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FEEDING ECOLOGY OF VENDACE, *COREGONUS ALBULA* (L.), IN LAKE WIGRY (NORTHEASTERN POLAND)

Tomasz K. Czarkowski, Andrzej Martyniak*, Andrzej Kapusta**, Anna Wójcik*, Magdalena Bowszys***, Bogdan Wziątek*, Urszula Szamańska*, Jacek Kozłowski**

*Department of Fish Biology and Pisciculture, University of Warmia and Mazury in Olsztyn, Poland
**Department of Ichthyology, The Stanisław Sakowicz Inland Fisheries Institute in Olsztyn, Poland
***Department of Applied Ecology, University of Warmia and Mazury in Olsztyn, Poland

ABSTRACT. The aim of the study was to present selected issues concerning the feeding of adult vendace, *Coregonus albula* (L.) in Lake Wigry. Seasonal changes in dietary composition, feeding intensity, and vendace preferences for the most important prey taxa were determined. Fish were caught monthly from April to October in 2001 and 2002. The main food components were *Cyclops vicinus* and *Daphnia* spp. Significant seasonal variation in diet composition was confirmed in both study years. In spring and fall, this species fed on large copepods, particularly *Cyclops vicinus*, while in summer it consumed cladocerans, primarily *Daphnia cucullata*. *Chaoborus* sp. larvae and chrysalises were a substantial component of vendace food . The most intense feeding was noted in April and May, while the least intense was recorded in July and August. The highest percentage of fish with empty digestive tracts (40%) were confirmed in July, while in spring and fall prey was noted in the digestive tracts of all the individuals examined.

Key words: VENDACE, ZOOPLANKTON, FOOD, *CYCLOPS VICINUS*, LAKE WIGRY

INTRODUCTION

Fish exhibit a high degree of feeding plasticity depending on the habitat they live in and the food resources it offers (Dill 1983, Smith and Skulason 1996). Food dependencies are the primary type of relationship between individuals and among species. The analysis of fish food permits identifying these relationships in an aquatic ecosystem while simultaneously providing a necessary element of fisheries management (Opuszyński 1983). Due to their occurrence on a mass scale, planktivorous fish that inhabit lake pelagic zones are a significant link in the matter cycle.

CORRESPONDING AUTHOR: Tomasz K. Czarkowski, Warmińsko-Mazurski Ośrodek Doradztwa Rolniczego, Dział Ekologii i Ochrony Środowiska, ul. Jagiellońska 91, 10-356 Olsztyn, Tel./Fax: +48 89 5357684; e-mail:t.czarkowski@wodr.olsztyn.pl

Vendace, *Coregonus albula* (L.), which is a member of the family Salmonidae, is a medium-sized fish occurring in lake pelagic zones in northern Europe and the Gulf of Finland and Bothnian Bay. It has also been introduced to basins outside of its original range of occurrence. As with other representatives of the genus Coregonus, vendace prefers water with a high oxygen content and a low temperature (Dembiński 1971, Winfield et al. 2004). It is also a typical zooplanktivorous species. The diet of juvenile specimens has been confirmed to contain rotifers and small crustaceans (Sutela and Huusko 1997), while adult specimens have been noted to feed on crustacean zooplankton and, sporadically, Chironomidae and *Chaoborus* sp. larvae and chrysalises (Marciak 1962).

Repeated attempts have been made to use biomanipulation to limit progressing lake eutrophication caused by both natural aging processes and anthropogenic pressure (Prejs et al. 1994, Mehner et al. 2002). Monitoring the structure of fish assemblages in Lake Wigry along with the results of vendace feeding and the analysis of the dietary components of other planktivorous species can be used in concert with other potential projects aimed at preserving this lake. The authors of the current paper attempted to present chosen issues regarding vendace feeding in Lake Wigry. Seasonal variation in dietary composition, feeding intensity, and vendace preferences were determined for the most important prey taxa.

MATERIALS AND METHODS

STUDY AREA

Lake Wigry (53°59'–54°04' N, 22°59'–23°08' E) is located in northeast Poland in the mid reaches of the Czarna Hańcza River in the Neman basin. It is one of the largest Polish lakes and is the largest among the 42 lakes located in Wigry National Park. The surface area of the lake is 2186.7 ha, including islands with a surface area of 68.4 ha, and it has a maximum depth of 73.0 m and a mean depth of 15.8 m. In the eutrophic northern part of the lake, anoxia is noted in the hypolimnion in summer (Górniak 2006), while in the mesotrophic central basin of Lake Wigry the oxygenation range in the hypolimnion is 20-30%. The period of full ice cover usually lasts three months from December to March.

