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EFFECTS OF SIZE-SELECTIVE MORTALITY ON ESTIMATES OF THE GROWTH RATE OF ZANDER, *SANDER LUCIOPERCA* (L.) FROM LAKE JEZIORAK

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Background. Fish growth rate is usually determined based on a single sample or a number of sub-samples considered jointly. A study on cisco, *Coregonus artedi*, successively collected within 6 years in Canada, had demonstrated a possibility of determining size-selective mortality in relation to larger- or smaller fish. Three recent papers on the growth of zander, *Sander lucioperca* from the Odra River estuary, suggested a higher mortality of smaller fish (a *negative Lee's phenomenon in inclusive sense*). On the other hand zander from Lake Jeziorak, collected by the present authors, exhibited a size-selective mortality in relation to the larger fish (a *positive Lee's phenomenon in inclusive sense*). The aim of this paper is to discuss this issue.
Material and methods. The zander were collected from Lake Jeziorak with a summer seine in 1970 (328 specimens), 1971 (72 spec.), 1972 (73 spec.), and in 1973 (143 spec.). The fish were aged 2- through 5-years, representing three year-classes (i.e. hatched in 1967, 1968, and 1969). The age and growth rates of the fish were determined based on scales and verified based on cross sections of fin rays. Growth rate indices were based on empirical relationship between the standard length and the oral radius of scale, which assured elimination of the phenomenon of apparent change of growth rate.
Results. Despite the above assumption, the lengths attained at the moment of establishing sequential annuli decreased with age of fish studied. The differences between individual year-classes, however, were decreasingly smaller. Those regularities were tested on individual year-classes as well as on individual age groups caught within a single season. It reflects a higher mortality of faster-growing fish. The length frequency distribution curves of both empirical and back-calculated values for sequentially collected samples were plotted, separately for each of three year-classes. The intention was to verify whether the higher mortality of larger fish could contribute to a skewness of length distribution curves. Skewness was not observed, but it turned out that each year-class had

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its specific frequency distribution of length, persisting from their second- through fourth year of life. The occurrence of *positive-* and *negative Lee's phenomenon in inclusive sense* in fish stocks of the same species, inhabiting different bodies of water, is discussed. **Conclusion**. This paper defines the following research problem: What are the reasons of different size-selective mortality of different populations of the same species, living under similar climatic and hydrological conditions?

Key words: fish, zander, *Sander lucioperca*, growth rate of individual year classes, size selective mortality, length frequency distribution

INTRODUCTION

The paper of E. Lea (1910) on the growth of length of herring, determined from its scales, provoked a vivid reaction within the years to come. The authors, who used this method for describing growth of sprat, herring, haddock, and trout, have noticed that the growth indices determined based on the scales collected from older fish were lower than those determined based on the scales from younger and smaller fish. This phenomenon, which received a highly publicised attention, was referred to as the *Lee's phenomenon in inclusive sense* (Ricker 1969).

Ricker (1969), in his overview paper on size-selective mortality listed, based on earlier authors, three causes of this phenomenon:

• Technical—where back reading is based on a wrong relationship between the size of scale and the size of the body.

• Biased sampling—where the distribution of fish length in the analysed sample of scales or otoliths does not reflect the proportions of different size fish in the population.

• Selective mortality—where the mortality rate of larger fish of an age group differs from that of the smaller fish. The reasons of the selective mortality of larger (or smaller) fish may arise from natural conditions or from different catchabilities of different fish sizes (when the principal cause of the mortality is fishing).

According to Ricker (1969) the size-selective mortality, contrary to two of the above-mentioned causes of the *Lee's phenomenon* is the property of a fish population rather then of a technique, and therefore it may have an effect on the biological statistics of the stock surveyed.

Assuming, that the investigated sample was representative and the growth calculation was based on a correct relationship between the body length and the scale radius—and despite that older fish show slower growth—it would mean that the faster-growing fish were subjected to a higher mortality and vice-versa. The best way to observe this phenomenon is to separately determine the growth of sequential age groups of the same year-class (Ricker 1969, 1979). The present authors decided to use their scale collections of zander, caught with a summer seine in 1970, 1971, 1972, and 1973 to carry out such analysis for three year-classes of fish hatched in 1967, 1968, and 1969.

The aim of this work was to compare the growth indices of the seine-caught fish:

a) Representing the same year-class, but caught in sequential years of life.

b) Representing the same year-class, but caught in sequential months, June through December.

c) Representing the analysed year-classes, with separately determined growth of 3-year-old and 4-year-old fish.

d) Representing individual year-classes, caught within a single fishing season.

e) Representing individual year-classes of zander from Lake Jeziorak and from other bodies of water of northern Poland.

In addition to that, length growth distributions determined from back readings, separately for each of three year-classes were compared. The aim of the analysis of those three distributions was to answer the question raised by Ricker (1969)—Does a persistent elimination of the largest fish translate into a progressively skewed distribution curve?

A number of papers on the growth of zander have been published in Poland (Nagięć 1961, 1964, Ciepielewski 1977, Szypuła 1996, 2002, Neja and Turowska 1998, Błaszczyk 1999), non of them, however, had mentioned the effect of size-selective mortality on estimated growth parameters.

DESCRIPTION OF THE ENVIRONMENT

Lake Jeziorak, situated within the drainage basin of the Drwęca River (right-hand side tributary of the Vistula River), covers the area of 3219 ha. Its average depth is 4.3 m, its shoreline is well developed, and the water transparency is poor. The dominant item of the partly-submerged, tall vegetation is the reed whereas the submerged vegetation is poorly-represented. Phytoplankton consists of a small number of species. The crustaceans are represented by 4 dominant species of copepods and 3 species of cladocerans. There are 7 abundant species of rotifers and a higher number of sporadically occurring ones. The benthic fauna is relatively poor.

Within the period of 1952–1991 the catch registers recorded 14 fish species with the carp bream as the dominant one. The total annual yield ranged from 18.0 to 41.0 kg per ha. The annual yield of zander ranged from 1.9 to 9.4 kg per ha, on average 5.14 kg per ha (SD = 1.52)(Draganik and Nagięć 1995).

MATERIAL AND METHODS

The growth rate of zander was determined based on the scales sampled from left-hand side of each specimen, above its lateral line, near the end of pectoral fin. Each fish was also measured (standard length SL, total length TL to the nearest 0.5 cm). The material covers the data of 639 specimens acquired from commercial catches, performed with the aid of a summer seine, within four sequential years: 1970, 1971, 1972, and 1973. The seine parameters were as follows: wing length 180 m, wing height near the bag 11.5 m, mesh size in the bagend 28 mm. The growth of 2-year-old fish, caught in the autumn of 1969 was taken from the paper of Karaś (1970).

The standard length of fish ranged from 31.0 to 60.5 cm while its age—from 2+ to 6+ with domination of fish aged 3+ and 4+. The samples were collected from July to December. Measurements and scales were always collected from all fish caught on a given day with the seine. Detailed data are listed in Tables 1, 2, 3, 4.

Age determination was easy, because the scales were well readable. In order to verify the reliability of the age readings, 10 specimens were subjected to simultaneous examination of scales, hard rays of pelvic- and dorsal fins. In zander aged 2–7 years the numbers of annuli on the scales were consistent with the number of growth inhibition lines in the bone structure (Nagięć et al. 1996).

The growth rate was determined considering empirical relationship between the standard length and the oral radius of scale (Nagięć 1961). Therefore—assuming that the fish caught by the summer seine, starting from the legal size (1000 g), constituted representative samples—it can be concluded that the observed *Lee's phenomenon* could have been caused by non-technical reasons (Ricker 1969, 1979).

During the collection of samples not all fish were weighed. The weight values were calculated from the weight–length relationship calculated for the zander population of Lake Jeziorak (Nagięć 1978)

$$W = 0.0143 \cdot l^3$$

where: W, weight [g]
l, standard length [cm]

According to the above relationship the standard length of the protected size of 1000 g is 41.2 cm.

Significance of differences of the standard length determined through back readings was calculated based on single classification using the F test (ANOVA).

Statistical comparisons were made only on age groups comprising not fever than 10 specimens.

In cases where back-calculated length distributions were monomodal, the coefficients of skewness were calculated based on the formula

$$\text{w.s.} = \frac{lx - Dx}{\text{SD}}$$

where: w.s., coefficient of skewness
lx, mean length of individual age group
SD, standard deviation of this length
Dx, the mode (modal value)(Szulc 1972).

Table 1

The growth of zander, *Sander lucioperca* captured in 1970 at Lake Jeziorak by summer seine

Date of capture	Age at capture	Year class	Number of fish	Mean standard length at capture [cm]	Length range at capture [cm]	Computed size at scale annuli				
						l_1 [cm]	l_2 [cm]	l_3 [cm]	l_4 [cm]	l_5 [cm]
			N	$\bar{x} \pm SD$		$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$
20 Aug 70	2+	1968	3	39.0 ± 0.71	38.0–39.5	19.7 ± 1.11	31.3 ± 1.70			
9 Sep 70			8	39.4 ± 1.07	37.0–40.5	19.9 ± 0.82	30.7 ± 1.81			
9 Oct 70			3	37.0 ± 2.45	34.0–40.0	16.0 ± 2.95	25.1 ± 3.90			
11 Nov 70			5	41.7 ± 0.87	41.0–43.0	19.6 ± 0.74	30.9 ± 1.81			
17 Dec 70			8	41.7 ± 1.46	40.0–45.0	20.2 ± 1.63	32.0 ± 1.77			
			27		34.0–45.0	$\bar{x}$ =19.5 ± 1.31	$\bar{x}$ = 30.6 ± 2.02			
16 Jul 70	3+	1967	20	42.8 ± 1.72	39.0–45.5	18.9 ± 1.43	30.6 ± 2.84	40.9 ± 2.12		
20 Aug 70			80	42.7 ± 2.24	38.5–47.5	16.9 ± 2.32	26.7 ± 3.90	37.0 ± 3.23		
9 Sep 70			63	43.9 ± 2.00	40.0–48.0	16.7 ± 2.61	26.4 ± 3.71	36.9 ± 2.87		
9 Oct 70			36	43.4 ± 1.86	39.0–47.0	15.8 ± 2.52	24.8 ± 3.96	35.6 ± 2.16		
11 Nov 70			26	45.5 ± 1.42	43.0–48.0	17.0 ± 1.92	26.3 ± 2.86	37.2 ± 2.22		
17 Dec 70			50	46.4 ± 2.25	42.0–50.0	18.1 ± 2.37	28.1 ± 3.79	38.9 ± 2.77		
			275		38.5–50.0	$\bar{x}$ = 17.1 ± 2.32	$\bar{x}$ = 26.0 ± 3.67	$\bar{x}$ = 37.4 ± 2.75		
16 Jul 70	4+	1966	2	49.0 ± 2.00	47.0–51.0	17.2 ± 0.90	29.5 ± 0.05	40.0 ± 0.55	48.3 ± 2.25	
20 Aug 70			4	48.3 ± 1.92	46.0–51.0	16.1 ± 0.68	26.7 ± 1.03	38.9 ± 2.00	45.5 ± 2.20	
9 Sep 70			5	49.5 ± 0.45	49.0–50.0	16.9 ± 1.34	27.2 ± 1.49	39.9 ± 1.44	45.4 ± 0.78	
9 Oct 70			1	50		16.0	22.5	34.2	43.7	
11 Nov 70			2	51.5 ± 1.50	50.0–53.0	16.6 ± 0.10	27.1 ± 0.45	40.7 ± 0.45	46.1 ± 0.90	
17 Dec 70			7	52.9 ± 2.59	48.0–57.0	17.3 ± 1.76	26.9 ± 2.27	38.3 ± 1.69	47.0 ± 2.18	
			21		46.0–57.0	$\bar{x}$ = 16.8 ± 1.13	$\bar{x}$ = 27.0 ± 1.36	$\bar{x}$ = 39.0 ± 1.38	$\bar{x}$ = 46.2 ± 1.73	
9 Sep 70	5+	1965	2	53.3 ± 1.75	51.5–55.0	18.1 ± 0.05	26.5 ± 0.90	35.1 ± 0.10	44.0 ± 1.00	49.3 ± 1.25
17 Dec 70			3	59.7 ± 0.84	58.5–60.5	19.7 ± 1.57	29.7 ± 2.33	41.3 ± 1.91	50.3 ± 1.28	55.3 ± 0.57
			5		51.5–60.5	$\bar{x}$ = 19.1 ± 0.96	$\bar{x}$ = 28.5 ± 1.76	$\bar{x}$ = 38.8 ± 1.19	$\bar{x}$ = 48.1 ± 1.17	$\bar{x}$ = 52.9 ± 0.84
			328			$\bar{x}$ = 17.3 n = 328 ± 2.14	$\bar{x}$ = 26.5 n = 328 ± 3.36	$\bar{x}$ = 37.5 n = 301± 2.63	$\bar{x}$ = 46.6 n = 26 ± 1.62	$\bar{x}$ = 52.9 ± 0.84

