes than in later periods (Krzywosz et al. 1995). Crayfish under pressure from predatory fish, especially eel, *Anguilla anguilla* (L.), were of a larger size (Krzywosz et al. 1995). The results presented in the current study indicate a similar dependence; in Lake Dgał Wielki, which the crayfish had inhabited for the shortest period and in which the eel population was the largest, the crayfish were the largest.

According to Strużyński (1994), small spinycheek crayfish body size, the effort required to catch them, and problems with transporting them, are the primary causes of the lack of commercial interest in the spinycheek crayfish since the percentage of meat in this species is close to that of indigenous Polish species (Kossakowski 1966, Własow et al. 2002), and the share of protein proper and total protein in the meat of spinycheek crayfish are even higher than in indigenous species (Dabrowski et al. 1966).

Due to their labor intensity, morphometric studies of crayfish are not numerous. Studies of the morphometric characters of crayfish have been conducted as follows: on the noble crayfish by Kossakowski (1962) and Podsiadło and Olech (1994); on narrow-clawed crayfish by Kossakowski (1962) and Andrzejewski et al. (2001); on spinycheek crayfish by Kossakowski (1962) and Chybowski (2000). Some proportions in the spinycheek crayfish were also analyzed by Seligo (1895), Lehmann and Quiel (1927), and Pieplow (1938), and in the noble crayfish by Seligo (1895), Fevolden and Hessen (1989), and Sint et al. (2005). According to Kossakowski (1962), the proportions of the noble, narrow-clawed, and spinycheek crayfish are very similar. Further, in their comparison of narrow-clawed crayfish proportions, Andrzejewski et al. (2001) indicated that there are differences in the proportions of particular populations. These preceding authors all note the highest variability in the proportions related to cheliped size.

The detailed analysis of spinycheek crayfish body proportions presented in the present work indicate that the differences between the studied populations are not substantial (Table 6). The differences noted within the same sex and male form, although very small, are still statistically significant. These differences were detectable only thanks to the large quantity of study material. The differences between females and form I males were substantially larger (Table 6). Form I males have decidedly longer and wider chelipeds and a wider abdomen than did females. These differences are large enough to permit easy, visual differentiation of form I males from females. The body proportions of form II males, although significantly statistically different, are generally close to those of females and did not permit decisively differentiating form II males from females (Table 6).

Most of the proportions studied exhibited high variability (Table 6), and the highest were noted in relation to cheliped size. This variability even exceeded 10%. Among the proportions analyzed, only the variability of total length to abdomen length and to cephalothorax length (TL/AL and TL/CL) in females and form I males was lower than 3%. Variability in the proportions of form II males is distinctly higher than in either females of form I males.

In comparison with female signal, narrow-clawed, and noble crayfish, female spinycheek crayfish have different body proportions (Table 19). With the exception of cheliped length to cheliped thickness (ChL/ChT) in female spinycheek and noble crayfish, total length to cephalothorax length (TL/CL), and total length to anterior cephalothorax length (TL/CfL) in female spinycheek and narrow-clawed crayfish, were statistically significant (Fisher test, P ≤ 0.05). The body proportions of spinycheek crayfish were most similar to those of the female narrow-clawed crayfish.

TABLE 19

Values of mean proportions (M) and variability coefficients (V) for females of four crayfish species

	Spinycheek crayfish[1]		Signal crayfish[2]		Narrow-clawed crayfish[3]		Noble crayfish[4]	
	n = 1772		n=320		n=85		n=26	
Proportion	M	V (%)	M	V (%)	M	V (%)	M	V (%)
TL/AL	1.920[a]	2.5	1.951[b]	5.7	1.915[a]	4.7	2.011[c]	5.1
TL/CL	2.090[c]	2.8	2.059[b]	3.3	2.103[d]	5.2	2.001[a]	6.4
TL/CfL	3.178[c]	3.4	3.007[b]	4.7	3.199[c]	5.3	2.925[a]	2.5
TL/ChL	3.765[c]	9.4	2.749[a]	8.8	3.162[b]	10.6	2.816[a]	6.4
TL/CW	4.217[d]	3.7	4.037[c]	4.9	3.971[b]	7.5	3.828[a]	5.4
TL/ChW	9.285[d]	12.7	6.180[a]	9.3	8.172[c]	14.6	6.230[b]	10.0
AL/AW	2.203[c]	7.7	1.851[a]	10.1	2.048[b]	13.7	1.990[b]	13.3
CL/CW	2.019[c]	3.8	1.962[b]	4.6	1.892[a]	8.4	1.917[a]	5.9
ChL/ChW	2.464[c]	6.6	2.255[a]	8.8	2.586[d]	10.4	2.353[b]	7.0
ChL/ChT	4.287[b]	9.0	4.142[a]	9.6	5.059[c]	10.9	4.417[a]	9.3

1 – Mean value of body proportions of the three studied populations of spinycheek crayfish
2 – Mean values of proportions of signal crayfish from Lake Pobłędzie and the ponds of the Dgał Experimental Hatchery (author's unpublished materials)
3 – Mean values of proportions of narrow-clawed crayfish from Lake Samin and the ponds of the Dgał Experimental Hatchery (author's unpublished materials)
4 – Mean values of the proportions of noble crayfish from the Czarna River and the ponds of the Dgał Experimental Hatchery (author's unpublished materials)
Values with a different letter index in the same row differ significantly statistically (Fisher test, P ≤ 0.05)

In comparison to the signal, narrow-clawed, and noble crayfish, form I and II spinycheek crayfish males of the same total length have longer abdomens, shorter cephalothoraces, shorter anterior cephalothorax segments, narrower cephalothoraces, and shorter and thicker chelipeds (Table 20). These differences were statistically significant (Fisher test, P ≤ 0.05). The most notable differences were in the size of the spinycheek crayfish cheliped, which was much smaller in comparison with the chelipeds of the other crayfish species.

TABLE 20

Values of mean proportions (M) and variability coefficients (V) for males of four crayfish species

Proportion	Spinycheek crayfish[1]				Signal crayfish[2]		Narrow-clawed crayfish[3]		Noble crayfish[4]	
	form I		form II							
	n = 2255		n=290		n=419		n=98		n=109	
	M	V (%)	M	V (%)	M	V (%)	M	V (%)	M	V (%)
TL/AL	1.971[b]	2.8	1.955[a]	3.0	2.039[c]	5.7	2.057[d]	6.0	2.104[e]	5.0
TL/CL	2.033[d]	3.0	2.050[e]	3.3	1.972[c]	3.8	1.957[b]	5.4	1.913[a]	4.3
TL/CfL	3.120[c]	3.7	3.112[c]	4.0	2.922[b]	4.5	3.016[b]	5.1	2.854[a]	4.2
TL/ChL	2.623[d]	10.1	3.364[e]	15.5	2.048[a]	12.3	2.309[c]	22.2	2.162[b]	15.2
TL/CW	4.043[c]	3.8	4.283[d]	5.4	3.841[b]	5.5	3.638[a]	6.9	3.624[a]	6.1
TL/ChW	7.448[d]	9.9	9.912[e]	15.9	4.714[a]	13.9	6.583[c]	19.0	5.388[b]	16.0
AL/AW	2.379[c]	5.6	2.499[d]	6.9	2.111[a]	8.0	2.205[b]	8.4	2.178[b]	9.0
CL/CW	1.989[d]	3.3	2.089[e]	4.8	1.948[c]	4.7	1.861[a]	6.4	1.895[b]	5.2
ChL/ChW	2.845[d]	6.0	2.951[e]	7.0	2.304[a]	7.4	2.883[c]	10.8	2.496[b]	7.3
ChL/ChT	4.655[c]	7.9	4.998[d]	11.2	4.207[a]	8.8	5.420[e]	10.3	4.523[b]	8.8

1 – Mean value of body proportions of the three studied populations of spinycheek crayfish
2 – Mean values of proportions of signal crayfish from Lake Pobłędzie and the ponds of the Dgał Experimental Hatchery (author's unpublished materials)
3 – Mean values of proportions of narrow-clawed crayfish from Lake Samin and the ponds of the Dgał Experimental Hatchery (author's unpublished materials)
4 – Mean values of the proportions of noble crayfish from the Czarna River and the ponds of the Dgał Experimental Hatchery (author's unpublished materials)
Values with a different letter index in the same row differ significantly statistically (Fisher test, $P \leq 0.05$)

Crayfish body weights were correlated with the basic linear body measurements of total length and cephalothorax length. As with other animals, the dependence of crayfish body weight and length was most often presented by a multiplicative equation (Pieplow 1938, Brink et al. 1988, Krzywosz 1994, Kozák and Policar 2001). This dependence in spinycheek crayfish was also best described by a multiplicative equation (Tables 7 and 8). These equations were highly statistically significant ($P < 0.0001$) and fit the empirical data well. Based on these and with data regarding total length or cephalothorax length, crayfish body weight could be estimated precisely. The curves that described this dependency in the studied spinycheek crayfish population overlapped indicating that the dependence between body weight and length was similar in all of the studied populations (Fig. 16-18). However, this dependence was distinctly different in females than it was in form I males and was slightly different from form II males (Fig. 19). The body weight of form I males increased faster than that of females or form II males, which is why form I males at the same body length generally attained a higher body weight. Pieplow (1938), Orzechowski (1984), and Brink et al. (1988) also reported that males had higher body weights than did females. Additionally, Pieplow (1938) indicated that form II males had distinctly lower body weights than did form I males. The results of the present study concur fully with Pieplow's (1938) observations since in each of the analyzed cases form I males had higher body weights than did form II males, while the latter had similar body weights to that of females (Fig. 19).