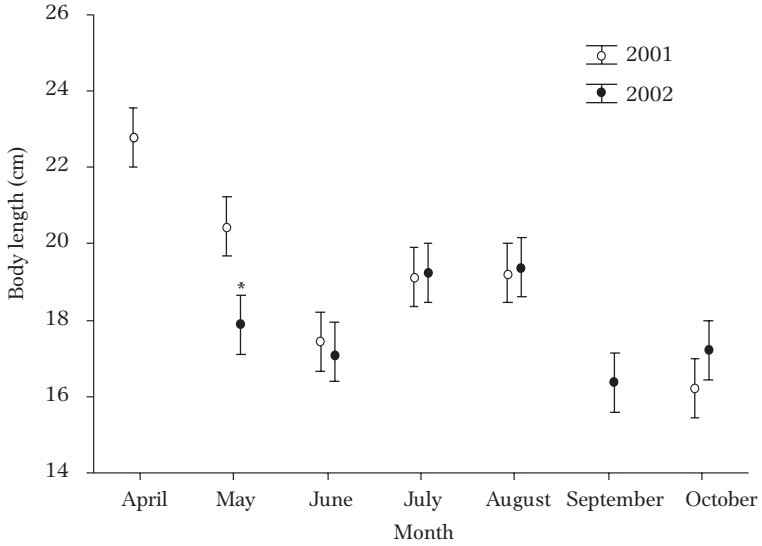

Fig. 1. Difference in mean body length of vendace caught in 2001-2002 in Lake Wigry. Open circles indicate means for fish in 2001, solid circles for fish in 2002. Asterisks indicate significant differences ($P < 0.05$) between mean body lengths of vendace sampled for feeding analyses.

FISHING

The fish used in the study were caught monthly in 2001and 2002 from April to October. The fish were caught at night using gillnets with 16, 18, 20, 22, 24, and 28 mm mesh sizes. Samples of crustaceous zooplankton were collected in the areas fished with a Patalas sampler. Using a plankton net with a mesh size of 50 μm, 50 dm^3 of water was reduced to a volume of 100 ml and then preserved with Lugol's solution and formalin. At each sampling event 30 fish were collected for the analysis of stomach contents (360 fish total). After measuring body length (Lt), the digestive tracts were removed from the fish and preserved in a 4% formalin solution. Although the mean length of the vendace submitted to stomach content analysis in both years was similar, it did differ significantly between months (ANOVA, $P < 0.001$; Fig. 1). The largest fish were caught in spring (135-278 mm) and summer (170-230 mm).

ANALYSIS OF MATERIAL

The differentiation in the crustaceous zooplankton in subsequent months was calculated with the Shannon-Wiener diversity index (Magurran 1988):

$$H' = -\Sigma p_i (\ln p_i)$$

where: H' – species diversity index, p_i – share of specimens of species i in the assemblage.

The analysis of the stomach contents entailed determining the taxonomic composition and the specimen length of individuals from the various taxa. The food biomass was calculated based on this and using the dependence between prey length and body weight. The results obtained were used to calculate the index of relative importance (IRI; Hyslop 1980):

$$IRI = (\%N + \%V) \times \%F$$

where: N – number share, V – weight share, F – frequency of occurrence.

Vendace food preferences were calculated with Ivlev's electivity index (Ivlev 1961):

$$D = (r - p) / (r + p) - (2r \times p)$$

where: D – food preference coefficient, p – share of prey from a selected class in the environment (%), r – share of prey from a selected class in the stomach contents (%).

Feeding intensity was expressed as the share of full digestive tracts in the sample, the fullness index (mean weight of food per fish weighing 100 g), and the mean number of prey per fish.

STATISTICAL ANALYSIS

Statistical analysis was preceded by a normal distribution test (Shapiro-Wilk W test) and the equality of variance of variables (Levene's test). The data used in the analysis was log transformed (log(x+1)). The comparison of the density of crustacean zooplankton in each of the study years was performed with the Mann-Whitney U test, while seasonal differentiation in feeding intensity (number of prey identified in the stomachs) was analyzed with two factor analysis of variance (two-way ANOVA). After significant results were obtained from the analysis of variance, the groups that differed from one and other were identified with the Tukey test.