Table 2

The growth of zander, *Sander lucioperca* captured in 1971 at Lake Jeziorak by summer seine

Date of capture	Age at capture	Year class	Number of fish	Mean standard length at capture [cm]	Length range [cm]	Computed size at scale annuli l_1 [cm]	l_2 [cm]	l_3 [cm]	l_4 [cm]	l_5 [cm]
			N	$\bar{x} \pm SD$		$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$
29 Oct 71	2+	1969	4	41.5 ± 0.94	40.0–42.5	19.6 ± 0.95	31.9 ± 0.99			
27 Jul 71 29 Oct 71	3+	1968	20 18	41.6 ± 1.76 45.3 ± 2.54	38.5–45.0 39.5–49.5	16.9 ± 1.76 17.1 ± 1. 60	25.7 ± 2.74 27.0 ± 2.92	37.3 ± 2.20 37.8 ± 2.55		
			38		38.5–49.5	$\bar{x}$ =17.0 ± 1.68	$\bar{x}$ =26.3 ± 2.83	$\bar{x}$ =37.5 ± 2.37		
27 Jul 71 29 Oct 71	4+	1967	26 2	46.3 ± 2.36 54.3 ± 0.75	42.0–51.0 53.5–55.0	16.5 ± 1.82 18.6 ± 1.50	24.0 ± 3.24 33.3 ± 0.15	34.7 ± 3.72 43.2 ± 0.65	43.5 ± 2.37 50.6 ± 0.10	
			28		42.0–55.0	$\bar{x}$ =16.7 ± 1.80	$\bar{x}$ =24.7 ± 3.01	$\bar{x}$ =35.3 ± 3.50	$\bar{x}$ =44.0 ± 2.21	
27 Jul 71 29 Oct 71	5+	1966	1 1	55.0 54.0		15.7 14.9	27.4 21.5	41.1 34.0	46.4 42.5	51.5 50.5
			2	54.5		$\bar{x}$ =15.3 ± 0.40	$\bar{x}$ = 24.5 ± 2.95	$\bar{x}$ =37.6 ± 3.55	$\bar{x}$ =44.5 ± 1.95	$\bar{x}$ =51.0 ± 0.50
			72			$\bar{x}$ =17.00 ± 1.65 n = 72	$\bar{x}$ =25.94 ± 2.80 n = 72	$\bar{x}$ =36.59 ± 2.87 n = 68	$\bar{x}$ =44.03 ± 2.19 n = 30	$\bar{x}$ =51.0 ± 0.50 n = 2

Table 3

The growth of zander, *Sander lucioperca* captured in 1972 at Lake Jeziorak by summer seine

Date of capture	Age at capture	Year class	Number of fish	Mean standard length at capture [cm]	Length range at capture [cm]	Computed size at scale annuli					
						l_1 [cm]	l_2 [cm]	l_3 [cm]	l_4 [cm]	l_5 [cm]	
			N	$\bar{x} \pm SD$		$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	
8 Sep 72	2+	1970	1	40.5		20.1	31.6				
19 Jul 72	3+	1969	23	42.4 ± 1.23	40.5–45.5	19.1 ± 0.67	29.7 ± 1.38	38.9 ± 1.22			
5 Aug 72			21	44.3 ± 1.29	42.0–45.0	18.9 ± 0.79	28.3 ± 1.67	39.1 ± 1.55			
8 Sep 72			11	43.4 ± 2.47	40.0–49.0	17.1 ± 1.98	25.6 ± 3.37	36.0 ± 3.26			
			55		40.0–49.0	$\bar{x}$ = 18.6 ± 0.98	$\bar{x}$ = 28.3 ± 1.89	$\bar{x}$ =38.4 ± 1.75			
19 Jul 72	4+	1968	3	48.5 ± 0.41	48.0–49.0	19.1 ± 1.47	28.8 ± 2.45	39.1 ± 1.13	46.0 ± 0.62		
5 Aug 72			4	48.1 ± 1.29	46.0–49.5	17.1 ± 1.19	24.6 ± 2.28	36.0 ± 2.90	44.3 ± 1.92		
8 Sep 72			3	50.7 ± 3.79	45.5–54.5	16.7 ± 2.57	26.1 ± 4.30	38.2 ± 3.64	45.9 ± 2.17		
			10		45.5–54.5	$\bar{x}$ = 17.6 ± 1.69	$\bar{x}$ = 26.3 ± 2.94	$\bar{x}$ = 37.6 ± 2.59	$\bar{x}$ = 45.3 ± 1.61		
19 Jul 72	5+	1967	4	52.1 ± 1.70	50.5–54.5	19.9 ± 0.80	29.8 ± 1.67	38.8 ± 0.38	45.6 ± 0.94	50.4 ± 1.33	
5 Aug 72			1	52.0		17.7	26.7	37.0	45.5	50.0	
8 Sep 72			1	56.5		18.1	26.5	36.6	46.0	53.0	
			6		50.5–56.5	$\bar{x}$ = 19.2 ± 1.13	$\bar{x}$ = 28.7 ± 2.03	$\bar{x}$ =38.1 ± 1.01	$\bar{x}$ =45.7 ± 0.78	$\bar{x}$ =50.8 ± 1.59	
19 Jul 72	6+	1966	1	60.5		18.3	26.4	33.5	46.5	53.9	58.9
			73			$\bar{x}$ = 18.5 ± 1.06 n = 73	$\bar{x}$ = 28.1 ± 1.99 n = 73	$\bar{x}$ = 38.2 ± 1.78 n = 72	$\bar{x}$ = 45.5 ± 1.22 n = 17	$\bar{x}$ =51.2 ± 1.36 n=7	$\bar{x}$ = 58.9 n=1

Table 4

The growth of zander, *Sander lucioperca* captured in 1973 at Lake Jeziorak by summer seine

Date of capture	Age at capture	Year-Class	Number of fish	Mean standard Length at capture [cm]	Length range [cm]	Computed size at scale annuli					
						l_1 [cm]	l_2 [cm]	l_3 [cm]	l_4 [cm]	l_5 [cm]	l_6 [cm]
			N	$\bar{x} \pm SD$		$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x}$
27 Sep 73	2+	1971	2	32.0 ± 1.00	31.0–33.0	19.4 ± 0.2	26.3± 0.6				
27 Jun 73	3+	1970	28	42.0 ± 1.36	38.0–44.5	19.7 ± 1.11	29.5 ± 1.61	39.4 ± 1.56			
27 Sep 73			6	45.3 ± 2.46	40.0–47.5	19.0 ± 1.10	27.8 ± 1.82	38.7 ± 1.70			
11 Oct 73			8	45.2 ± 1.54	43.0–47.5	18.8 ± 1.05	28.4 ± 1.47	38.5 ± 1.35			
			42		38.0–47.5	$\bar{x}$ = 19.4 ± 1.10	$\bar{x}$ = 29.0 ± 1.61	$\bar{x}$ = 39.1 ± 1.54			
27 Jun 73	4+	1969	42	45.3 ± 1.56	39.0–47.5	17.7 ± 1.15	26.4 ± 1.92	36.6 ± 1.58	44.6 ± 1.81		
27 Sep 73			33	49.8 ± 1.73	47.0–54.0	18.0 ± 1.01	26.7 ± 1.70	36.6 ± 1.87	45.2 ± 1.81		
11 Oct 73			13	48.2 ± 1.76	45.5–51.5	17.6 ± 0.82	26.0 ± 0.98	34.9 ± 1.74	43.3 ± 1.71		
			88		39.0–54.0	$\bar{x}$ = 17.8 ± 1.05	$\bar{x}$ = 26.5 ± 1.70	$\bar{x}$ = 36.3 ± 1.71	$\bar{x}$ = 44.6 ± 1.80		
27 Jun 73	5+	1968	9	49.7 ± 1.27	48.0–51.5	17.1 ± 0.81	25.1 ± 1.83	35.2 ± 1.51	43.4 ± 1.29	48.8 ± 1.47	
27 Sep 73			1	53.0	53.0	18.5	27.6	37.1	45.5	49.5	
			10		48.0–53.0	$\bar{x}$ = 17.3 ± 0.87	$\bar{x}$ = 25.7 ± 1.84	$\bar{x}$ = 35.4 ± 1.54	$\bar{x}$ = 43.6 ± 1.37	$\bar{x}$ = 48.9 ± 1.41	
27 Sep 73	6+	1967	1	64.0		20.7	29.6	38.5	46.1	51.5	59.0
			143			$\bar{x}$ = 18.3 ± 1.03 n = 143	$\bar{x}$ = 27.2 ± 1.66 n = 143	$\bar{x}$ = 37.2 ± 1.64 n = 141	$\bar{x}$ = 44.5 ± 1.74 n = 99	$\bar{x}$ = 49.1 ± 1.28 n = 11	

The authors assumed the standard length as the base for the back readings. To compare the growth of zander from Lake Jeziorak with zander from the Szczecin Lagoon and Lake Dąbie (Neja and Turowska 1998) based on total length, the data for fish longer than 26 cm were calculated using a formula developed by Szypuła (1996):

$$TL = 1.5572 + 1.0882\ SL$$

The data for smaller fish were calculated according to Nagięć 1961):

$$SL = 0.87\ TL$$

RESULTS

The material in our disposal enabled determination of the growth rate separately for each of three year-classes under survey i.e. fish hatched in 1967, 1968, and 1969 for sequential age groups (Fig. 1A, B, C).

The growths of each age group were computed as weighted mean from a number of samples collected in a given fishing season (Tables 1, 2, 3, 4, 5)

Fig. 1A, B, C and Table 5 illustrate back-calculated growth indices declining throughout life. The fish captured as 2-year-old exhibited a faster growth rate than 3-year-olds, which means that they grew faster than the fish of the same year-class caught one year later. Three-year-old fish of the year-classes 1967 and 1969 (Fig. 1A, C) grew faster than four-year olds. Four-year-olds of the year-class of 1968 (Fig. 1B) grew faster than the five-year-olds. Only in this case (year-class of 1968) a quantity of 10 five-year-old specimens, deemed as sufficient, was available. There was also an exception. The fish caught in 1971 as 3-year-old showed a similar growth rate than those caught in 1972 as 4-year-olds (Fig. 1B—a statistically insignificant difference). Respectively for l_1, l_2, l_3 the values of F test were $F_1 = 1.905$ $P < 0.174$; $F_2 = 0.000543$ $P < 0.982$; $F_3 = 0.043$ $P < 0.837$).

The phenomenon of growth parameters, declining throughout life can be expressed in a form of inequality:

$$l_{1(2+)} > l_{1(3+)} > l_{1(4+)}$$

$$l_{2(2+)} > l_{2(3+)} > l_{2(4+)}$$

The range of differences between the curves reflecting fish growth at age of n and those for the age n + 1, decreases with the age.

$$l_{1(n)} - l_{1(n+1)} > l_{1(n+1)} - l_{1(n+2)} > l_{1(n+2)} - l_{1(n+3)}$$

$$l_{2(n)} - l_{2(n+1)} > l_{2(n+1)} - l_{2(n+2)} > l_{2(n+2)} - l_{2(n+3)}$$

where:

$l_{1(n)}$, first year reading from scales of fish at the age of n

$l_{1(n+1)}$, first year reading from scales of fish at the age of n + 1

$l_{2(n)}$, second year reading from scales of fish at the age of n

$l_{2(n+1)}$, second year reading from scales of fish at the age of n + 1.