The condition of female spinycheek crayfish, expressed by the dependence between body weight and total length, was lower than that of female noble or signal crayfish and close to that of the female narrow-clawed crayfish (Table 21, Fig. 20). The condition of form I male spinycheek crayfish, similarly to females, was poorer than that of noble or signal crayfish but almost identical to that of narrow-clawed crayfish males. Form II spinycheek crayfish males were in the lowest condition (Table 21, Fig. 21).

TABLE 21

Parameters of the multiplicative regression equation ($W = b_0 TL^{b_1}$) that best explains the dependence of body weight (W, g) on total length (TL, mm) in females and males of four crayfish species, n – number (specimens). b_0, b_1 – regression coefficient with 95% confidence intervals, SE – standard error, R^2(%) – determination coefficient, $P < 0.0001$

	Species	n	b_0	b_1	SE	R^2(%)
Females	Spinycheek crayfish[1]	1772	0.00002 ± 0.00000	3.09 ± 0.02	1.09	98.0
	Signal crayfish[2]	320	0.00003 ± 0.00001	3.03 ± 0.09	1.09	93.0
	Narrow-clawed crayfish[3]	84	0.00002 ± 0.00000	3.08 ± 0.04	1.09	99.7
	Noble crayfish[4]	26	0.00000 ± 0.00001	3.64 ± 0.60	1.15	86.8
Males	Spinycheek crayfish form I[1]	2255	0.00002 ± 0.00000	3.14 ± 0.02	1.08	96.9
	Spinycheek crayfish form II[1]	290	0.00001 ± 0.00000	3.18 ± 0.04	1.10	98.7
	Signal crayfish[2]	419	0.00000 ± 0.00000	3.55 ± 0.10	1.14	92.1
	Narrow-clawed crayfish[3]	98	0.00001 ± 0.00000	3.24 ± 0.05	1.11	99.3
	Noble crayfish[4]	109	0.00000 ± 0.00000	4.03 ± 0.19	1.16	94.5

1 – Three studied populations of spinycheek crayfish

2 – Signal crayfish from Lake Pobłędzie and the ponds at the Dgał Experimental Hatchery (author's unpublished materials)

3 – Narrow-clawed crayfish from Lake Samin and the ponds of the Dgał Experimental Hatchery (author's unpublished materials)

4 – Noble crayfish from the Czarna River and the ponds at the Dgał Experimental Hatchery (author's unpublished materials)

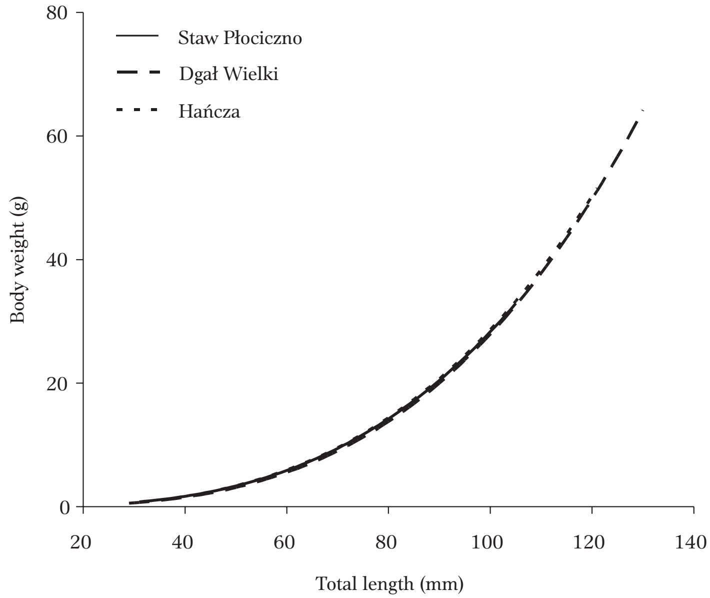

Fig. 16. Relationship between body weight and total length in female spinycheek crayfish from lakes Staw Płociczno, Dgał Wielki, and Hańcza.

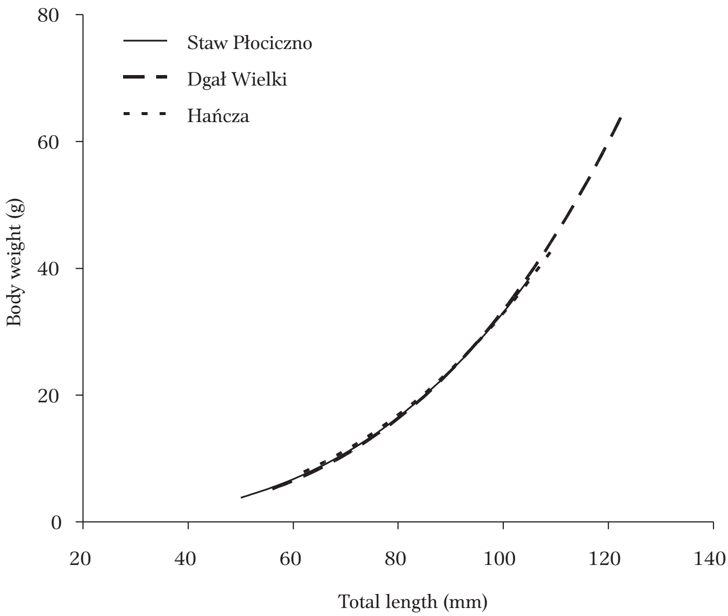

Fig. 17. Relationship between body weight and total length in form I male spinycheek crayfish from lakes Staw Płociczno, Dgał Wielki, and Hańcza.

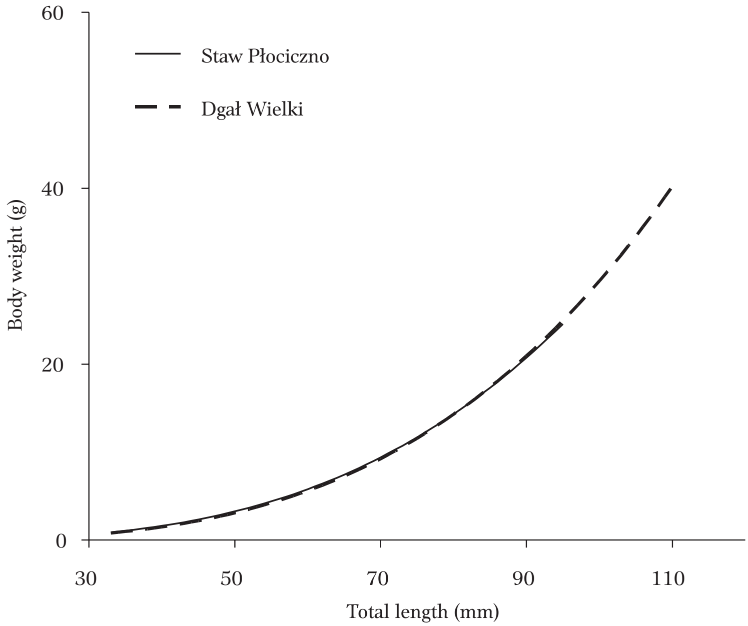

Fig. 18. Relationship between body weight and total length in form II male spinycheek crayfish from lakes Staw Płociczno and Dgał Wielki.