RESULTS

COMPOSITION OF LAKE PLANKTON

During the studied period, the Crustacea assemblage in Lake Wigry was comprised of nine Copepoda and twelve Cladocera species. In each of the two years, the zooplank-

ton abundance and biomass were similar (Mann-Whitney U test, $P > 0.05$; Table 1). The highest density was noted in summer (196.8 indiv. dm^{-3}), while the lowest was in April (18.2 indiv. dm^{-3}) and October (20.0 indiv. dm^{-3}). Crustacea diversity in 2002 was statistically significantly higher in comparison to that in 2001 (Mann-Whitney U test $P<0.01$; Table 1).

TABLE 1

Characteristics of the zooplankton in Lake Wigry

Year	Month	Species richness	Diversity H'	Abundance (indiv. dm^{-3})	Biomass (mg dm^{-3})
2001	April	5	0.461	18.2	0.54
	May	14	0.710	163.2	4.81
	June	13	0.907	178.0	16.24
	July	11	0.845	193.6	16.43
	August	10	0.582	51.0	1.20
	October	9	0.847	23.0	1.88
2002	May	16	0.890	156.6	7.91
	June	18	0.962	164.2	16.75
	July	18	0.925	196.8	19.53
	August	17	0.920	48.0	3.01
	September	14	0.998	32.0	3.27
	October	11	0.937	20.0	1.35

FOOD COMPOSITION

The vendace in Lake Wigry fed on copepods (*Cyclops vicinus*, *Mesocyclops leuckarti*, copepodits, *Eudiaptomus gracilis*, *Eudiaptomus graciloides*), cladocerans (*Daphnia cucullata*, *Daphnia cristata*, *Daphnia hyalina*, *Bosmina longirostris*, *Bosmina coregoni*), and the larvae and pupae of insects (*Chaoborus* sp., *Microtendipes* sp.). The principle food components were *Cyclops vicinus* and *Daphnia* spp. Significant seasonal variation in the dietary composition of the vendace diet was confirmed in both study years (Fig. 2). In April and May, the main vendace dietary component was *Cyclops vicinus* (IRI from 78.7 to 90.0%), but in June it was *Daphnia* spp., at an IRI of nearly 80%. In subsequent months, the importance of *Daphnia* spp. in the vendace diet decreased. The importance of *Chaoborus* sp. larvae and pupae, which occurred in the food only in July and August, was not large (IRI from 3.7 to 18.0%).