Table 5

The growth rate of zander, *Sander lucioperca* estimated following a single year-class throughout its entire life

Period of capture	Age at capture	Number of fish	Computed size at scale annuli					The body size differences				
			l_1 [cm]	l_2 [cm]	l_3 [cm]	l_4 [cm]	l_5 [cm]	l_1 [cm]	l_2 [cm]	l_3 [cm]	l_4 [cm]	
		N	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x}$	$\bar{x}$	$\bar{x}$	$\bar{x}$	
1967 year-class												
Sep Oct Nov 1969	2+	23	20.1 ± 1.02	32.1 ± 2.14								mean of 3 samples
differences								3.0	6.1			
16 Jul–17 Dec 1970	3+	275	17.1 ± 2.32	26.0 ± 3.67	37.4 ± 2.75							mean of 6 samples
differences								0.4	1.3	2.1		
27 Jul–29 Oct 1971	4+	28	16.7 ± 1.80	24.7 ± 3.01	35.3 ± 3.50	44.0 ± 2.21						mean of 2 samples
differences*												
19 Jul–8 Sep 1972	5+	6	19.2 ± 1.13	28.7 ± 2.03	38.2 ± 1.00	45.7 ± 0.78	50.8 ± 1.59					mean of 3 samples
1968 year-class												
20 Aug–17 Dec 1970	2+	27	19.5 ± 1.31	30.6 ± 2.02								mean of 5 samples
differences								2.5	4.3			
27 Jul–29 Oct 1971	3+	38	17.0 ± 16.8	26.3 ± 2.83	37.5 ± 2.37							mean of 2 samples
differences								–0.6	0.0	–0.1		
19 Jul–8 Sep 1972	4+	10	17.6 ± 1.69	26.3 ± 2.94	37.6 ± 2.59	45.3 ± 1.61						mean of 3 samples
differences								0.3	0.6	2.2	1.7	
27 Jun–27 Sep 1973	5+	10	17.3 ± 0.87	25.7 ± 1.84	35.4 ± 1.54	43.6 ± 1.37	48.9 ± 1.41					
differences												
1969 year-class												
29 Oct 1971	2+	4	19.6 ± 0.95	31.9 ± 0.99								one sample
differences*												
19 Jul–8 Sep 1972	3+	55	18.6 ± 0.98	28.3 ± 1.89	38.4 ± 1.75							mean of 3 samples
differences								0.8	1.8	2.1		
27 Jun–11 Oct 1973	4+	88	17.8 ± 1.05	26.5 ± 1.70	36.3 ± 1.71	44.6 ± 1.80						mean of 3 samples

* age groups comprising fewer than 10 specimens were not included in the statistical processing of the material

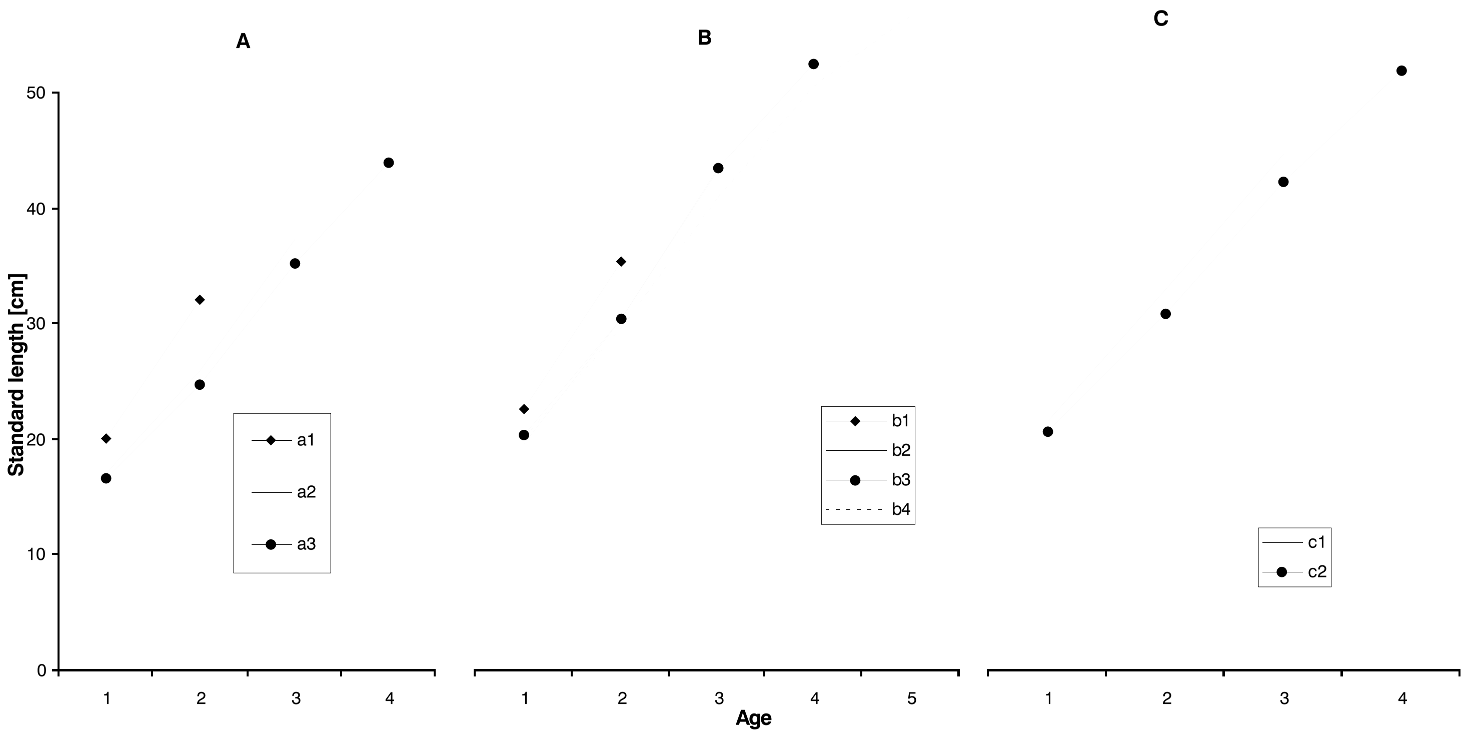


Fig. 1. Zander, *Sander lucioperca* in Lake Jeziorak; the growth rate estimated following a single year-class throughout its entire life; examples of a *positive Lee's fenomenon*; A, year-class 1967; B, year-class 1968; C, year-class 1969; a1, 2+ fish captured in 1969 (n = 23); a2, 3+ fish captured in 1970 (n = 275); a3, 4+ fish captured in 1971 (n = 28); b1, 2+ fish captured in 1970 (n = 27); b2, 3+ fish captured in 1971 (n = 38); b3, 4+ fish captured in 1972 (n = 10); b4, 5+ fish captured in 1973 (n = 10); c1, 3+ fish captured in 1972 (n =55); c2, 4+ fish captured in 1973 (n = 88)

The most extensive differences are between fish aged 2+ and those aged 3+ that is in the period of attaining the legal size (Fig. 1A, B; Table 5). The magnitude of the differences between the fish aged 3+ and 4+ is smaller. For example for an abundant year-class of 1967 those differences were:

$$l_{1(2+)} - l_{1(3+)} = 20.1 - 17.1 = 3.0 \text{ cm}$$
$$l_{1(3+)} - l_{1(4+)} = 17.1 - 16.7 = 0.4 \text{ cm}$$
$$l_{2(2+)} - l_{2(3+)} = 32.1 - 26.0 = 6.1 \text{ cm}$$
$$l_{2(3+)} - l_{2(4+)} = 26 - 24.7 = 1.3 \text{ cm}$$

The existence and the magnitude of differences between the growth parameters of fish aged 4+ and 5+, consisting solely of legal size specimens, were recorded for only one year-class (1968). Therefore it is difficult to draw general conclusions.

As it is evident from Table 5, the differences, in each pair of readings in all quoted examples, grow with the age:

$$l_{1(n)} - l_{1(n+1)} < l_{2(n)} - l_{2(n+1)} < l_{3(n)} - l_{3(n+1)}$$

For example the mean differences between the readings for two- and three-year-olds (1967 and 1968) were:

$$l_{1\,(2+)} - l_{1(3+)} = 2.75 \text{ cm for } \frac{3.0 + 2.5}{2} = 2.75$$

$$l_{2\,(2+)} - l_{2(3+)} = 5.20 \text{ cm for } \frac{6.1 + 4.3}{2} = 5.20$$

Analogous differences between the readings for three- and four-year-olds for three year-classes (1967, 1968, 1969) were:

$$l_{1\,(3+)} - l_{1(4+)} = 0.20 \text{ cm for } \frac{0.4 + (-0.6) + 0.8}{2} = 0.20$$

$$l_{2\,(3+)} - l_{2(4+)} = 1.03 \text{ cm for } \frac{1.3 + 0.0 + 1.8}{3} = 1.03$$

$$l_{3\,(3+)} - l_{3(4+)} = 1.36 \text{ cm for } \frac{2.1 + (-0.1) + 2.1}{3} = 1.36$$

This phenomenon indicates that the factor responsible for the differences observed was predominantly the faster growth within the last year, which is visualised on the graph as diverging growth curves.

Zander in Lake Jeziorak lives up to 10 years, whereas its exploitation is in 80% based on fish aged 3+ and 4+ (Nagięć 1978). This explains the deficiency of 5-year-old and older fish in the samples.

Assuming the representativeness of the samples of the exploited stock, collected with the summer seine, the declining growth rate, observed in sequential years for three zander year-classes, can be used as another example of a *positive Lee's phenomenon in inclusive sense* caused by a higher mortality of faster growing fish (Ricker 1969, 1979).

The legal size (TL) of zander is 1000 g, which is associated with the standard length of 41.2 cm. Such size is attained by zander specimens aged 2+ and 3+, that is being in their third and fourth year of life, respectively (Tables 1, 2, 3, 4, 6). Those two age groups captured with a seine consisted of both legal-size and undersized specimens (Table 6).

Two-year-old fish attain the legal size by the end of their third growth season[1]. First 2-year-olds in beach-seine catches were encountered in August (1970). Their mean weight was 849 g. The period of attaining the legal size is extended throughout one year (Table 6). For example, the weight of five 2-year-old fish captured in November 1969 ranged from 1007 to 1145g (1062 g on average) which means that they all reached the legal size. The weight of 36 three-year-olds in October 1970 ranged from 848 to 1485 g (1176 g on average). The undersized fish constituted 17% of that group and they weighed 951 g, on average. Analogous data can be found for the year-class of 1968.

Table 6

Recruitment of the exploited stock of zander, *Sander lucioperca*

Data of capture	Age at capture	Year class	Number of fish	Mean Body weight at capture [g]	Fish approaching the minimum size			Fish exceeding the minimum size		
			N	$\bar{x} \pm SD$	N	%	Mean Body weight [g] $\bar{x} \pm SD$	N	%	Mean Body weight [g] $\bar{x} \pm SD$
Sep 1969	2+	1967	8	943 ± 126.23	5	62.5	863 ± 79.86	3	37.5	1078 ± 53.20
Oct 1969			10	1003 ± 69.07	5	50.0	944 ± 2.84	5	50.0	1062 ± 51.29
Nov 1969			5	1062 ± 51.29	0	0.00	—	5	100.0	1062 ± 51.59
			23		10	43.5		13	56.5	
20 Aug 70		1968	3	849 ± 45.53	3	100	849 ± 45.53	0	0	
9 Sep 70			8	879 ± 69.18	8	100	879 ± 69.18	0	0	
9 Oct 70			3	734 ± 144.35	3	100	734± 144.35	0	0	
11 Nov 70			5	1038 ± 65.74	3	60	985 ± 0.0	2	40	1117 ± 19.60
17 Dec 70			8	1039 ± 113.38	4	50	959 ± 29.17	4	50	1120 ± 108.79
			27		21	78		6	22	
16 Jul 70	3+	1967	20	1127 ± 132.46	4	20	916 ± 48.51	16	80	1179 ± 86.59
20 Aug 70			80	1124 ± 179.13	25	31	934 ± 51.26	55	69	1212 ± 146.24
9 Sep 70			63	1193 ± 207.93	6	10	956 ± 31.56	57	90	1241 ± 152.09
9 Oct 70			36	1176 ± 149.82	6	17	951 ± 52.58	30	83	1221 ± 118.93
			199		41	21		158	79	
27 Jul 71		1968	20	1031 ± 131.96	10	50	920 ± 51.40	10	50	1143 ± 85.06
29 Oct 71			18	1342 ± 222.38	1	6	881	17	94	1369 ± 197.80
			38		11	29		27	71	
19 Jul 72		1969	23	1094 ± 97.20	3	13	962 ± 16.73	20	87	1114 ± 88.43
5 Aug 72			21	1247 ± 109.54	0	0	—	21	100	1247 ± 109.54
8 Sep 72			11	1178 ± 210.36	2	18	950 ± 35.15	9	82	1228 ± 199.47
			55		5	9		50	91	
27 Jun 73		1970	28	1060 ± 99.91	7	25	922 ± 70.41	21	75	1106 ± 56.45
27 Sep 73			6	1336 ± 200.26	1	17	915	5	83	1421 ± 74.49
11 Oct 73			8	1324 ± 136.48	0	—	—	8	100	1324 ± 136.48
			42		8	19		34	81	

[1] Zander is a thermophilous species and under Polish climatic conditions it grows best in summer (Nagięć 1980).

Among the three-year-olds (3+), the last undersized specimens were captured in October. Their percentage share between July and December (1970) declined from month to month (Table 6). Those fish were either in the course of their fourth vegetation season or they completed four growth seasons. Zander in Lake Jeziorak grows from June to the end of September (Nagięć 1980).

The above-mentioned data, along the back readings of the length, illustrate the growth range of the recruitment year-class.