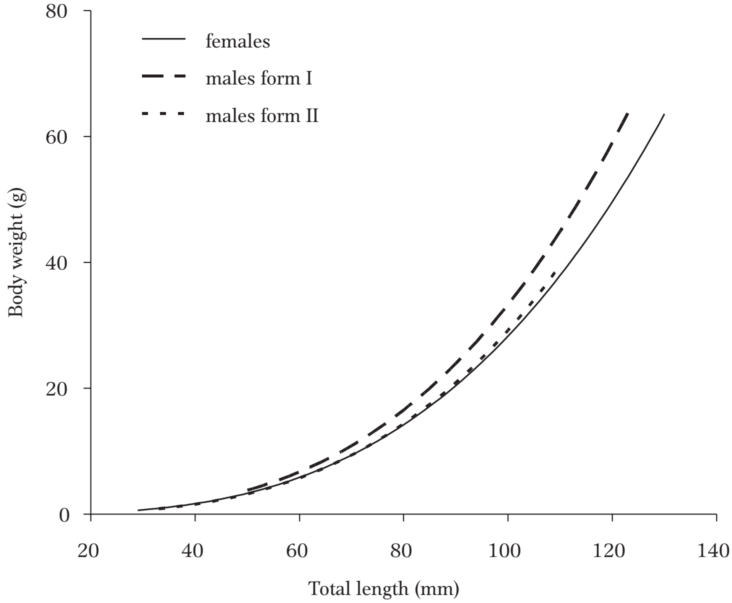

Fig. 19. Relationship between body weight and total length in spinycheek crayfish.

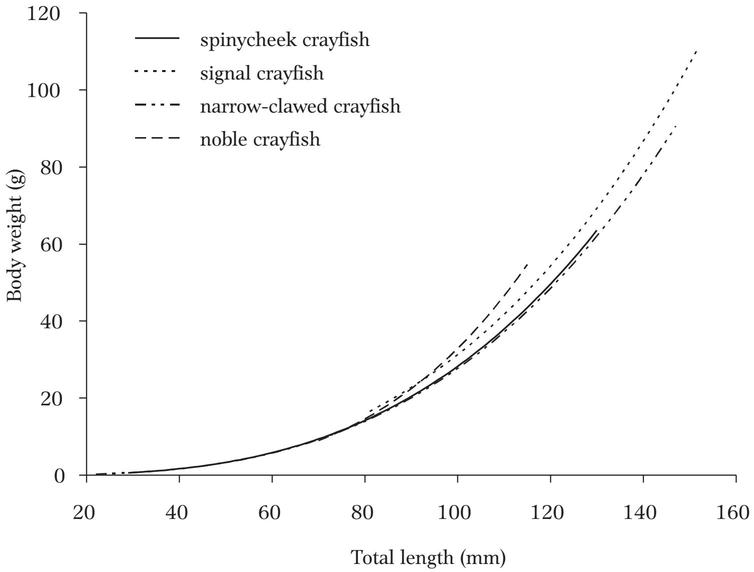

Fig. 20. Relationship between body weight and total length in females of four crayfish species: spinycheek crayfish from lakes Staw Płociczno, Dgał Wielki, and Hańcza (current work); signal crayfish from Lake Pobłędzie and the ponds at the Dgał Experimental Hatchery (author's unpublished materials); narrow-clawed crayfish from Lake Samin and the ponds at the Dgał Experimental Hatchery (author's unpublished materials); noble crayfish from the Czarna River and the ponds at the Dgał Experimental Hatchery (author's unpublished materials).

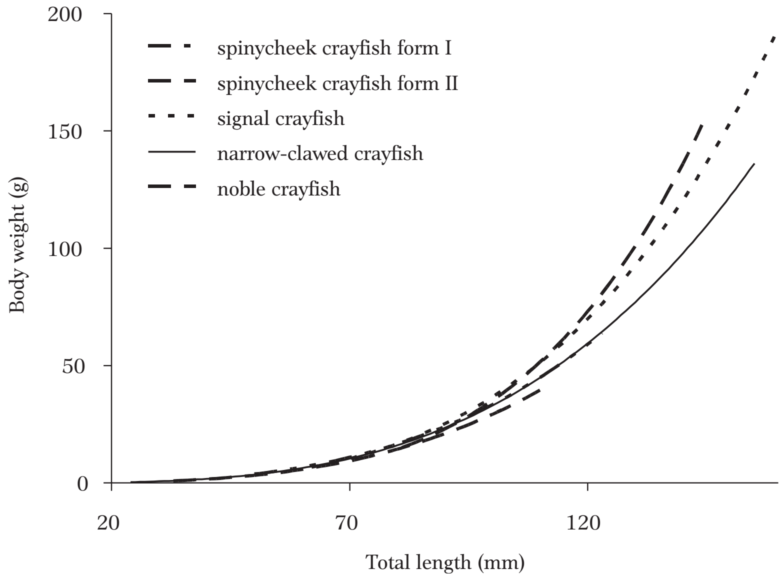

Fig. 21. Relationship between body weight and total length in males of four crayfish species: form I spinycheek crayfish males from lakes Staw Płociczno, Dgał Wielki, and Hańcza (current work); form II spinycheek crayfish males from lake Staw Płociczno and Dgał Wielki (current work); signal crayfish from Lake Pobłędzie and the ponds at the Dgał Experimental Hatchery (author's unpublished materials); narrow-clawed crayfish from Lake Samin and the ponds at the Dgał Experimental Hatchery (author's unpublished materials); noble crayfish from the Czarna River and the ponds at the Dgał Experimental Hatchery (author's unpublished materials).

The total length of crayfish was related strongly to cephalothorax length. This dependency was best expressed by linear equations (Table 9), which were very well fitted to the empirical data. Both Stypińska et al. (1978) and Brink et al. (1988) described this dependence in spinycheek crayfish as linear. Romaire et al. (1977), in turn, determined a linear dependency between total length and cephalothorax length in two other crayfish from the genus Procambarus. Knowledge of this dependency might be useful when taking measurements of crayfish. Total length, measured from the tip of the rostrum to the end of the abdomen, is the most frequently used parameter to describe crayfish size. The abdomen and the fins at the end of it are mobile, and when live crayfish are measured errors occur caused by the curling or curving of the abdomen. Measurements of the cephalothorax are more precise since it is a fixed, stiff structure. The equations presented above can be used to calculate easily and precisely total length based on measurements of the cephalothorax.

The chelipeds of crayfish grow faster proportionally than does total length or cephalothorax length. This was described by Pieplow (1938) in spinycheek crayfish, by

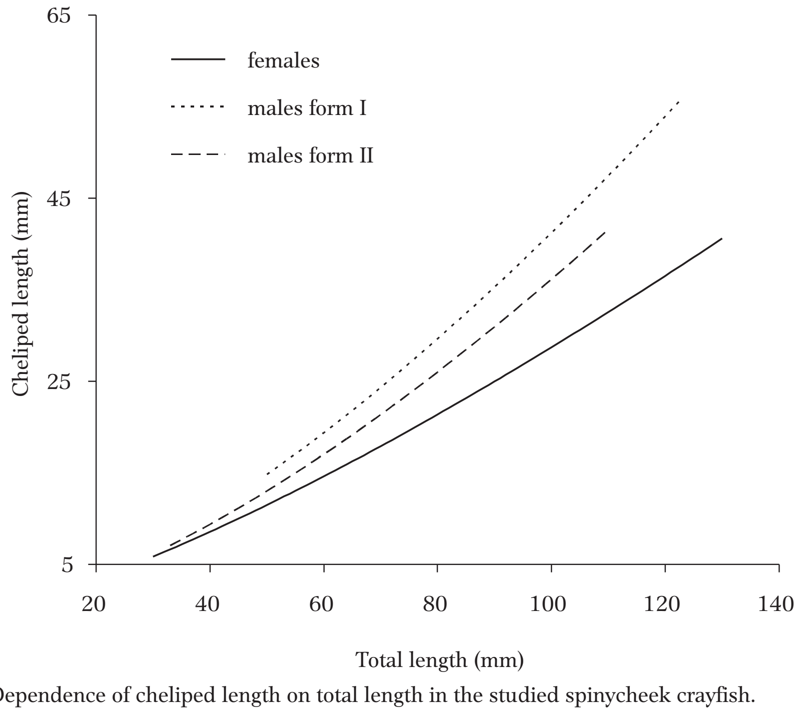

Fig. 22. Dependence of cheliped length on total length in the studied spinycheek crayfish.

Kossakowski (1967) in narrow-clawed crayfish, and by Metelski et al. (1980) in noble crayfish. The chelipeds of the spinycheek crayfish from the present study also grew faster proportionally than did total length and cephalothorax length. This growth is well described by a multiplicative equation (Tables 10 and 11). The chelipeds of form I males were larger than those of form II males and females (Fig. 22).