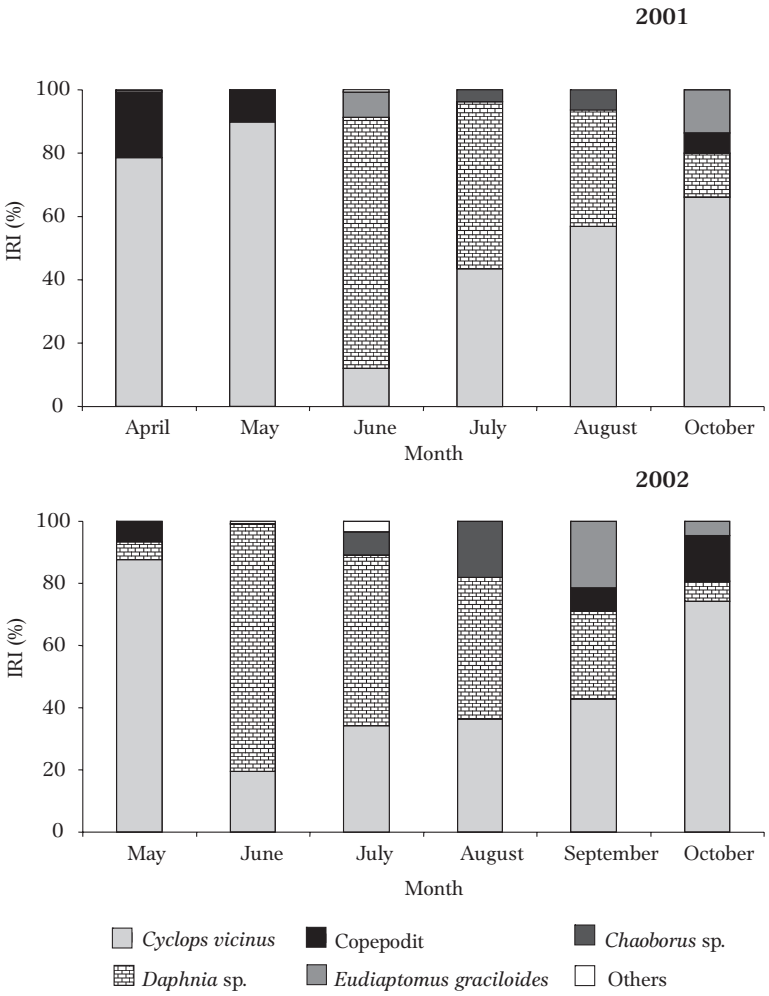

Fig. 2. Index of Relative Importance (%) of food components in the vendace diet in Lake Wigry.

FEEDING INTENSITY

Vendace feeding intensity exhibited significant seasonality (ANOVA, $P<0.001$). The highest values of the vendace stomach fullness index was confirmed in April and May (Table 2), while the least intense feeding in both years was noted in July and August. Changes in the shares of fish with empty stomachs were identical (Table 2).

TABLE 2

Seasonal variability in vendace feeding intensity in Lake Wigry

Year	Month	Fish analyzed	Mean body length (mm)	Mean body weight (g)	Mean gut fullness (g wet weight/100 g fish wet weight)	Percentage of full stomachs (%)
2001	April	30	22.8	148.1	0.43	100
	May	30	20.5	107.7	0.57	100
	June	30	17.4	65.8	0.20	100
	July	30	19.1	87.1	0.11	40.0
	August	30	19.2	88.5	0.09	63.3
	October	30	16.2	53.1	0.51	100
2002	May	30	17.9	71.7	0.81	100
	June	30	17.2	63.6	0.19	100
	July	30	19.2	88.5	0.09	40.0
	August	30	19.4	91.3	0.05	66.6
	September	30	16.4	55.1	0.29	100
	October	30	17.2	63.6	0.49	100

The lowest share of feeding fish was noted in summer; in July only 40% of the examined individuals had food in their stomachs. However, 100% of the fish examined in spring and fall had prey in their stomachs. The mean number of prey varied significantly during the study period; in April it was fifty fold higher than it was in July or August (two-way ANOVA, $P<0.001$; Fig. 3).

FOOD PREFERENCE

In both of the study years the vendace exhibited similar food preferences with regard to the main food components (Table 3). Seasonal variation in the Ivlev's index was most frequently insignificant. Vendace exhibited the most decided food preferences for *Cyclops vicinus* and *Chaoborus* sp. *Eudiaptomus graciloides* was chosen by vendace in the first year of the study, but it was avoided in 2002. Only in September 2002 was a clear preference expressed by vendace for this species of copepod. Among the Cladocera, vendace preferred only *Daphnia cucullata* and avoided other species of the genus Daphnia (*Daphnia cristata*, *Daphnia hyalina*), as they did with smaller cladocerans (e.g., *Bosmina longirostris*).

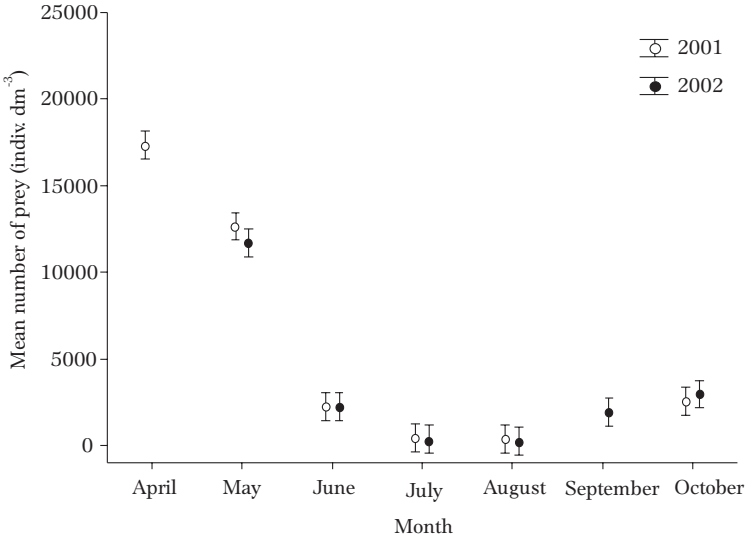

Fig. 3. Mean number of prey in the digestive tracts of vendace in Lake Wigry (mean ± 0.95% range).