The earlier-mentioned comparison of the growth curves of four age groups (2+, 3+, 4+, 5+), separately for each year class (Fig. 1A, B, C; Table 5), permits, what have been mentioned earlier, to formulate a hypothesis, that in the population of zander inhabiting Lake Jeziorak the faster-growing fish are more available to fishing gear (summer seine). This provokes a question whether the process of earlier retreat of the faster-growing fish can be observed during analysing fish samples collected in sequential months of a fishing season?

The material in the present authors' disposal enabled to plot the growth curves of:

- three-year-old fish of the year-class 1967 in sequential 6 months (July–December) of the season of 1970 (Table 1, Fig. 2A)[2],
- three-year-old fish of the year-class 1968 within two months (July, October) of the season 1971 (Table 2, Fig. 2B),
- three-year-old fish of the year-class 1969 in sequential 3 months (July, August, September) of the season of 1972 (Table 3, Fig. 2C), and
- four-year-old fish of the year-class 1969 in sequential 3 months (June, September, October) of the season of 1973 (Table 4, Fig. 2D).

The year-class of 1967 first appeared in the catches in the autumn of 1969. From this date on, till October 1970 (i.e. in July, August, September, and October) the fish caught showed distinctly declining growth rates (Table 1, Fig. 2A). This means that the regularity observed for individual year-classes repeated itself once again.

[2] Fairly similar data from August and September 1970 and November and December 1970 were merged to ensure a better clarity of Fig. 2A.

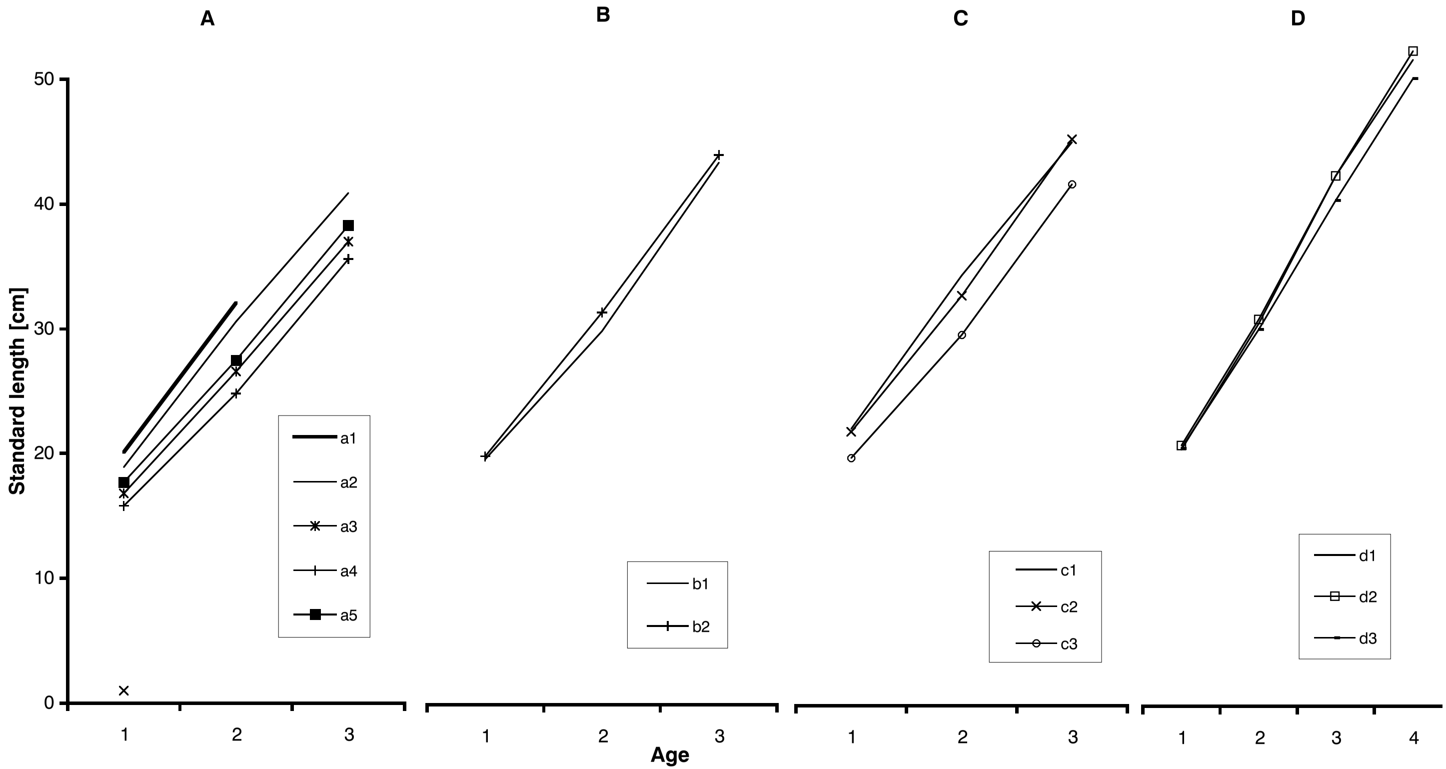


Fig. 2. The growth rate of zander, *Sander lucioperca*, representing a single year-class captured by summer seine; examples of a *positive Lee's phenomenon*: A, year-class 1967; B, year-class 1968; (the exception proves the rule); C, year-class 1969; D, year-class 1969; a1, Sep Oct Nov 1969 (n = 23); a2, 16 Jul 1970 (n = 20); a3, Aug Sep 1970 (n = 143); a4, 9 Oct 1970 (n = 36); a5, Nov Dec 1970 (n = 76); b1, 27 Jul 1971 (n = 20); b2, 29 Oct 1971 (n = 18); c1, 19 Jul 1972 (n = 23); c2, 5 Aug 1972 (n = 21); c3, 8 Sep 1972 (n = 11); d1, 27 Jun 1973 (n = 42); d2, 27 Sep 1973 (n = 33); d3, 11 Oct 1973 (n =13)

On the other hand, the growth curves of fish captured in November and December 1970 (76 specimens) appeared to be higher than those of the fish caught in August, September, and October of the same year. Higher growth indices occurred only in recruits caught in autumn of the previous year and in July 1970 (Table 1, Fig. 2A). An explanation of this “inconsistency” is given in Discussion.

Only two low-number samples were taken within the fishing season of 1971 (Fig. 2B, Table 2). The growth rate of fish captured in October (18 specimens) was faster than that of the fish collected in July (20 specimens).

In the season of 1972 the fish aged 3+, present in the catches from July through September, consequently grew decreasingly slower (Fig. 2C, Table 3).

In the season of 1973 the fish aged 4+, caught in June and in August, grew at a similar pace, whereas the fish captured in October—a little bit slower (Table 4; Fig. 2D).

The growth curves of 3- and 4-year-old fish of individual year-classes (1967, 1968, and 1969) were presented on Fig. 3A, B. In both cases, the year-class of 1969 was the fastest growing.

To characterise further the length growth of the three analysed year-classes the back-calculated length distributions and the real lengths at capture were plotted for sequential samples within individual year-classes (Table 7, Figs. 4, 5, 6, 7).

Table 7

Average growth rate (SL) [cm] of zander, *Sander lucioperca*, from different reservoirs

Age group	No. of specimens	l_1	l_2	l_3	l_4	l_5	l_6
2+	57	19.72	31.16				
3+	410	17.53	26.64	37.72			
4+	147	17.43	26.21	36.58	44.76		
5+	23	18.01	26.99	37.03	45.20	50.45	
6+	3	19.50	28.00	36.00	46.30	52.70	58.95
	639	17.73	26.96	37.39	44.84	50.63	58.95
		639	639	582	172	25	2
Individual years							
1970		17.3	26.5	37.5	46.6	57.9	
n		328	328	301	26	5	
1971		17.0	25.9	36.6	44.0	510	
n		72	72	68	30	2	
1972		18.5	27.9	38.2	45.5	51.1	53.9
n		73	73	72	17	7	1
1973		18.3	27.2	37.1	44.5	49.1	59.0
n		143	143	141	99	11	1

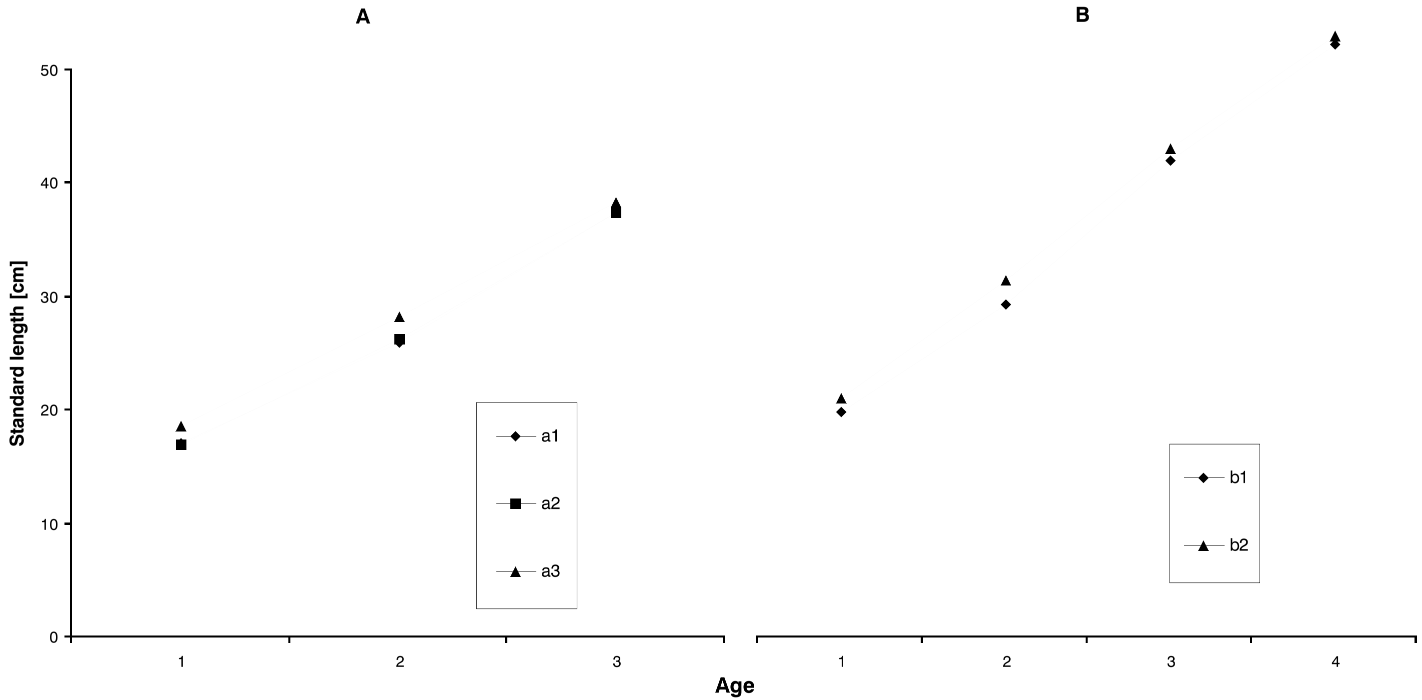


Fig. 3. The growth rate (SL, cm) of three- (A) and four-year-old (B) zander, *Sander lucioperca*, calculated for individual year-classes; a1, year-class 1967 (n = 275) captured in 1970; a2, year-class 1968 (n = 38) captured in 1971; a3, year-class 1969 (n = 55) captured in 1972; b1, year-class 1967 (n = 28) captured in 1971; b2, year-class 1969 (n = 88) captured in 1973