5. 2. STRUCTURE AND INDEXES OF THE CATCHABLE PORTION OF THE SPINYCHEEK CRAYFISH POPULATION

The share of females and males in the catchable segment of the population does not always adequately reflect the actual sex ratio in the entire population since the share caught is often related to the type of gear applied and the catch method (Brink et al. 1988, Cukerzis 1989, Anwand 1993, Krzywosz et al. 1995). Catches made with crayfish traps catch decidedly more males than females. The share of males in this type of catch can be as high as 98% (Krzywosz et al. 1995). In turn, towed gear such as seines catch decidedly more females. For example, the share of females in trap and seine catches in Lake Okrągłe in the Suwałki district was 2% and 40%, respectively (Krzywosz et al. 1995). Generally, the sex disproportion in catches made with trap and towed gear can be explained by the greater aggression, mobility, and strength of males, which, once having found food in a trap, do not allow in smaller and weaker females. This phenomenon does not occur during catches with seines, which are less selective and capture all crayfish encountered. Thus, it can be assumed that the sex ratio determined using towed gear is closer to that in reality. In the present work, the sex ratio of the spinycheek crayfish was determined based on the share of females and males caught with towed (seine) and trap (fyke net frame) gears. Although the fyke net frame is a type of trap gear, it is not as selective at crayfish traps as it catches passively without using bait. This is also why the results of the sex ratio of the catchable segment of the spinycheek crayfish population was not related to the catch method. The share of females among the spinycheek crayfish caught with seines was only slightly higher (45.2%) than that caught with the fyke net frame (40.9%). In his study of crayfish from Lake Wdzydze, Kossakowski (1961) determined the share of females was 46%, while Orzechowski (1984) reported it to be 44% in the Koronowski Reservoir. The results of the present author's own studies and those of the cited authors are similar, and they all oscillate at just above 40%.

The size structures of the catchable segment of the crayfish population caught with fyke net frames and seines were slightly dissimilar. Typically, fyke net frame catches had a nearly zero share of crayfish with a total length of less than 51 mm (Fig. 9), while in catches made with seines crayfish of this size occurred regularly (Fig. 10).

The majority of the crayfish caught in the fyke net frame exceeded 60 mm in length, while all sizes were caught with seines (Figs. 9, 10). Deploying seines and fyke net frames in addition to traditional crayfish traps permitted collecting study material that included nearly the entire size range occurring in the lake. It does appear, however, that the size structure presented is a reliable reflection of the structure of only the larger group of the natural population. This hypothesis is confirmed by the results of a study of the catchable segment of a noble crayfish population reported by Cukerzis (1989), in which the catches were always dominated (80-90%) by larger, older crayfish.

The individual absolute fecundity of female spinycheek crayfish in Lake Staw Płociczno ranged from 56 to 431 eggs for females weighing from 4.7 g to 23.4 g and from 138 to 926 eggs for females from Lake Dgał Wielki that weighed from 3.3 g to

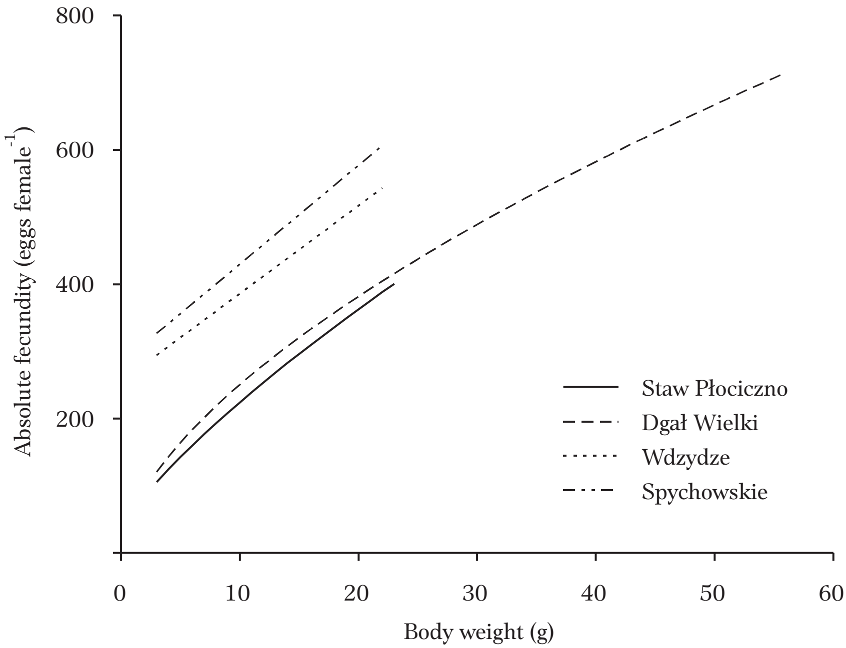

Fig. 23. Dependence of individual absolute fecundity with body weight of female spinycheek crayfish from lakes Staw Płociczno and Dgał Wielki (current work), Wdzydze (Stypińska 1978), and Spychowskie (Stypińska 1978).

56.0 g. To date, the individual absolute fecundity of spinycheek crayfish in Polish waters has ranged from 290 to 685 eggs (Stypińska 1972, 1973, 1978). In North American waters, Smith (1981) determined that fecundity ranged from 57 to 440 eggs. Although the individual absolute fecundity attained by females from Lake Dgał Wielki was larger than that noted to date in Poland, it was substantially lower than that of spinycheek crayfish of the same size from lakes Wdzydze and Spychowskie (Stypińska 1978) and Dąbie (Schulz and Smietana 2001) (Fig. 23 and 24). However, the fecundity of the Lake Dgał Wielki females was similar to that of females in the Koronowski Reservoir (Orzechowski 1984) (Fig. 25). The mean individual absolute fecundity of female spinycheek crayfish from Lake Staw Płociczno (247 eggs) was lower than the mean individual fecundity of females from Lake Dgał Wielki (499 eggs), and the difference was statistically significant (Fisher test, $P \leq 0.05$). According to Leńkowa (1962), Kossakowski (1966), Stypińska (1973), and Schulz and Smietana (2001), spinycheek crayfish in Poland attain sexual maturity earlier (as soon as in the first or second year of life), and their mean absolute fecundity is higher than that of noble or narrow-clawed crayfish. However, signal and spinycheek crayfish are similarly fecund,

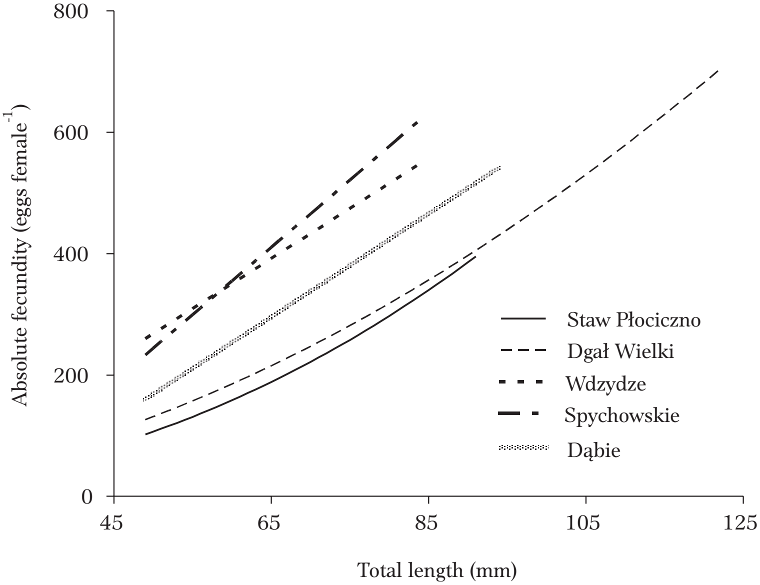

Fig. 24. Dependence of individual absolute fecundity on total length of female spinycheek crayfish from lakes Staw Płociczno and Dgał Wielki (current work), Wdzydze (Stypińska 1978), Spychowskie (Stypińska 1978), and Dąbie (Shulz and Smietana 2001).