TABLE 3

Feeding preferences (Ivlev's index) of vendace in Lake Wigry in 2001 and 2002

Year	Month	*Cyclops vicinus*	*Eudiaptomus graciloides*	Copepodit	*Bosmina longirostris*	*Daphnia cristata*	*Daphnia cucullata*	*Daphnia hyalina*	*Chaoborus* sp.
2001	April	0.8	1.0	-0.1*					
	May	0.9		-0.5	-1.0	-0.5			
	June	1.0	1.0	-0.8	-0.7	-0.4	0.8	-0.9	
	July	1.0		-1.0	-1.0	-1.0	0.4	-1.0	1.0
	August	1.0		-1.0	-1.0		1.0		1.0
	October	0.2*	0.4	-0.4		0.1*	0.3	-0.2*	
2002	May	0.9	-0.1*	-0.5	-1.0	0.7	-1.0	-1.0	
	June	0.9	-1.0	-0.8	-0.8	-0.6	0.8	-1.0	
	July	1.0	-1.0	-1.0	-0.1*	-1.0	0.5	-1.0	1.0
	August	0.9	-1.0	-1.0	-1.0	-1.0	0.5	-1.0	1.0
	September	0.6	0.7	0.2*	-1.0	-1.0	0.1*	-1.0	
	October	0.4	0.1*	0.1*		0.1*	0.4	0.4	

Values marked with asterisks (*) indicate that selectivities were do not significant

DISCUSSION

The results presented in the current paper were used to analyze the feeding ecology of adult vendace in two study years. The food composition of vendace has been ana-

lyzed in several research projects (Marciak 1962, Szypuła 1965, 1970, Mamcarz and Błoniarz 1995, Więski 2002). The species composition and the significance of the individual prey taxa in the vendace diet differs fairly significantly in the lakes this species inhabits (Table 4).

TABLE 4

Overview of dominant prey of vendance in European waters
(SL – standard length, TL – total length)

Lake (Country)	Time period	Fish length (mm)	Dominant prey	Reference
Lake Miedwie (Poland)	June-September	184-250 SL	*Leptodora kindtii*	Więski (2002)
Lake Pluszne (Poland)	July-December	(1+ – 2+)	*Daphnia* spp.	Marciak (1962)
Lake Pluszne (Poland)	November-June	(1+ – 2+)	*Eurytemora lacustris*	Marciak (1962)
Lake Legińskie (Poland)	May-July	170-265 SL	*Daphnia cucullata* *Bythotrephes longimanus*	Szypuła (1965)
Lake Legińskie (Poland)	November-February	170-265 SL	*Cyclops* spp. *Eudiaptomus* spp.	Szypuła (1965)
Lake Charzykowskie (Poland)	March-June	161-181 SL	*Cyclops strenuus* *Daphnia* spp.	Mamcarz and Błoniarz (1995)
Lake Suomunjärvi (Finland)	April-October	82-234 TL	Cladocera *Cyclops scutifer*	Viljanen (1983)
Lake Bolmen (Sweden)	July, October		*Bosmina coregoni* *Holopedium gibberum*	Hamrin (1983)
Lake Mälaren (Sweden)	June-October		*Bosmina* spp.	Northcote and Hammar (2006)
Lake Wigry	April-October	160-230 SL	*Cyclops vicinus* *Daphnia* spp.	current study

In Lake Miedwie the basic food component was *Leptodora kindtii* (Więski 2002), in Lake Bolmen it was *Holopedium gibberum* (Hamrin 1983), in Lake Mälaren it was *Bosmina* spp. (Northcote and Hammar 2006), and in Lake Charzykowski it was *Cyclops strenuus* (Mamcarz and Błoniarz 1995). Nonetheless, the vendace feeding patterns in these lakes was similar to those confirmed in Lake Wigry. Copepods dominate the adult vendace diet in spring and fall, while in summer cladocerans are prevalent. The variation in dietary composition of fish inhabiting different basins might stem from varied zooplankton structure and differing availability of the various dietary components (Opuszyński 1983, Northcote 1988). The seasonal and temporal changes in the food composition of planktivorous fish depends, among other factors, on the availability of food, environmental conditions, pressure exerted by piscivorous fish,

inter-species and intra-species competition, and also on the behavior of the prey and its predator (Vijverberg et al. 1990, Alajärvi and Horppila 2004, Mous et al. 2004).