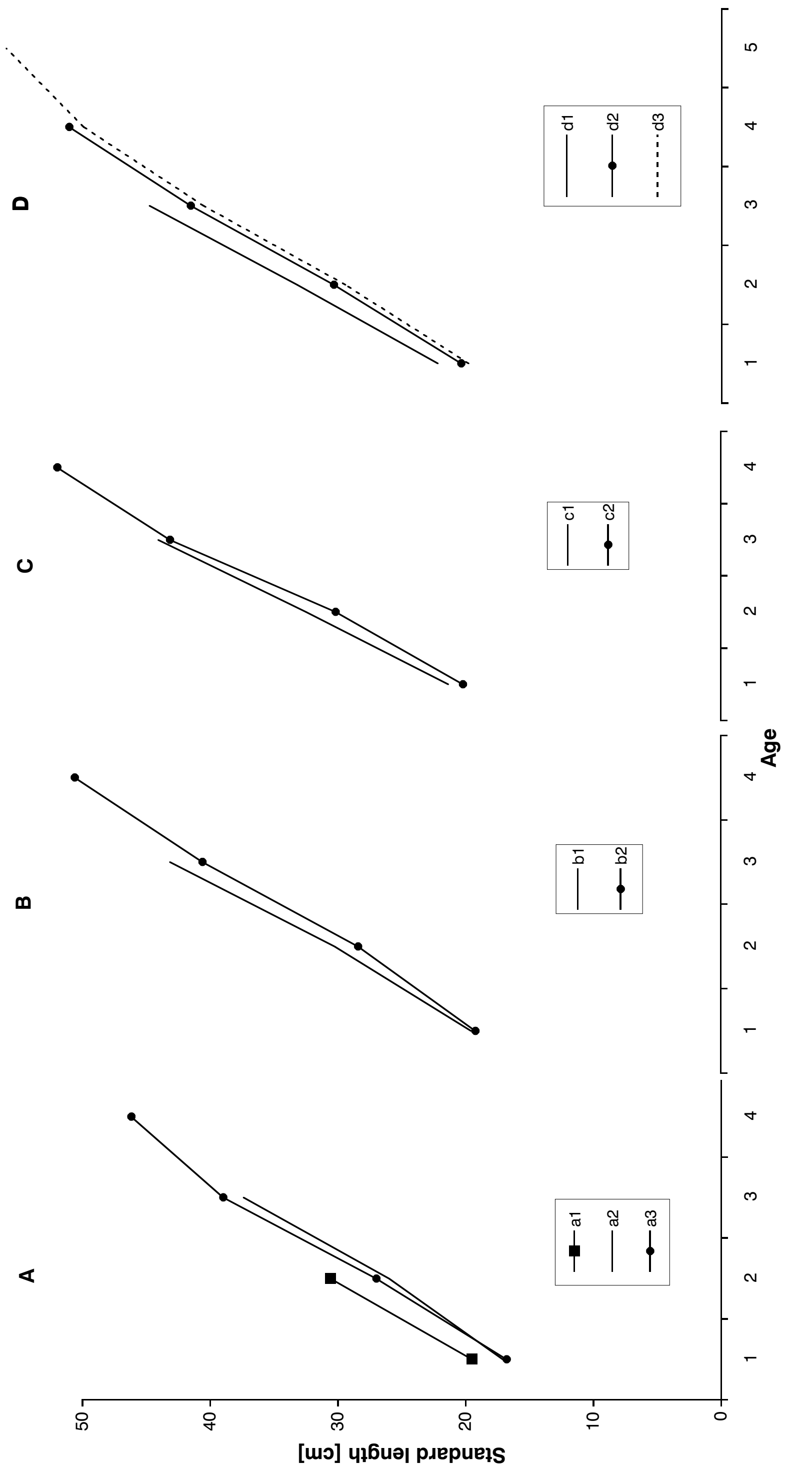


Fig. 4. Zander, *Sander lucioperca*, in Lake Jeziorak; the growth rate of single age groups captured in one fishing season: A, 1970; B, 1971; C, 1972; D, 1973; examples of a *positve Lee's phenomenon*; a1, 2+ fish, year-class 1968 (n = 27); a2, 3+ fish, year-class 1967 (n = 275); a3, 4+ fish, year-class 1966 (n = 21); b1, 3+ fish, year-class 1968 (n = 38); c1, 3+ fish, year-class 1969 (n = 55); c2, 4+ fish, year-class 1968 (n = 10); d1, 3+ fish, year-class 1970 (n = 42); d2, 4+ fish, year-class 1969 (n = 88); d3, 5+ fish, year-class 1968 (n = 10)

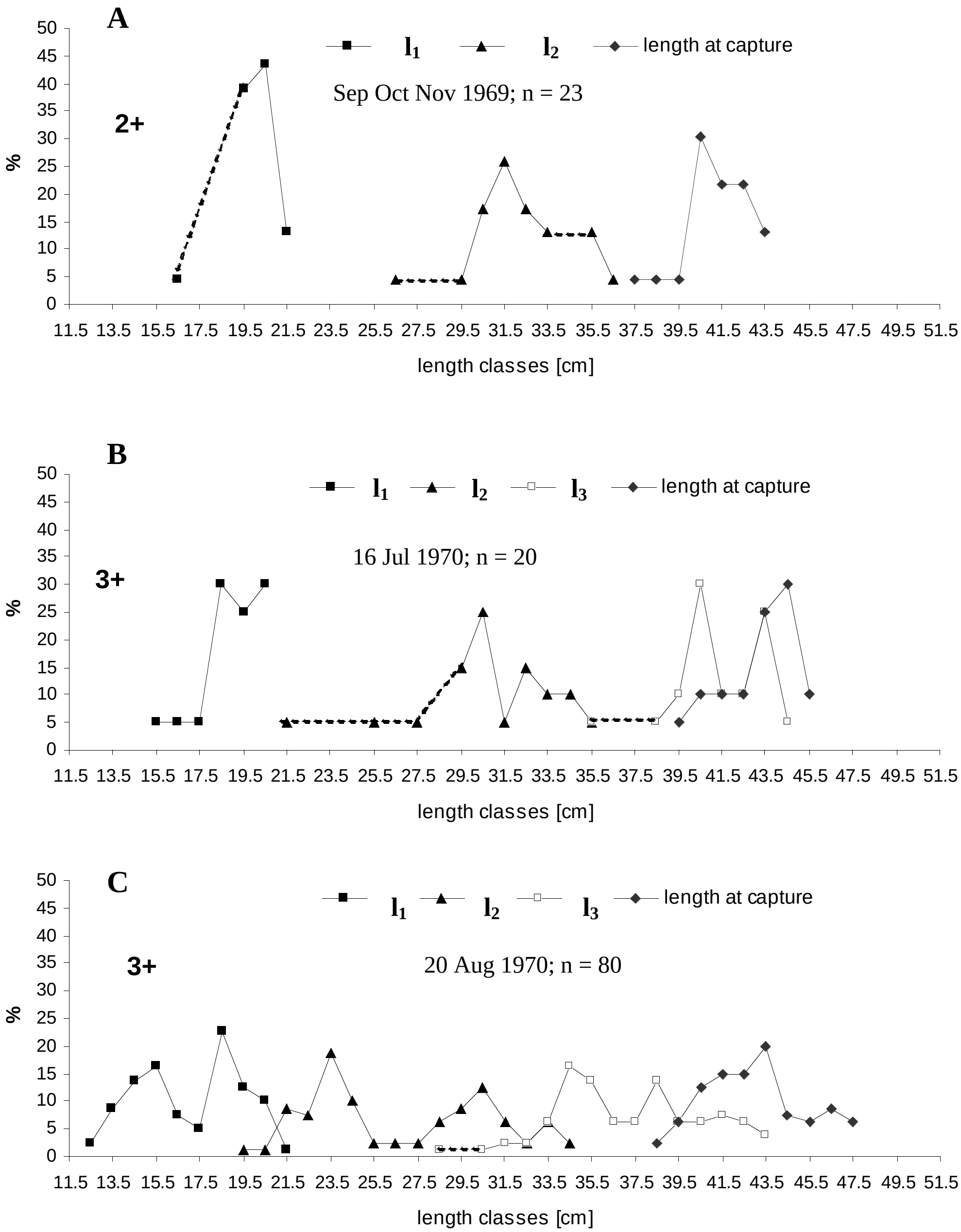


Fig. 5 A–C. Zander, *Sander lucioperca*, in Lake Jeziorak; year-class 1967; length frequency distributions of calculated growth (l_1, l_2, l_3) and of lengths measured at capture

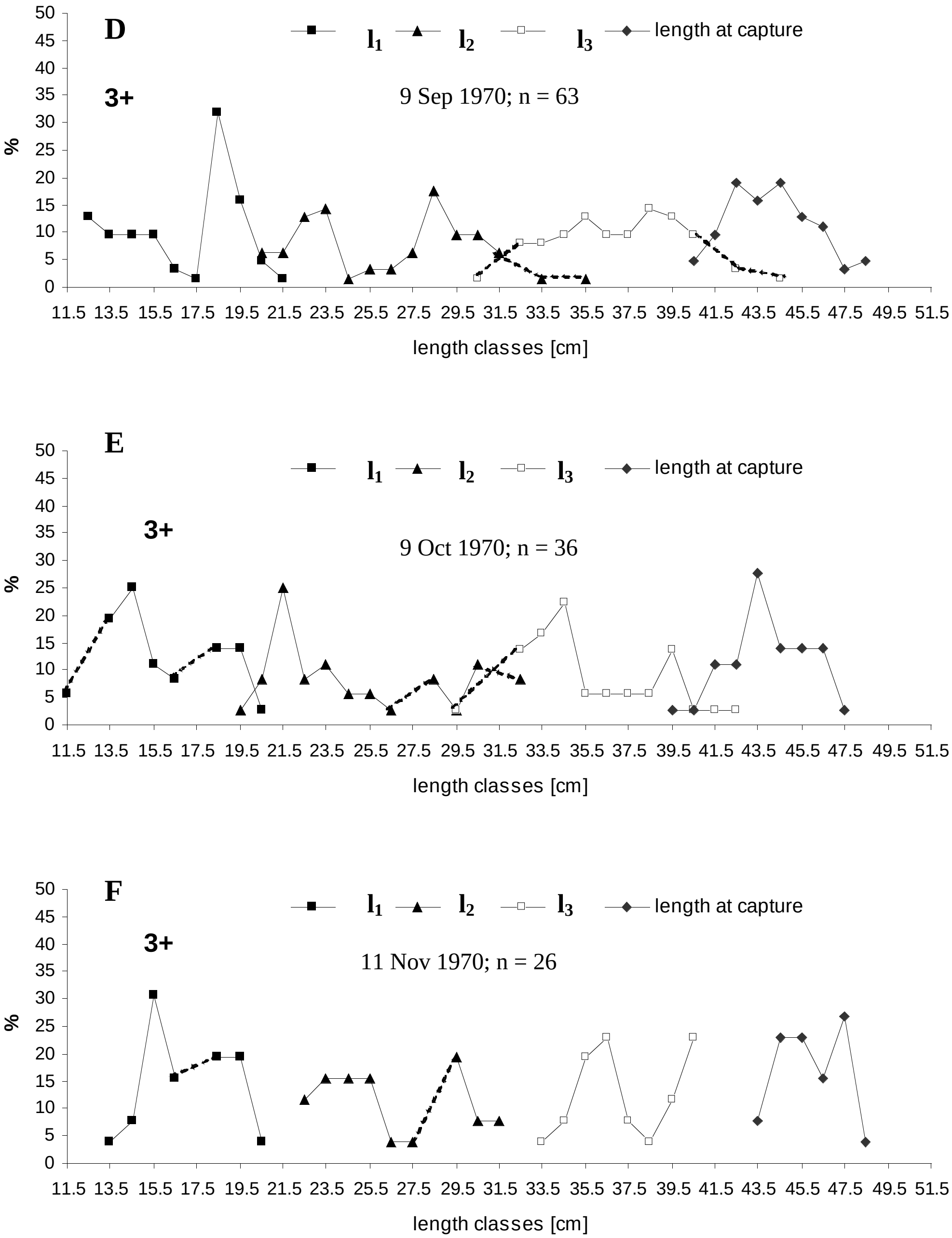
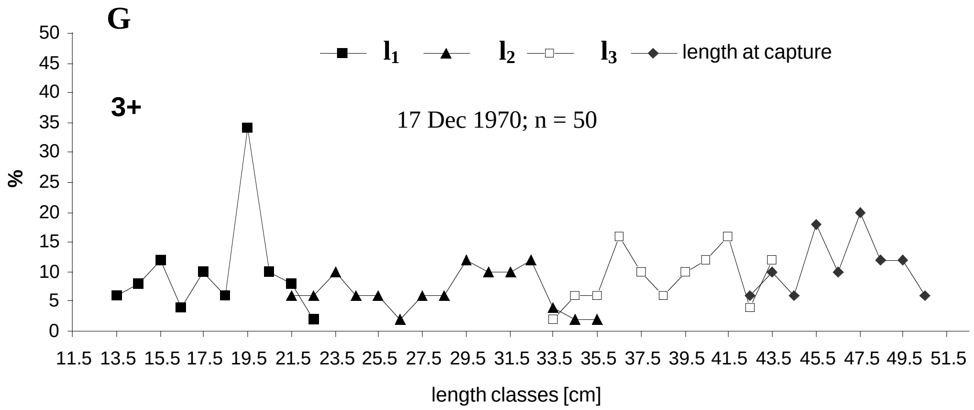


Fig. 5 D–F. Zander, *Sander lucioperca*, in Lake Jeziorak; year-class 1967; length frequency distributions of calculated growth (l_1, l_2, l_3) and of lengths measured at capture