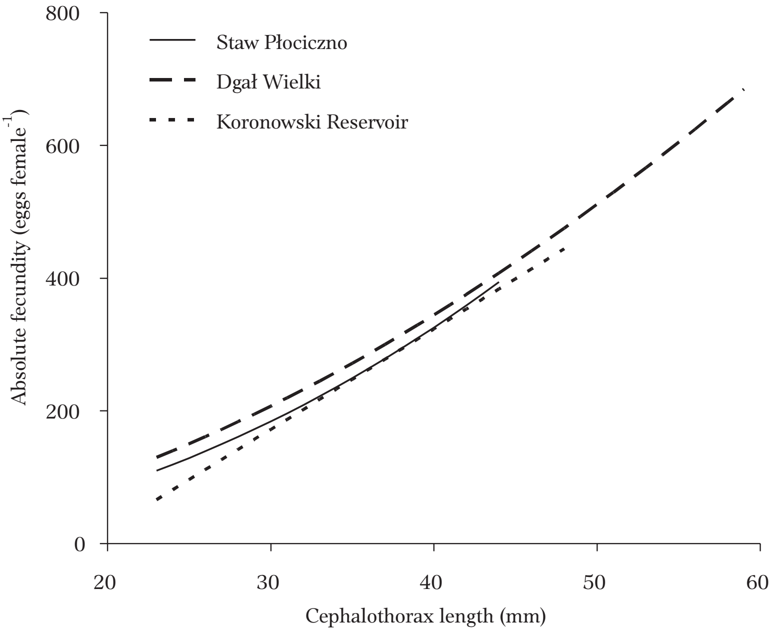

Fig. 25. Dependence of individual absolute fecundity of spinycheek crayfish females on cephalothorax length from lakes Staw Płociczno and Dgał Wielki (current work) and the Koronowski Reservoir (Orzechowski 1984).

even though spinycheek crayfish attain sexual maturity in the first or second year of life and signal crayfish attain it in the second or third year of life (Krzywosz 1994).

As do all the other crayfish species occurring in Polish waters, the spinycheek crayfish mates in the fall from September to November. At this time, however, the male only passes his sperm to the female's spermatheca. Fertilization does not occur until the spring (in April at the earliest), when the female deposits mature eggs on her abdomen. If a female spinycheek crayfish loses the sperm or did not mate in the fall, it can do so again in the spring (Ulikowski and Borkowska 1999, Chybowski and Juchno 2002). Fertilization and egg deposition occurs immediately in the fall in the three other crayfish species (noble, Galician, signal) that inhabit Polish waters. The egg incubation period in spinycheek crayfish lasts only 5-6 weeks (April and May), and not 5-6 months (November - April), as is the case with the other crayfish species. Attaining sexual maturity earlier, the higher absolute fecundity, and the shorter incubation time ensure that the spinycheek crayfish is a more successful breeder.

The biomass of the catchable segment of the population of spinycheek crayfish in Lake Staw Płociczno was 32.3 kg ha^{-1} (2690 indiv. ha^{-1}) of the area inhabited by the crayfish. The biomass estimated by Krzywosz et al. (1995) in over a dozen lakes in the Mazurian and Suwałki districts ranged from 28.9 to 58.1 kg ha^{-1} (1600-5105 indiv. ha^{-1}), while the biomass analyzed by Orzechowski (1984) in the Koronowski Reservoir ranged from 60.0 to 3100.0 kg ha^{-1} (to 720000 indiv. ha^{-1}). The results obtained for Lake Staw Płociczno coincide with those reported by Krzywosz et al. (1995), who, as in the present study, estimated the crayfish biomass in natural basins using the Petersen method. The estimations by Orzechowski (1984), performed in an artificial dam reservoir with another calculation method, were disproportionally large and appear to be incomparable to the results of the current work.

5.3. SPINYCHEEK CRAYFISH FEEDING INTENSITY

The index of stomach fullness, which was considered to be the measure of feeding intensity, was highly variable in the studied spinycheek crayfish in both daily and annual cycles. The lowest mean stomach fullness index was confirmed at the lowest water temperature in March, while the highest was noted at the highest water temperature in July. Białokoz (1997) noted similar stomach fullness intensity variability in fish (silver carp, *Hypophthalmichthys molitrix* (Val.), roach, *Rutilus rutilus* (L.), perch, *Perca fluviatilis* L.) that consume neutral and low caloric food, which is similar to crayfish food. However, the dependency between the mean stomach fullness index and water temperature in spinycheek crayfish was not unequivocal. In October, when the water temperature was only 9.4°C, this index was as high as 11.2‰ body wet weight and was just slightly less than the figure from July when the water temperature was 19.8°C (11.4‰ body wet weight) and was substantially higher than it was in August at a temperature of 18.0°C (7.0‰ body wet weight) (Table 14). Despite irregular fluctuations of this index with water temperature, a statistically significant dependence was determined. This dependence, however, was loaded with relatively high error and had a low determination coefficient, which indicated that the size of the stomach fullness index, especially during the spring and early autumn, can be affected by other factors. It appears that in spinycheek crayfish the physiological state of the animal (moulting, mating period, egg deposition) has the greatest impact on the value of the stomach fullness index. This supposition is clearly supported by the substantial decrease in the index in August, when both males and females moult synchronously. The disproportionally small increase in this index noted in May at high water temperatures might also be related to the physiological state of the crayfish. Some females already deposit their eggs in May, while others mate again (Ulikowski and Borkowska 1999, Juchno and Chybowski 2003). In turn, some males underwent the first spring moult, while others were mating (Ulikowski and Borkowska 1999, Chybowski and Juchno 2002). In late fall and winter the stomach fullness index decreases as the water temperature decreases. During this period, when water temperatures are low, it is in fact water temperature that is the decisive factor influencing the value of the stomach fullness index. The spinycheek crayfish does not feed in winter from January to March, and their stomachs are practically empty during this period (Table 16).

Daily variability in the stomach fullness index is linked to the daily activity patterns of the crayfish. According to Kossakowski (1966), Cukerzis (1989), Strużyński (1994), and Lozan (2000), the crayfish are active both nocturnally and during the day, however, they are decidedly more active at night. Higher nocturnal crayfish activity is noted, among other factors, in the more intense feeding that occurs at night. The stomach fullness index of the studied spinycheek crayfish was most often at the maximum at night, while during the day it was at its minimum (Fig. 14). Thus, these crayfish fed mostly in the evening and at night.

The gastric evacuation time varied throughout the year and ranged from 15.7 h in July when the water temperature was 19.8°C to 393.6 h in March when the water temperature was 3.2°C. Evacuation time exhibited a strong negative statistically significant dependence on water temperature. This dependence was exponential in character and was well fitted to the empirical data. The high value of the determination coefficient (R^2(%) = 91.6) indicates that there is little impact from other factors. The dependence between evacuation time and water temperature might also be of another character. Loya-Javellana et al. (1995) confirmed a linear dependence between evacuation time and water temperature in the crayfish *Cherax quadricarinatus* fed daily and an arcus sinus dependence in the same crayfish when they were fed every second day. Unfortunately, no descriptions of gastric evacuation in crayfish in natural conditions were found in the available literature. This dependence has been studied much more frequently in fish, and it can be linear (Prejs 1978), multiplicative (Molnar et al. 1967, Białokoz 1997), or exponential (Elliott 1972, Persson 1979, Białokoz 1997) and depends mainly on the type of food consumed.

The stomach fullness index is one of the factors that can have an impact on the evacuation time. The dependence between evacuation time and the stomach fullness in fish has been confirmed by, among others, Prejs (1978) and Białokoz (1997). In the current work, no statistically significant dependence between these factors was observed.

The daily food ration of the spinycheek crayfish in Lake Staw Płociczno fluctuated substantially throughout the year with the highest values in the summer period and the lowest in March. The daily food rations calculated with the Kogan and Thorpe methods were the highest in May (55.5‰ and 28.2‰ body wet weight, respectively) and in September (63.0‰ and 36.1‰ body wet weight, respectively) (Table 15), while those calculated with the Bajkov and Elliot and Persson methods were 11.4‰ and 39.3‰ body wet weight, respectively, in June and 17.4‰ and 38.4‰ body wet weight, respectively, in July (Table 15). In August, the daily ration calculated with the Kogan, Thorpe, and the Elliot and Persson methods were disproportionally low in comparison with July and September. This fact, similarly to the stomach fullness index, can be explained by the physiological state of the spinycheek crayfish. In August, the crayfish moult synchronously and food consumption is significantly limited by it.

The results obtained with the Bajkov and Elliot and Persson methods, which determine the daily food ration based on gastric evacuation time, the largest daily food ration was noted in months when the gastric evacuation period was the fastest. However, with the Kogan and Thorpe methods, in which the daily food ration is based on daily fluctuations in the fullness index, the largest daily food ration is noted in months when maximum daily decreases in fullness index were the highest.