The vendace inhabiting Lake Wigry exhibited the greatest preference for *Cyclops vicinus* and *Chaoborus* sp. larvae and pupae. While the preference for insect larvae and pupae can be easily explained by their marked size and weight, that for copepods is not. Due to their small size and ability to escape, copepods are less advantageous energetically than are cladocerans for planktivorous fish (Persson 1987). Planktivorous fish often feed in low light and pursue zooplankton that migrate in the evenings to the near-surface water layer (Gliwicz 1986). Under these conditions, copepods, with their particularly aggressive movements and fairly high amplitude, may attract the attention of fish more so than cladocerans (Milinski 1984).

Variation in both vendace food composition and feeding intensity are noted in different basins. Depending on the lake, the highest feeding intensity is in the spring month of June (Northcote and Hammar 2006), summer in July and August (Marciak 1962), or in winter in February (Szypuła 1965). In Lake Wigry feeding intensity was highest in April and May, it decreased in July and August, but increased again in September and October. It is plausible that the decreased vendace feeding intensity in the summer period despite the high density of zooplankton might have been caused by the disadvantageous physicochemical conditions in the water during summer stagnation (Górniak 2006). The high temperature and decrease in oxygen content might have narrowed the area which the vendace are able to penetrate, which could have affected feeding intensity (Szypuła 1970). Doubtless, the rapid digestion rate in the summer also had an impact on low feeding intensity (Szypuła 1965). The nature of gillnet fishing also required that the caught fish spent a fairly long period in the net, which, in turn, at the high water temperatures in summer, could have contributed to the decline in prey quantity and the biomass of the food consumed.

Due to ease with which vendace stocking material is produced, this species' resistance to disease, and its high market value, it is the most valuable commercial component of the ichthyofauna of Polish lakes (Wołos and Mickiewicz 1998). Simultaneously, it is an endangered species in many countries (Winfield et al. 2004), which is evidenced by its listing in Annex III of the Bern Convention and Annex V of the EC Habitats and Species Directive. In Lake Wigry, this species occurs abundantly

(Świerzowski 1999). The results presented in this paper can be used in proposed work for the protection and management of vendace populations.

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STRESZCZENIE

EKOLOGIA ODŻYWIANIA SIĘ SIELAWY, *COREGONUS ALBULA* (L.) W JEZIORZE WIGRY

Celem badań było przedstawienie wybranych zagadnień odżywiania się dorosłej sielawy, *Coregonus albula* (L.) w jeziorze Wigry. W pracy określono strukturę, zagęszczenie i różnorodność zoooplanktonu skorupiakowego (tab. 1). Dokonano oceny wielkości złowionych ryb (rys. 1) oraz scharakteryzowano sezonowe zmiany składu pokarmu, intensywność żerowania oraz wybiórczość sielawy w stosunku do najważniejszych taksonów ofiar. Ryby łowiono raz w miesiącu od kwietnia do października w latach 2001-2002. Głównym składnikiem pokarmowym był *Cyclops vicinus* i *Daphnia* spp. W obu latach stwierdzono istotną zmienność sezonową składu diety sielawy (rys. 2). Wiosną i jesienią odżywiała się dużymi widłonogami, szczególnie *Cyclops vicinus*, natomiast latem dużymi wioślarkami, przede wszystkim *Daphnia cucullata*. Okresowo również larwy i poczwarki *Chaoborus* sp. stanowiły istotny składnik pokarmu sielawy. Największą intensywność żerowania stwierdzono w kwietniu i maju, a najniższą w lipcu i sierpniu (tab. 2, rys. 3). Największy udział ryb z pustymi przewodami (40%) stwierdzono w lipcu. Natomiast wiosną i jesienią w przewodach pokarmowych wszystkich osobników występowały ofiary. Sielawa w jeziorze Wigry największą wybiórczość wykazywała w stosunku do *Cyclops vicinus* oraz larw i poczwarek *Chaoborus* sp. (tab. 3). W pracy przeprowadzono analizę zmienności składu pokarmu sielawy w areale jej występowania (tab. 4). Wzorzec odżywiania sielawy w tych jeziorach jest podobny do stwierdzonego w jeziorze Wigry. Wiosną i jesienią podstawę diety dorosłej sielawy stanowią widłonogi, natomiast latem wioślarki.