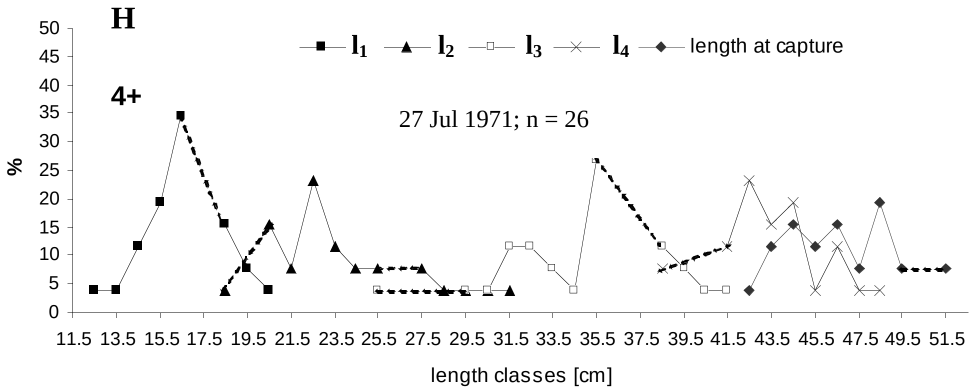


Fig. 5 G–H. Zander, *Sander lucioperca*, in Lake Jeziorak; year-class 1967; length frequency distributions of calculated growth (l_1, l_2, l_3, l_4) and of lengths measured at capture

Each of the year-classes represents a different type of distribution. The first sample of the most numerous year-class of 1967, consisting of autumn recruits, aged 2+ had a monomodal, almost symmetrical distribution (Fig. 5A). On the other hand, a high-span distribution, without distinctly developed peaks, persisted starting from August 1970 (Table 7, Fig. 5C, D, E, F, G, H). Among three-year fish there were specimens of standard lengths ranging from 38.5 to 50.0 cm (Table 8). Among the back-read values, a particularly wide range was observed for the second year of life (l_2). For 2-year-olds of the year-class of 1967, captured in 1970 the standard lengths were from 19.7 to 35.5 cm, on the average 13.5 cm (for 6 samples). Such wide range covered the pre-recruitment period, because the zander after completing their second year of life,

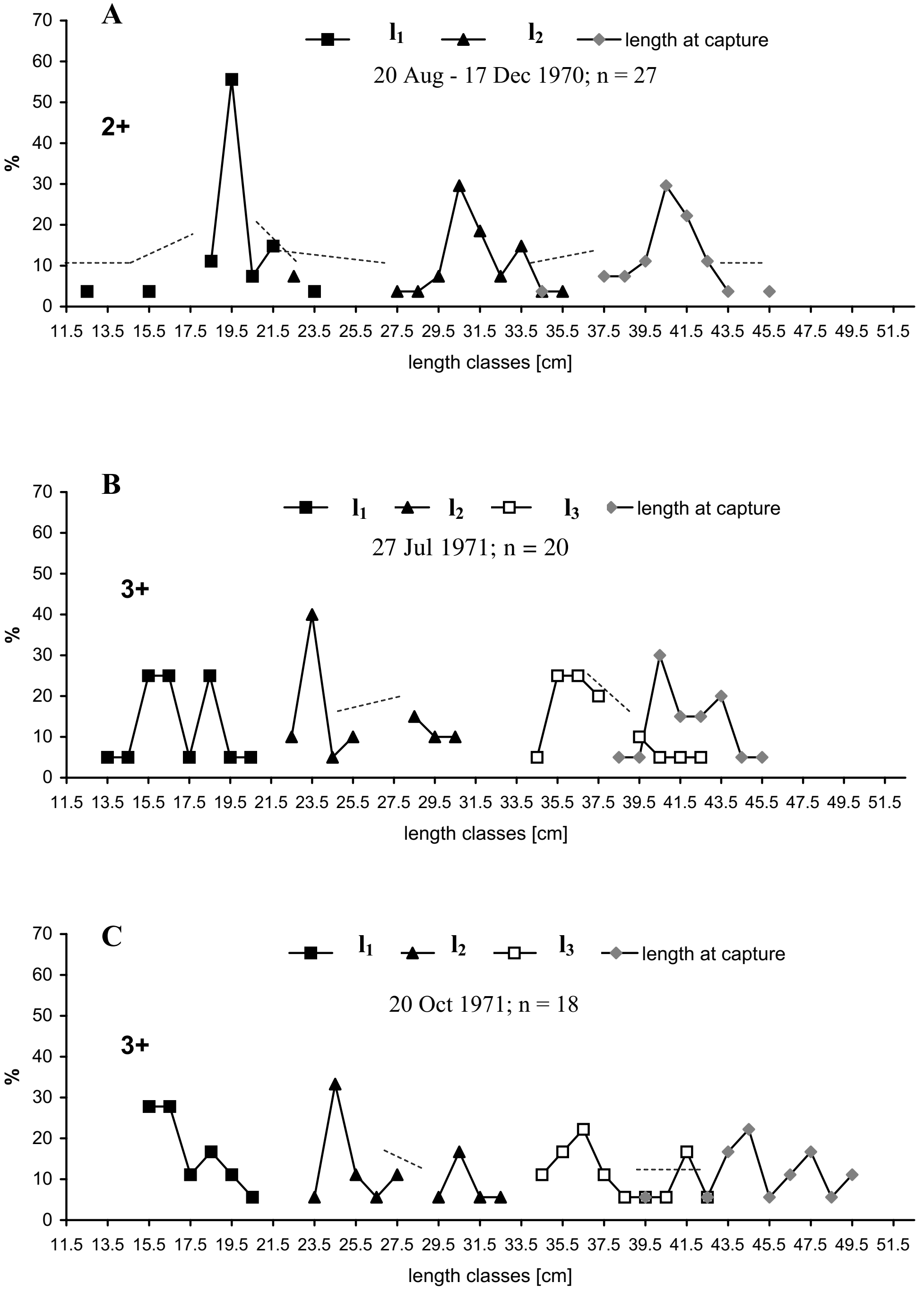


Fig. 6. Zander, *Sander lucioperca*, in Lake Jeziorak; year-class 1968; length frequency distributions of calculated growth (l_1, l_2, l_3) and of lengths measured at capture

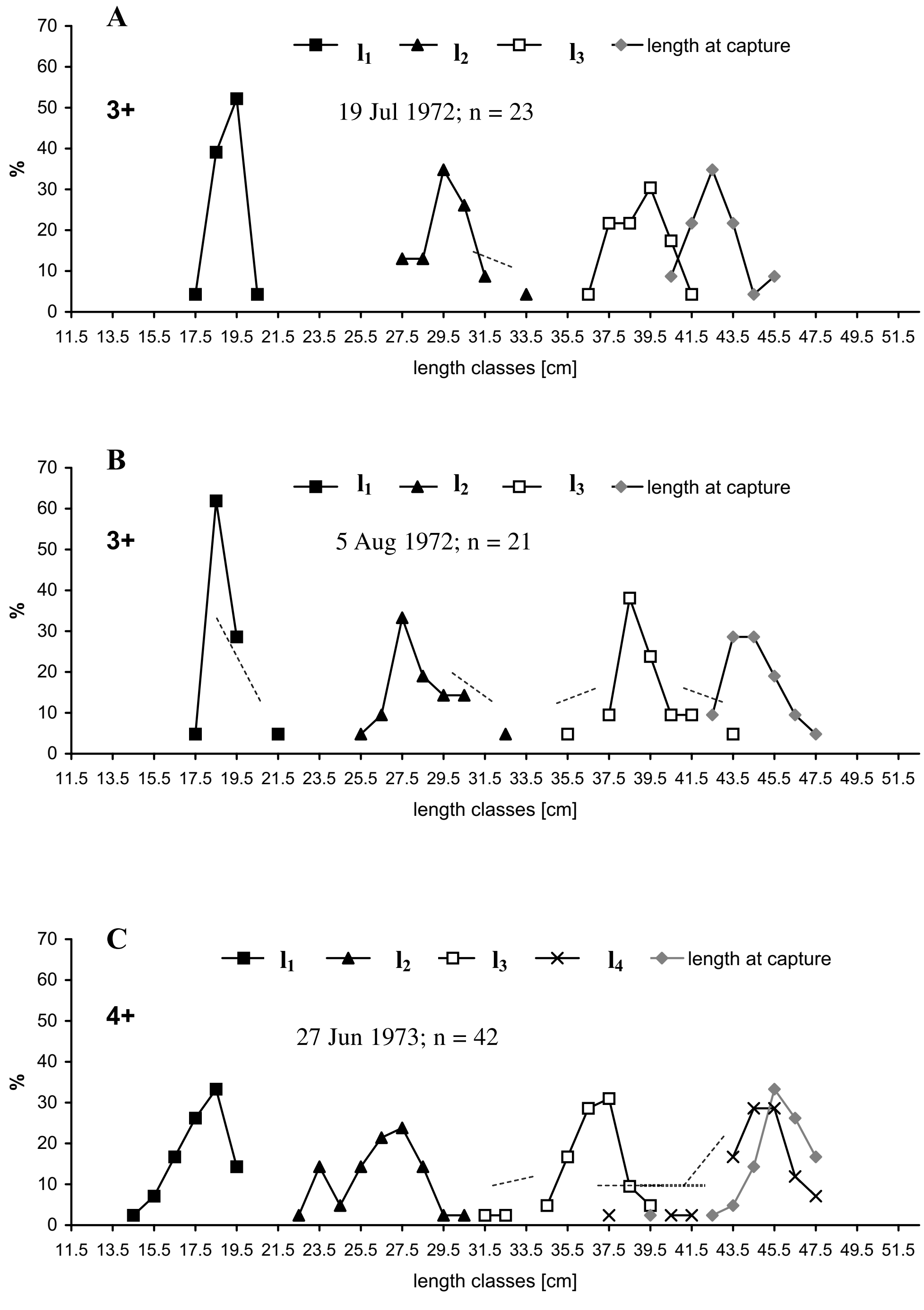


Fig. 7 A–C. Zander, *Sander lucioperca*, in Lake Jeziorak; year-class 1969; length frequency distributions of calculated growth (l_1, l_2, l_3, l_4) and of lengths measured at capture

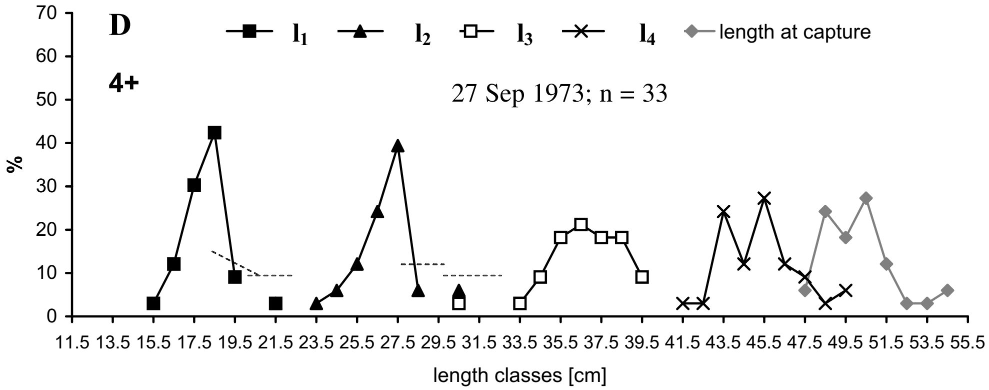


Fig. 7 D. Zander, *Sander lucioperca*, in Lake Jeziorak; year-class 1969; length frequency distributions of calculated growth (l_1, l_2, l_3, l_4) and of lengths measured at capture

by the end of their third growth season become available for fishing (Table 6).

Three, low-numbered, samples of the year-class of 1968, represented bimodal length distributions (Fig. 6A, B, C).

On the other hand, the distributions of the year-class of 1969 were represented by two samples taken in 1972 and two—taken at 1973 (Fig. 7A, B, C, D) were consequently monomodal of a small growth length frequency distribution. For example, the range of the back-readings for the first year (l_1) was from 14.9 to 21.7 cm, on the average 4.3 cm. For the second year (l_2) it was from 21.5 to 33.5 cm (7.1 cm on average) (Table 7).

The monomodal distribution allowed, according to Ricker (1969) to calculate coefficients of skewness. Those indices ranged from 0.05 to 0.69 and nine times they were negative (–) and six times positive (+). It suggests a weakly-expressed and non-directed asymmetry. According to Szulc (1972) we deal with a substantial asymmetry when the coefficient of skewness exceeds values of +1 or –1. In the frames of four sequential samples (from July 1972 to September 1973) the values of this factor fluctuated but they did not grow (Table 8). The year-class of 1969, exhibiting the slowest length frequency distribution, among the discussed three year-classes, was among the fastest-growing year-classes (Fig. 3A, B).

Comparative analysis of the length distributions requires very numerous materials. This requirement has not been met for all samples. Nevertheless, the materials presented above indicate that each year-class exhibits its own length distribution, both back-calculated one as well as measured at capture.