The daily food ration required for sustenance was calculated with the Winberg method and was the highest in July at the highest water temperature (44.5‰ body wet weight) and the lowest at the lowest water temperature (0.8‰ body wet weight) (Table 15), because water temperature was the only influential factor on variability.

The daily food ration calculated with the Bajkov method was much lower than the values calculated with the other methods. The formula used to calculate the daily food ration with the Bajkov method does not employ the widely used multipliers that level the differences between the period of full evacuation and the actual evacuation period. Applying an additional multiplier, for example 3, would increase the value of the daily ration calculated with this method to the values calculated with the remaining methods.

The comparison of daily food ration calculated with the methods presented above permits designating the Elliott and Persson method as the most applicable for the needs of calculating the daily food ration of the spinycheek crayfish. This method assumes that evacuation time from stomach is exponential, which was confirmed for spinycheek crayfish in the current work, and takes into consideration the periodic, actual stomach fullness index. The disadvantages of this method are that it is both time and labor intensive.

The daily ration calculated with the Elliott and Persson method was strongly correlated with the mean daily stomach fullness index and water temperature. This permitted creating empirical formulae that allowed making quite accurate predictions of the daily food ration based on the same fullness index ($RdP = 1.483\ If^{1.238}$, $SE = 1.60$, $R^2(\%) = 74.5$, $P = 0.0013$). The predictions were more accurate when based on water temperature ($RdP = 0.567\ t^{1.383}$, $SE = 1.27$, $R^2(\%) = 93.2$, $P < 0.0001$), and very accurate when based on these two factors together ($\ln RdP = 0.397 + 0.094\ t + 0.614 \ln If$, $SE = 0.11$, $R^2(\%) = 98.7$, $P < 0.0001$). Formulas that permitted predicting the daily food ration based on the fullness index and water temperature fit the empirical data very well (Fig. 15). This was confirmed by the t-test (method of paired comparisons), which did not indicate statistically significant differences ($\alpha = 0.05$, $P = 0.98$) between the predicted and observed values. It is thus possible to assume that the prediction of the daily food ration based on the stomach fullness index and water temperature is accurate and greatly simplifies calculating the daily food ration of the spinycheek crayfish.

To date, the daily food ration of spinycheek crayfish has only been studied under laboratory conditions. The daily food ration of spinycheek crayfish fed clams at a water temperature of 20°C was studied by Simon and Garnier-Laplace (2005). They estimated that this ration to be 39‰ body wet weight. In turn, Staszak and Szaniawska (2006) estimated the daily food ration of crayfish fed green algae at a water temperature of 12°C was 43.77 J $indiv.^{-1}\ h^{-1}$, which was approximately 42‰ body wet weight, and at 18°C it was 50.88 J $indiv.^{-1}\ h^{-1}$, which was approximately 49‰ body wet weight. Although these food rations were obtained under laboratory conditions and with a different type of food, the values are close to the daily rations calculated in the current paper.

The annual food ration of the spinycheek crayfish was calculated with data obtained with the Elliott and Persson method and was 638% body wet weight (Table 16). The results obtained with other calculation methods were highly divergent and ranged from 173% body wet weight (calculated with the Bajkov method) to 1117%

body wet weight (calculated with the Kogan method) (Table 16). Crayfish fed the most intensely from May to October, and during this period they consumed more than 80% of the annual food ration as calculated with the Elliott and Persson method.

The spinycheek crayfish in Lake Staw Płociczno fed primarily on plant matter. The mean weight of plant matter in the stomach contents was 84.8%, while animal matter comprised 15.2%. In particular , the share of plant matter in the food fluctuated, but it never decreased below 50% (Table 17). According to Pieplow (1938), Kossakowski (1966), Anwand (1993), MacIsaac (1994), Anwand and Valentin (1996), as well as Reynolds and O'Keeffe (2005), crayfish are omnivores although their diet is dominated decisively by plant matter. Pieplow (1938) also determined that in early spring, spinycheek crayfish feed mostly on animal matter, in early summer plant matter has the advantage, while later the diet becomes mixed. It is Momot's (1995) opinion that crayfish feed primarily on animal matter. The results presented in the current paper are to closest to the thesis proposed by Pieplow (1938), because in spring the share of animal food in the diet of crayfish from Lake Staw Płociczno was the highest and later it decreased distinctly over the course of the summer. Aquatic plants, which are the primary food of spinycheek crayfish, also proved a habitat for invertebrate organisms, which sometimes even occur in significant quantities (Soszka 1975). This, it would appear that under natural conditions crayfish consume plant matter along with the attached invertebrate organisms, and that the high density of these animals may be decisive in the weight share of animal food in the crayfish diet.

The biomass of the studied spinycheek crayfish population was 3.2 g m^{-2} of the area inhabited by the crayfish. Annually, the population consumed 20.6 g m^{-2} of food, including 17.5 g m^{-2} of plant matter. This comprised just 0.27% of the aquatic plant wet weight found in the zone inhabited by the crayfish. Substantially more aquatic vegetation is consumed by other aquatic invertebrates. Kornijów (1994) estimated that they consume from 2.5% to 20.3% of the total vegetation biomass. There are, however, data from the literature that crayfish can reduce radically the amount of aquatic vegetation. According to Lodge and Lorman (1987), one adult *Orconectes rusticus* crayfish with a biomass of 19 g living in one square meter is capable of reducing 64% of the vegetation, and crayfish with a biomass of 140 g m^{-2}, can within seven days eliminate totally vegetation. According to Flint and Goldman (1975), signal crayfish with a biomass exceeding 69 g m^{-2} reduce decisively the biomass of macrophytes. In the case of other herbivores, such as grass carp, *Ctenopharyngodon idella* (Val.) substantial reductions in vegetation biomass occur when the biomass of the herbivores is at least 1% that of the aquatic vegetation (Krzywosz 1997). In Lake Staw Płociczno, the crayfish biomass was in excess of twenty fold lower than that reported by Flint and Goldman (1975). Simultaneously, it comprised just 0.05% of the plant biomass, which was twenty fold lower than the biomass that Krzywosz (1997) reported as critical for aquatic vegetation in the case of herbivorous fish. Thus, it can be assumed that in the studied lakes the quantity of plant matter consumed by the spinycheek crayfish does not have a significant impact on the biomass of the vegetation. Simultaneously, the food composition and annual rhythm of spinycheek crayfish feeding refutes the commonly held belief concerning the negative impact these crayfish have on the ichthyofauna through the consumption of fish eggs in spawning grounds. No fish eggs were noted in the stomachs of the studied crayfish, even though the crayfish samples were collected during the perch, roach, bream, *Abramis brama* (L.) and rudd, *Scardinius erythrophthalmus* (L.) spawning season directly from the spawning grounds. Pieplow (1938), Sakowicz and Kompowski (1962) as well as Savino and Miller (1991), all of whom studied the food of spinycheek crayfish, concluded that although fish eggs did occur in the food of the crayfish, they were incidental and were not a constant component of the crayfish diet. More frequently, crayfish are food for fish and are a preferred prey item of eel (Draganik 1962, Blake and Hart 1995, Tulonen et al. 1998), European wels, *Silurus glanis* L. (Czarnecki et al. 2003), perch (Terlecki 1987, Tulonen et al. 1998, Svensson 1992, Blake and Hart 1995, Dubois et al. 1999), ruffe, *Gymnocephalus cernuus* (L.) (Tulonen et al. 1998), burbot, *Lota lota* (L.) (Tulonen et al. 1998), and even roach (Blake and Hart 1995, Tulonen et al. 1998).

6. CONCLUSIONS

1. In Poland, spinycheek crayfish attain smaller body sizes than do noble, narrow-clawed, or signal crayfish.
2. At the same total length, spinycheek crayfish females have a longer abdomen, shorter cephalothorax, shorter anterior cephalothorax segment, and shorter chelipeds than do form I and II males. The chelipeds of the females are narrower than those of form I males, but wider than those of form II males.

3. At the same total length, form II spinycheek crayfish males have a longer abdomen, a shorter cephalothorax, a longer anterior cephalothorax segment, and shorter, narrower, and heavier chelipeds than do form I males.
4. The body proportions of the spinycheek crayfish differ from those of the noble and signal crayfish, but they are nearly identical to those of the narrow-clawed crayfish.
5. At the same total length, the mean absolute fecundity of the spinycheek crayfish from Lake Staw Płociczno was substantially lower than that of the spinycheek crayfish from Lake Dgał Wielki.
6. The catchable biomass of the studied population of spinycheek crayfish was within the range calculated for crayfish inhabiting other Mazurian and Suwałki lakes.
7. The stomach fullness index, food evacuation period, and daily food ration exhibited strong dependencies on water temperature. No statistically significant dependence was noted between evacuation time and the stomach fullness index.
8. Of the five methods tested for calculating the daily food ration, that by Elliott and Persson (1978) occurred to be the most applicable for calculating the ration for spinycheek crayfish.
9. There was a very strong dependence between the daily food ration of the crayfish and the stomach fullness index and water temperature, which permitted estimating the daily ration based on the following equation: $\ln RdP = 0.397 + 0.094\,t + 0.614 \ln If$, where RdP – predicted daily food ration (‰ body wet weight), If – mean stomach fullness index (‰ body wet weight), t – water temperature (°C).
10. The crayfish fed most intensely from May to October, during which period they consumed in excess of 80% of the annual food ration.
11. The primary food of the spinycheek crayfish was plant matter since the mean share of plants in the crayfish food was more than 80%.
12. Annually, the spinycheek crayfish population from Lake Staw Płociczno consumed barely 0.27% wet weight of the aquatic vegetation located in the crayfish area of occurrence. Thus, they could not have had a significant impact on the plant biomass.
13. The spinycheek crayfish in the studied basin did not feed on fish eggs. No such food was noted in the stomach content of the studied crayfish even though the specimens studied were collected during the perch, roach, bream, and rudd spawning season directly from the spawning grounds.

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7. SUMMARY

The subject of the study was three populations of spinycheek crayfish, *Orconectes limosus* (Raf.) from lakes Staw Płociczno, Dgał Wielki, and Hańcza. The study material was collected in 1999-2003. The mean total length (TL) of female and male (forms I and II) spinycheek crayfish was the smallest in Lake Staw Płociczno (75.3, 78.3, 68.1 mm, respectively) and the largest in Lake Dgał Wielki (95.7, 95.8, 75.5

mm). It was also in the latter lake that a crayfish of the longest ever recorded total length (130 mm) was caught. The analysis of the spinycheek crayfish body proportions confirmed there is a small, yet significant, difference between the studied populations of spinycheek crayfish (Table 6). Generally, body proportions of form II males are close to those of females, while those of form I males differ decidedly from those of females and form II males. The body proportions of female and male spinycheek crayfish differed from those of signal crayfish, *Pacifastacus leniusculus* Dana, narrow-clawed crayfish, *Astacus leptodactylus* Esch., or noble crayfish, *Astacus astacus* (L.), and these differences were statistically significant (Tables 19 and 20). Crayfish body weight was correlated with total length and cephalothorax length. This dependence in the spinycheek crayfish was best described by multiplicative equations (Tables 7 and 8). Form I males that were the same size as females and form II males were usually heavier (Fig. 19). The body weight of female spinycheek crayfish that were the same size as their counterparts were lower than that of female noble or signal crayfish and close to that of female northern crayfish (Table 21, Fig. 20). Form I male spinycheek crayfish were lighter than noble and signal crayfish of the same body size (Table 21, Fig. 21). The chelipeds of form I males were larger than those of form II males and females (Table 10 and 11, Fig. 22).

The mean share of females in the catchable segment of the population of spinycheek crayfish was 40.9% when catches were made with fyke net frames and 45.2% when made with seines. The mean total length of the crayfish caught with fyke net frames was 80.5 mm, which was statistically significantly higher than the mean body length (75.2 mm) of the crayfish caught with seines. The crayfish caught with fyke net frames were dominated by individuals with a total body length range of 81 to 90 mm (Fig. 9), while those caught with seines measured from 71 to 80 mm (Fig. 10).

The individual absolute fecundity of spinycheek crayfish in Lake Staw Płociczno ranged from 56 to 431 eggs, while in Lake Dgał Wielki it was from 138 to as much as 926 eggs. The mean individual absolute fecundity of female spinycheek crayfish from Lake Staw Płociczno was 247 eggs and was statistically significantly higher than the mean individual fecundity of females from Lake Dgał Wielki (499 eggs).

The biomass of the catchable part of the spinycheek crayfish population in Lake Staw Płociczno was 32.3 kg ha^{-1} of surface area inhabited by them.

The stomach fullness index exhibited high variability in both daily and yearly cycles. The lowest mean stomach fullness index was determined at the lowest water temperature in March, while the highest was noted at the highest water temperature in July. The dependence of the stomach fullness index on water temperature was determined to be statistically significant. The daily variability in the stomach fullness indices of the studied crayfish resulted from varied levels of crayfish activity throughout the daily cycle. The stomach fullness index of the studied spinycheek crayfish generally reached the maximum at night, and was at the minimum during the daytime (Fig. 14), which indicates that they fed primarily in the evening and at night. The gastric evacuation time varied throughout the year and ranged from 15.7 h in July when the water temperature was 19.8°C to 393.6 h in March when the water temperature was 3.2°C (Table 14). There was a strong negative statistically significant dependence with water temperature. This dependence was exponential and fit well with the empirical data. The daily food ration of the spinycheek crayfish in Lake Staw Płociczno was highly variable throughout the annual cycle. The daily food rations calculated with the Kogan and Thorpe methods were the highest in May (55.5 and 28.2‰ body wet weight, respectively) and in September (63.0 and 36.1‰ body wet weight, respectively; Table 15). However, when calculated with the Bajkov or Elliot and Persson methods, it was the highest in June (11.4 and 39.3‰ body wet weight, respectively) and July (17.4 and 38.4‰, body wet weight, respectively; Table 15). In August, when the crayfish moult synchronously, the daily feed ration decreased, and in September increased again. This variability in the daily feed ration was not noted when it was calculated with the

Winberg method (Table 15) since this method of calculating the daily feed ration depends exclusively on water temperature. The comparison of the daily feed rations calculated with the chosen methods indicated that the Elliott and Persson method was the best suited for calculating the daily feed ration of spinycheek crayfish. This method assumes the that gastric evacuation time is exponential, and this was confirmed for spinycheek crayfish in the present work and it takes into consideration the actual daily variability in the stomach fullness indexes. The disadvantage of this method is that it is both highly time consuming and labor intensive.

The daily feed ration was also correlated with both the mean daily stomach fullness index and water temperature. This permitted creating empirical formulas that allowed forecasting the daily ration based on simple measurements. The daily feed ration can be forecast quite precisely based only on the stomach fullness index ($RdP = 1.483\ If^{1.238}$, SE = 1.60, $R^2(\%) = 74.5$, P = 0.0013), much more precisely based on water temperature ($RdP = 0.567\ t^{1.383}$, SE = 1.27, $R^2(\%) = 93.2$, $P<0.0001$), and highly precisely based on these two parameters together ($\ln RdP = 0.397 + 0.094\ t + 0.614 \ln If$, SE = 0.11, $R^2(\%) = 98.7$, $P < 0.0001$). Equations that permit forecasting the daily ration based on the stomach fullness index and water temperature was fit very well to the empirical data (Fig. 15). Thus, it can be assumed that forecasting the daily feed ration based on the stomach fullness index and water temperature is precise and simplifies significantly calculating the daily feed ration in spinycheek crayfish.

The annual food ration of spinycheek crayfish calculated based on data obtained with the Elliott and Persson method was 638% of body wet weight. Results of the annual food ration varied widely depending on the method applied and ranged from 173% of body wet weight as calculated with the Bajkov method to 1117% of body wet weight when calculated with the Kogan method (Table 16).

The spinycheek crayfish in Lake Staw Płociczno fed intensively from May to October, when they consumed more than 80% of the annual food ration calculated with the Elliott and Persson method. They fed primarily on plant matter, and the mean share of plant matter in the diet was 84.8%, while animal matter comprised 15.2%. The contribution of plant matter to the food composition varied by month but did not, however, drop beneath 50% (Table 17). Annually, the crayfish population consumed 20.6 g m^{-2} of food, of which 17.5 g m^{-2} was plant matter. This was barely 0.27% of the wet weight of the aquatic vegetation in the zone inhabited by the crayfish.

The food composition and annual feeding rhythm of the spinycheek crayfish debunks the belief that these animals feed on fish eggs as none were noted in the stomachs of the crayfish samples caught during the spawning period of perch, roach, bream, and rudd.