Table 8

Length-frequency distributions of back-calculated lengths [cm] and indexes of skewness

Sampling date	age	No	l_1				l_2				l_3				l_4				SL			
			Range in SL	$\bar{x}$ ±SD	Dx	w.s.	Range in SL	$\bar{x}$ ±SD	Dx	w.s.	Range in SL	$\bar{x}$ ± δ	Dx	w.s.	Range in SL	$\bar{x}$ ± SD	Dx	w.s	Range in SL	$\bar{x}$ ± SD	Dx	w.s.
Year-class 1967																						
Sep Oct Nov 1969	2+	23	16.5–21.8 (5.3)	20.1 ± 1.02	20.5	0.39	26.7–36.4 (9.7)	32.1 ± 2.14	31.5	0.28									37.4–43.1 (5.7)	41.1 ± 1.42	40.5	0.42
16 Jul 1970	3+	20	15.4–21.4 (6.0)	18.9 ± 1.43	bi	—	23.5–35.5 (12.0)	30.6 ± 2.84	bi	—	35.5–44.0 (8.50)	40.9 ± 2.12	bi						39.0–45.5 (6.5)	42.8 ± 1.72	44.5	0.99
20 Aug 1970	3+	80	12.2–21.2 (9.0)	16.9 ± 2.32	bi	—	19.9–34.0 (14.1)	26.7 ± 3.90	bi	—	28.5–43.0 (14.5)	37.0 ± 3.23	bi						38.5–47.5 (9.0)	42.7 ± 2.24	43.5	0.36
9 Sep 1970	3+	63	12.0–21.4 (9.4)	16.7 ± 2.61	bi	—	20.3–35.3 (15.0)	26.4 ± 3.71	bi	—	32.1–44.0 (11.9)	36.9 ± 2.87	bi	—					40.0–48.0 (8.0)	43.9 ± 2.00	bi	—
9 Oct 1970	3+	36	11.0–20.6 (9.6)	15.8 ± 2.52	bi	—	19.7–32.9 (13.2)	24.8 ± 3.96	bi	—	29.8–42.0 (12.2)	35.6 ± 2.16	bi	—					39.0–47.0 (8.0)	43.4 ± 1.86	43.5	0.05
11 Nov 1970	3+	26	13.5–20.0 (6.5)	17.0 ± 1.92	bi	—	22.3–31.2 (8.9)	26.3 ± 2.86	bi	—	33.2–40.9 (7.7)	37.2 ± 2.22	bi	—					43.0–48.0 (5.0)	45.5 ± 1.42	bi	—
17 Dec 1970	3+	50	13.2–22.2 (9.0)	18.1 ± 2.37	poly	—	21.4–35.0 (13.6)	28.1 ± 3.79	bi	—	33.6–43.3 (9.7)	38.9 ± 2.77	bi	—					42.0–50.0 (12.0)	46.4 ± 2.25	poly	—
27 Jul 1971	4+	26	12.5–20.1 (7.6)	16.5 ± 1.82	16.5	0.00	18.8–31.5 (12.7)	24.0 ± 3.24	bi	—	25.1–41.4 (16.3)	34.7 ± 3.72	bi	—	38.3–48.5 (10.2)	43.5 ± 2.37	poly	—	42.0–51.0 (9.0)	46.3 ± 2.36	poly	—
Year-class 1968																						
Aug Sep Oct Nov Dec 1970	2+	27	12.6–23.8 (11.2)	19.5 ± 1.31	bi	—	22.0–35.6 (13.6)	30.6 ± 2.02	bi	—									34.0–45.0 (11.0)	40.2 ± 2.09	40.5	0.14
27 Jul 1971	3+	20	13.3–20.2 (6.9)	16.9 ± 1.76	bi	—	22.5–30.8 (8.3)	25.7 ± 2.74	bi	—	34.0–42.0 (8.0)	37.3 ± 2.20	36.0	0.59					38.5–45.0 (6.5)	41.6 ± 1.76	bi	—
29 Oct1971	3+	18	15.0–20.3 (5.3)	17.1 ± 1.60	bi	—	23.6–32.5 (8.9)	27.0 ± 2.92	poly	—	34.1–42.3 (8.2)	37.8 ± 2.55	bi	—					39.5–49.5 (10.0)	45.3 ± 2.54	bi	—
Year-class 1969																						
19 Jul 1972	3+	23	17.4–20.5 (3.1)	19.1 ± 0.67	19.5	0.59	27.5–33.5 (6.0)	29.7 ± 1.38	29.5	0.14	36.5–41.5 (5.0)	38.9 ± 1.22	39.5	0.49					40.5–45.5 (5.0)	42.4 ± 1.23	42.5	0.08
5 Aug 1972	3+	21	17.6–21.7 (4.1)	18.9 ± 0.79	18.5	0.51	25.3–32.9 (7.6)	28.3 1.67	27.5	0.48	35.5–43.0 (7.5)	39.1 ± 1.55	38.5	0.39					42.0–47.0 (5.0)	44.3 ± 1.29	44.0	0.23
27 Jun 1973	4+	42	14.9–19.7 (4.8)	17.7 ± 1.15	18.5	0.69	22.5–30.8 (8.3)	26.4 ± 1.92	bi	—	31.4–39.1 (7.7)	36.6 ± 1.58	37.5	0.57	37.2–47.4 (10.2)	44.6 ± 1.81	45.0	0.22	39.0–47.5 (8.5)	45.3 ± 1.56	45.5	0.13
27 Sep 1973	4+	33	15.9–21.0 (5.1)	18.0 ± 1.01	18.5	0.49	21.5–30.1 (8.6)	26.7 ± 1.70	27.5	0.47	30.8–39.1 (8.3)	36.6 ± 1.87	36.5	0.05	41.6–49.1 (7.5)	45.2 ± 1.81	bi	—	47.0–54.0 (7.0)	49.8 ± 1.73	bi	—

Dx, the dominant
w.s., coefficient of skewness
bi, bimodal distributions
poly, polymodal distributions
$\bar{x}$, arithmetical mean

DISCUSSION

The fish of different sizes, within individual year-classes, are subject to different mortality in relation to size. This usually takes a form of greater mortality among larger individuals than among smaller ones of a given age, except during the first year or two of life. This phenomenon concerns all or almost all populations (Ricker 1969).

The growth dynamics of the zander population in Lake Jeziorak illustrates the mentioned above regularity. The fish fry in this lake showed high growth variability and cannibalism within individual year-classes (Nagięć 1966a, b). It is therefore evident that the slowest-growing fish were eliminated in their first year of life. This phenomenon commonly occurs in the fish of the genus *Sander* and related genera. For example it was described by Fox (1989) in walleye, *Stizostedion vitreus* (Mitchill, 1818) cultured in experimental ponds and by van Densen (1985) in zander fry at a Dutch brackish-water Lake Issel. No data are available in the literature about the second year of life (1+) of these fish. In their third year of life (2+) the fastest-growing specimens attain the legal size (1000 g) and become subjects of the intensive exploitation carried out in Lake Jeziorak. It seems that the principal cause of the *positive Lee's phenomenon*, observed in this body of water, have been the summer seine catches. The phenomenon is evident despite the empirical body–scale relationship taken in consideration during the back readings.

A particularly big difference between the fish growth rate back-calculated from the scales of 2-year-old fish and the growth rate back-calculated from the scales of 3-year-old fish representing the same year-class (Table 5, Fig. 1A, B) results from a fast growth of the first recruits and possibly their particular availability to fishing gear at the attainment of the legal size. The persistence of lower growth rates, estimated for 1 year older fish, i.e. differences between the fish aged n and n + 1 was noted also for age groups, where all specimens attained market size. An example can be the faster growth of 4-year-old than 5-year-old zander within the year-class of 1968 (Tables 3, 4, Fig. 1B).

Ricker (1969) demonstrated a consistent decline of the growth rate indices for sequential age-groups (2 through 6 years) of the same year-class cisco, *Coregonus artedi* Lesueur, 1818 in Silver Lake, Wisconsin.

The magnitude of differences between the growth-rate indices in sequential years of life were analysed between 2- and 3-year-olds, 3- and 4-year-olds, and 4- and 5-year-olds (Table 5). In five- out of six pairs compared, the differences increased with each year, up to the third year.

$$l_{1(2+)} - l_{1(3+)} < l_{2(2+)} - l_{2(3+)}$$

$$l_{1(3+)} - l_{1(4+)} < l_{2(3+)} - l_{2(4+)} < l_{3(3+)} - l_{3(4+)}$$

As mentioned earlier, a similar growth of 3- and 4-year-old fish of the year-class of 1968, was an exception (Fig. 1B). Such increase of differences in sequential years is visible on the graphs as divergence of the curves illustrating the length growth (Fig. 1A, B, C).

Ricker (1969) who analysed six age-groups of cisco, *Coregonus artedi,* comparing 5 curves of growth, recorded a divergence of growth curves between the second and third and third and fourth years of life. On the other hand, between the fourth and fifth year of life the lines came closer again.

In the present study there is only one example of the growth rate comparison between 4- and 5-year-olds (year-class of 1968, Table 5). And this example also indicates that the curve lines of zander come closer again.

In the fishing season of 1970, between July and December a total of 328 zander were collected (Table 1). These materials permitted to compare the growth rate of 3-year-old fish (year-class of 1967) captured between the beginning of summer and the late autumn. The fish acquired during July, August, September, and October grew decreasingly slower. On the other hand, the growth indices of the fish caught in November and December 1970 were higher than those of August (Fig. 2A). Still higher indices were recorded only for 2-year-old fish caught in the autumn of 1969 and the fish from the earliest seine catches, i.e. from July. Such step-wise growth acceleration of fish caught in November and December might have been related to the change of behaviour caused by seasonal meteorological changes, such as water temperature drop, autumn winds, solar radiation decrease. Many fish species form winter concentrations or pre-spawning concentrations. Better fishing results after the rapid drop of water temperature may indicate an increased availability to fishing gear. The above-mentioned explanation should be treated as a hypothesis.

A similar pattern accompanied the distinct growth rate decline of 3-year-old zander caught in successive samples from July, August, and September 1972, representing the year-class hatched in 1969 (Table 3, Fig. 2C).

The following questions were prompted by the present study: “What is the percentage rate of the males among the earliest recruits?” and “Was the selective catching of males, growing faster in the first phase of life, responsible for the domination of females in the oldest age groups?” (The latter phenomenon was observed by the present authors.)[3]

Whenever we deal with a selective mortality, the same material can yield as many growth curves as there are the age groups (Figs. 1, 2, 3, 4). If all age groups aged n are captured, than we have n-1 growth curves. In addition we can obtain a growth estimate through arrangement of the last readings of each age-group. This prompts further questions: Which of the growth curves best represents the population? Does “the best” growth pattern exist? What can be the effect of the selection of growth indices on further populational computing?

It is evident that a growth curve obtained for zander is dependent on the age structure of the sample it was based on.

According to Jones (1958), based on the proven theoretical hypothesis, skewness is not visible in the back-calculated length frequency distributions despite the elimination of the largest fish. Ricker (1969) confirmed the Jones (1958) hypothesis

[3] A quantitative domination of females among pikes longer than 60 cm was described by Załachowski 1973

following the growth rate of a single year-class of cisco, *Coregonus artedi* from Silver Lake (Wisconsin).

Out of three analysed year-classes of zander, each represented another distribution (Figs. 5, 6, 7). They were either bimodal (broods of 1967, excluding 2-year-old fish and 1968) or monomodal (year-class of 1969). Coefficient of skewness ranged from +0.05 (positive skewness) to –0.69 (negative skewness). According to Szulc (1972), the values of coefficient of skewness exceeding +1 or –1 denote an advanced asymmetry. This also confirms the Jones (1958) hypothesis.

The bimodal frequency distributions were characterised by a wider growth range than the monomodal ones (Table 7, Figs. 5, 6, 7). Regardless, however of the absolute values of this range for all three year-classes, the widest range of the back-calculated lengths was noted for the second year (l_2)(Table 7).

Such particularly wide growth range of the fish approaching the legal size, which is shortly before being available to fishing gear, may reflect an intensified food competition and consequently—the growth competition. This remains an open question for a further study.

It is highly possible that the reason behind the variability of those frequency distributions can be found in the fry period of the development. Differences were found in the size of zander fry captured at the same time at two lakes differing in their hydrobiological parameters and particularly the availability of zooplankton (Nagięć 1966a). The fry size differences were accompanied by differences in the composition of the food found in the alimentary tracts (Nagięć 1966a). Fry sample from Czarna Kuta Lake (19 June 1963) consisted of 121 specimens. The size attained by the fry in Czarna Kuta Lake was larger than that attained by the fry from Lake Jeziorak (26 June 1963), although the range of the length and weight were smaller in Czarna Kuta Lake (Nagięć 1966a). The food composition was determined in 13 specimens. The dominant item, considering the occurrence frequency and the weight, was zooplankton. At the same time the alimentary tracts of the fish from Lake Jeziorak contained fish (Nagięć 1966b). Both lakes differed also in the quantitative composition of the food items. One fish specimen in Czarna Kuta Lake had, on the average, 243 planktonic crustaceans in its alimentary duct, while a zander from Jeziorak Lake—only 21 crustaceans. Similar values of mean indices of fullness (Czarna Kuta Lake 146 $^0/_{000}$, Lake Jeziorak 159 $^0/_{000}$) resulted from very wide ranges of this parameter in Jeziorak Lake, caused by the presence of fish in the alimentary tracts (Nagięć 1966b). The described above relationships were a result of much higher abundance of plankton in a fertile, pond-like Czarna Kuta Lake (Anonymous 1958).