8. STRESZCZENIE

Obiektem badań były trzy populacje raka pręgowatego *Orconectes limosus* (Raf.) z jezior: Staw Płociczno, Dgał Wielki i Hańcza. Materiały zbierano w latach 1999-2003. Średnia długość ciała (TL) samic i samców (w formach I i II) raków pręgowatych była najmniejsza w jeziorze Staw Płociczno (odpowiednio: 75,3, 78,3, 68,1 mm), a największa – w Dgale Wielkim (odpowiednio: 95,7, 95,8, 75,5 mm). W Dgale Wielkim złowiono również raka o rekordowej, dotychczas nierejestrowanej długości ciała – 130 mm. Analiza proporcji ciała raków pręgowatych wykazała istnienie niewielkich, istotnych statystycznie różnic pomiędzy badanymi populacjami raków pręgowatych (tab. 6). Na ogół proporcje ciała samców w formie II są zbliżone do proporcji ciała samic, a proporcje ciała samców w formie I zdecydowanie się różnią od proporcji samic i samców w formie II. Samice i samce raków pręgowatych charakteryzują się istotnie

statystycznie odmiennymi proporcjami ciała niż raki sygnałowe *Pacifastacus leniusculus* Dana, błotne *Astacus leptodactylus* Esch. i szlachetne *Astacus astacus* (L.) (tab. 19-20). Masa ciała raków jest skorelowana z długością całkowitą i długością głowotułowia. U badanych raków pręgowatych związek ten najlepiej opisywały równania potęgowe (tab. 7-8). Samce w formie I przy takich samych wymiarach ciała osiągają na ogół większą masę niż samice i samce w formie II (rys. 19). Natomiast masa ciała samic raków pręgowatych przy takich samych wymiarach jest niższa niż samic raków szlachetnych i sygnałowych, a zbliżona do masy samic raków błotnych (tab. 21, rys. 20). Samce raka pręgowatego w formie I przy takich samych wymiarach ciała mają niższą masę niż samce raków szlachetnych i sygnałowych i prawie identyczną z samcami raków błotnych. Natomiast samce raków pręgowatych w formie II – osiągają masę najniższą (tab. 21, rys. 21). Szczypce samców w formie I są większe niż samców w formie II i samic (tab. 10-11, rys. 22).

Średni udział samic w łownej części populacji raków pręgowatych wynosił 40,9%, gdy połowy prowadzono żakiem ramowym i 45,2%, gdy połowy prowadzono włoczkiem. Średnia długość ciała raków łowionych żakiem (80,5 mm) była istotnie statystycznie wyższa niż średnia długość ciała osobników (75,2 mm) łowionych włoczkiem. Wśród raków łowionych żakiem ramowym dominowały o długości całkowitej ciała od 81 do 90 mm (rys. 9), a u raków łowionych włoczkiem – od 71 do 80 mm (rys. 10). Indywidualna płodność absolutna raków pręgowatych w jeziorze Staw Płociczno wahała się od 56 do 431 jaj, a w jeziorze Dgał Wielki – od 138 do 926 jaj. Średnia indywidualna płodność absolutna samic raka pręgowatego z jeziora Staw Płociczno wynosiła 247 jaj i była istotnie statystycznie niższa niż samic z jeziora Dgał Wielki (499 jaj).

Biomasa łownej części populacji raków pręgowatych w jeziorze Staw Płociczno wynosiła 32,3 kg ha^{-1} powierzchni zasiedlanej przez raki.

Wskaźnik napełnienia żołądków treścią pokarmową wykazywał dużą zmienność zarówno w cyklu rocznym, jak i dobowym. Najniższy średni wskaźnik napełnienia żołądków stwierdzono w najniższej temperaturze wody, w marcu, a najwyższy – w najwyższej temperaturze wody, w lipcu. Stwierdzono istotny statystycznie związek tego wskaźnika z temperaturą wody. Dobowa zmienność wskaźników napełnienia żołądków związana jest z dobową zmiennością aktywności raków. Wskaźniki napełnienia żołądków badanych raków pręgowatych, najczęściej osiągały maksimum nocą, a minimum w porze dziennej (rys. 14), co wskazuje, że odżywiały się one głównie wieczorem i nocą. Czas ewakuacji pokarmu z żołądków zmieniał się w ciągu roku i wahał od 15,7 godzin w lipcu, gdy temperatura wody wynosiła 19,8°C, do 393,6 godzin w marcu, gdy temperatura wody wynosiła 3,2°C (tab. 14). Czas ten wykazywał silny, ujemny i istotny statystycznie, związek z temperaturą wody. Związek ten miał charakter wykładniczy i był dobrze dopasowany do danych empirycznych. Dobowe racje pokarmu raków pręgowatych w jeziorze Staw Płociczno wykazywały dużą zmienność w cyklu rocznym. Racje dobowe wyliczone metodą Kogan i Thorpego, były najwyższe w maju (odpowiednio: 55,5 i 28,2‰ mokrej masy ciała) i wrześniu (odpowiednio: 63,0 i 36,1‰ mokrej masy ciała) (tab. 15). Natomiast wyliczone metodą Bajkova oraz Elliota i Perssona były najwyższe w czerwcu (odpowiednio: 11,4 i 39,3‰ mokrej masy ciała) i lipcu (odpowiednio: 17,4 i 38,4‰ mokrej masy ciała). W sierpniu, w okresie masowego linienia raków, racje dobowe ulegały obniżeniu, a we wrześniu – ponownemu wzrostowi. Takiej zmienności nie zanotowano w racji dobowej liczonej metodą Winberga (tab. 15), gdyż racja dobowa wyliczona tą metodą zależy wyłącznie od temperatury wody. Porównując dobowe racje pokarmu, obliczone zastosowanymi metodami, należy wskazać metodę Elliotta i Perssona jako najbardziej przydatną do potrzeb obliczania racji dobowej u raków pręgowatych. Metoda ta zakłada wykładniczy charakter czasu ewakuacji, czyli taki, jaki stwierdzono w niniejszej pracy dla raków pręgowatych oraz uwzględnia rzeczywistą, dobową zmienność wskaźników napełnienia. Wadą tej metody jest jej bardzo duża czaso - i pracochłonność.

Racje dobowe były skorelowane zarówno ze średniodobowym wskaźnikiem napełnienia żołądków, jak i temperaturą wody. Pozwoliło to na stworzenie wzorów empirycznych umożliwiających prognozowanie racji dobowych na podstawie prostych pomiarów. Racje dobowe można dość dokładnie prognozować na podstawie samego wskaźnika napełnienia żołądków ($RdP = 1{,}483\ If^{1{,}238}$, SE = 1,60, R^2(%) = 74,5, P = 0,0013), dużo dokładniej – na podstawie temperatury wody ($RdP = 0{,}567\ t^{1{,}383}$, SE = 1,27, R^2(%) = 93,2, $P < 0{,}0001$) i bardzo dokładnie – na podstawie obu tych czynników naraz ($\ln RdP = 0{,}397 + 0{,}094\ t + 0{,}614 \ln If$, SE = 0,11, R^2(%) = 98,7, $P < 0{,}0001$). Równanie pozwalające na prognozowanie racji dobowej na podstawie wskaźnika napełnienia żołądków i temperatury wody było bardzo dobrze dopasowane do danych empirycznych (rys. 15). Można więc przyjąć, że prognozowanie racji dobowej na podstawie wskaźnika napełnienia i temperatury wody jest dokładne i znacznie upraszcza obliczanie racji dobowej u raków pręgowatych.

Roczna racja pokarmu raków pręgowatych wyliczona na podstawie danych uzyskanych metodą Elliotta i Perssona, wynosiła 638% mokrej masy ciała. Wyniki uzyskane za pomocą innych metod były bardzo rozbieżne i wynosiły od 173% mokrej masy ciała obliczonej metodą Bajkova do 1117% mokrej masy ciała – metodą Kogan (tab. 16).

Raki pręgowate w jeziorze Staw Płociczno odżywiały się intensywnie od maja do października, zjadając w tym czasie ponad 80% racji rocznej obliczonej metodą Elliotta i Perssona. Odżywiały się przede wszystkim pokarmem roślinnym. Średni wagowy udział pokarmu roślinnego wynosił 84,8%, a zwierzęcego – 15,2%. W poszczególnych miesiącach udział pokarmu roślinnego zmieniał się, jednak nigdy nie spadał poniżej 50% (tab. 17). Rocznie populacja raków spożywała 20,6 g m^{-2} pokarmu, w tym 17,5 g m^{-2} pokarmu roślinnego. Stanowiło to zaledwie 0,27% mokrej masy roślinności wodnej, znajdującej się w strefie bytowania raków.

Skład pokarmu i roczny rytm odżywiania się raków pręgowatych zaprzecza twierdzeniu o wyjadaniu ikry przez raki. W żołądkach badanych raków nie stwierdzono ikry ryb, chociaż próby raków pobierano w trakcie rozrodu okonia, płoci, leszcza i wzdręgi.