The growth and food of zander in its first year of life between June and October were studied in Lake Jeziorak within 1961 and 1962 (Nagięć 1966a, b). The growth rate of zander was distinctly higher in the warmer1961. Also in this warmer year there were more large planktonic forms (*Leptodora* sp. *Chaoborus* sp.) and two weeks earlier the fish switched to predation.

Although the data on the growth and feeding of fry were collected in 1961 and 1962 and the back-readings were performed for the fish hatched in 1967, 1968, and 1969, it can be assumed with a high probability that the type of growth of a given year class, expressed as the range of back-readings, is affected by the overall conditions of living encountered by zander in its first year of life.

Does the steady, equalised growth of the year-class of 1969 (Table 7, Fig. 7) constitute a continuation of a small length frequency distribution in the first year of life caused by the abundance of zooplankton or perhaps is a result of fierce cannibalism eliminating slower-growing fish? The above questions must be resolved in a future study.

It is very interesting that the similarity of frequency distributions of back-calculated lengths of a given year-class persists from the first to the fourth year of life of zander (Figs. 5, 6, 7), or perhaps even longer.

What is the possible correlation of the growth and type of frequency distribution and the abundance of the year-class? Out of the three discussed year-classes, the abundance estimated as the recruitment level of two-year old zander to the exploited population in Lake Jeziorak (Draganik and Nagięć 1995) amounted to:

Year-class 1967 : 22 100 specimens
1968 : 14 000
1969 : 20 000

For the period of 20 years (1967–1986) the estimated abundance ranged from 5596 specimens (year-class of 1985) to 33 000 specimens (year-class of 1980) and the mean value was 15 045 specimens (SD = 6892) (Draganik and Nagięć 1995).

Among the three year-classes compared, the fastest growing (as 3- and 4-year--olds) were the fish hatched in 1969 (Fig. 3A, B).

The combined data on the growth indices (Fig. 3A, B) the length frequency distributions of individual year-classes (Figs. 5, 6, 7) and their abundance within only three years may be not enough to draw conclusions on the factors affecting the stock dynamics, but it may be an important contribution to the way to learning mechanisms governing the establishment of the stock structure.

A *positive Lee's phenomenon* was observed based on the growth rates determined for individual year classes (Fig. 1A, B, C). The same conclusion may be drawn from growth readings based on a single sample or the cumulative one-fishing-season data covering different year-classes. It is well illustrated by Fig. 4A, B, C, D. The growth parameters of 2-year-old fish are higher than those of 3-year-olds (Fig. 4A), those of 3-year-olds—higher than 4-year-olds (Fig. 4B, C, D).

If a *positive Lee's phenomenon*, in particular case of zander in Lake Jeziorak, can be observed comparing the growth of individual age groups in a single sample (Fig. 4A, B, C, D) as well as analysing the growth of individual year-classes in individual years (Fig. 1A, B, C) it means that for other zander populations the growth rate of individual age groups present in a single sample (covering many year-classes) may also be an indicator of size-selective mortality. Growth rates of zander determined separately for individual age groups were studied by Błaszczyk (1999) for the populations from the Międzyodrze, by Neja and Turowska (1998) for the Szczecin Lagoon and Lake Dąbie, and by Szypuła (1996) for the Pomeranian Bay (Table 8, Figs. 8, 9, 10, 11, 12). In three bodies of water situated within the Odra River estuary, the fastest growth was noted in the oldest fish (in canals of the Międzyodrze—up to 6+, in the Szczecin Lagoon and the Pomeranian Bay—up to 5+) while the slowest in the youngest fish. These data indicate that in the zander populations inhabiting the estuary waters of the Odra River occurs a *negative Lee's phenomenon*. The exception is Lake Dąbie (Figs. 8B, 10). The above observation prompted the present authors to write this paper.

According to theoretical divagations of Ricker (1969) the *negative Lee's phenomenon* always reflects a selective mortality of one sort or another, whereas the *positive Lee's phenomenon* can arises from biased sampling.

In all four of the water bodies of the Odra River estuary a substantial share of the catches, including zander, is caught by deep-water fyke-nets (Table 8) commonly used since the 1960s, mainly for catching eels. This fishing gear consists of 7 rings of the diameter decreasing from 2.2 to 1.2 m. The first chamber and the guiding wall, which is 4.5 m high, are spread on rods inserted in the bottom. The last chamber works as a bag-end and the stretched mesh size in the bag-end ranges from 11 to 15 mm (Wysokiński and Garbacik-Wesołowska 1995). This fishing gear catches the fry and older undersized specimens of zander. In the Szczecin Lagoon one lifting up of a fyke-net yielded (year-average) 63 to 2690 specimens (depending on a year) of zander aged 0+. The highest fry concentrations were observed in September, when single catch produced 3500 to 4000 specimens (Wysokiński and Garbacik-Wesołowska 1995).

Błaszczyk (1999) based his analysis of age and growth on the fish caught with deep-water fyke nets (April 1996–May 1998) and he always collected the data on all zander caught during one day by a single fishermen crew. Undersized zander constituted 346 (66%) out of 546 specimens in the material collected this way. Among 353 sexually immature specimens there were 341 (94%) of undersized fish (Błaszczyk 1999: Tables 1, 2). They were the slowest-growing fish representing the age group of 2+. No data is available, however on the fish fry, very extensively captured along with industrial scale exploitation of zander in the Pomeranian Bay and the Vistula Lagoon.

What mechanisms lead to selective mortality of slower-growing fish? This will remain an unsolved problem. A selective role of large trap nets seems to be very possible in this process.

The principal advantage of determining the age and growth separately for individual year-classes is the possibility of distinct detection of size-selective mortality. This is not the only advantage. While reading the number of annuli on fish scales representing the same year-class, it is easy to notice a sclerite pattern, which is characteristic for a given brood, particularly within the first year of life. Such observations, having importance of natural tags may constitute an important decisionmaking element in the process of age determination (Sych 1971). Neja and Turowska (1998) and Szypuła (1996), while comparing the growth of zander in different years and different water bodies, concluded that the highest growth diversity occurred in the first year, reaching 8.6 cm in the Odra estuary.

An analogous diversity was observed based on direct measurements of fry in sequential two years in Lake Jeziorak (Nagięć 1966a). On the other hand Koonce et al. (1977) proposed a hypothesis that the abundance of species of the genus *Stizostedion* (valid name *Sander*) is determined in the first year both in Europe and in North America. This prompted the conclusion that information defined by the location and the structure of the first annulus on the scale and the sclerite pattern analysis in the centre may have a particular importance for learning the biology of a given year-class.

The above-mentioned authors, working on the growth rates of zander in the Odra River estuary, using the method of back reading did not comment on possible bad readability of the scales. Although there have been no methodological studies carried out on this subject there is a possibility of comparing the growth of zander populations living in those four bodies of water and Lake Jeziorak. These data are presented in Tables 7 and 9 and on Figs. 8, 9, 10, 11, 12. The average growth, which in all cases was based on a numerous material (Tables 7, 9) does not show big differences (Figs. 9A, 10A, 11A, 12A). Distinct differences, however, are visible during separate comparing the growth of individual age groups.

Table 9

Average growth rate (SL) [cm] (± SD) of zander , *Sander lucioperca*, representing successive age groups from: Szczecin Lagoon (A) and Lake Dąbie (B) (Neja and Turowska 1999), Międzyodrze Canal System (C)(Błaszczyk 1999), Pomeranian Bay (D)(Szypuła 1996), Lake Jeziorak (E)(present paper)

Age group	Body of water	Number of fish		Computed size at age annuli ($\bar{x}$ ±SD)					
		n	%	l_1	l_2	l_3	l_4	l_5	l_6
I	A	90	28.4	14.6 ± 2.2					
	B	18	14.5	15.3 ± 1.7					
	C	115	30.3	21.5					
	D	0.0	0.0						
	E	0.0	0.0						
II	A	66	20.8	14.9 ± 1.5	23.9 ± 2.5				
	B	20	16.1	15.7 ± 1.2	26.4 ± 2.5				
	C	89	23.5	19.4	28.3				
	D	56	35.9	18.9	26.3				
	E	57	8.9	19.8 ± 1.1	31.2 ± 2.0				
III	A	77	24.3	15.7 ± 1.6	28.1 ± 2.7	38.0 ± 3.1			
	B	59	47.6	15.4 ± 2.0	27.1 ± 3.5	36.9 ± 3.7			
	C	71	18.7	21.6	31.5	37.7			
	D	66	42.3	20.2	27.2	32.8			
	E	410	64.2	17.5 ± 1.9	26.6 ± 3.1	37.7 ± 2.5			
IV	A	64	20.2	16.0 ± 1.5	28.3 ± 2.5	40.4 ± 2.5	48.4 ± 2.5		
	B	21	16.9	16.8 ± 2.3	27.3 ± 4.6	38.7 ± 5.2	46.7 ± 5.5		
	C	59	15.6	22.0	32.7	39.8	43.8		
	D	19	12.2	22.3	30.1	36.3	41.2		
	E	147	23	17.4 ± 1.2	26.2 ± 2.0	36.6 ± 2.1	44.8 ± 1.9		

V	A	15	4.7	17.2 ± 0.9	28.3 ± 3.2	41.2 ± 4.2	49.4 ± 3.7	54.3 ± 2.9	
	B	5	4.0	17.2 ± 1.3	29.2± 2.1	42.4 ± 2.2	51.5 ± 2.4	56.8 ± 2.2	
	C	37	9.8	22.6	32.5	39.9	45.4	49.2	
	D	9	5.8	22.2	30.5	37.1	42.2	46.9	
	E	23	3.6	18.0 ± 0.9	27.0 ± 2.0	37.0 ± 1.5	45.2 ± 1.2	50.5 ± 1.3	
VI	A	2	0.6	17 ± 0.6	26.0 ± 1.8	36.8 ± 2.1	47.4 ± 1.2	54.9 ± 1.7	59.8 ± 0.6
	B	1	0.8	16.3	23.3	34.5	45.8	55.6	59.8
	C	8	2.1	22.9	34.4	42.7	48.8	52.6	55.6
	D	6	3.8	22.2	30.0	37.5	43.5	49.5	53.7
	E	2	0.3	19.5 ± 1.2	28.0 ± 1.6	36 ± 2.5	46.5 ± 0.2	52.7 ± 1.2	58.9 ± 0.1

Two-year-old zander grew faster in Lake Jeziorak that in any of four water bodies in the Odra estuary (Table 9, Figs. 9B, 10B, 11B, 12B). The growth of 3-year-old fish in the Szczecin lagoon and Lake Dąbie was similar to that of Lake Jeziorak (Table 9, Figs. 9C, 10C), whereas it was faster in canals of the Międzyodrze (Table 9, Fig. 11C). Four-year-old fish in all studied water bodies of the Odra estuary grew faster than in Lake Jeziorak (Table 9, Figs. 9D, 10D, 11D, 12D). Five-year-olds grew faster in Lake Dąbie and in the canals of Międzyodrze (Table 9, Figs. 10E, 11E), whereas in the Pomeranian Bay the back-readings for l1 and l 2 were higher than in Lake Jeziorak. On the other hand the readings for l4 and l5 were lower in the Pomeranian Bay (Fig. 12E).

In view of the facts presented a question arises: Why the same species living in the same climatic zone and under similar hydrobiological conditions, shows either a distinctly *positive*- or a distinctly *negative Lee's phenomenon*.

The above mentioned analysis shows also how much the indices of the mean growth can be dependent upon the age structure of the analysed sample.

Similarly as in the case of the described zander from Lake Jeziorak, a faster growth of fish captured in their early life was observed also for other species. For example Ciepielewski (1971) plotted the mean edge increments of 3-year-old vendace, *Coregonus albula* measured successively from June through November. Vendace was captured with anchored bottom gill-nets at Pluszne Lake (903 ha). The edge increments were increasing till August and in September they were smaller than in August. The same author (Ciepielewski 1974), analysing the growth of a defined (1966) year-class of vendace in Maróz Lake (333 ha), concluded that the values of back readings estimated based on scales of 2-year-old fish (2+) caught with anchored bottom gill-nets in the autumn of 1968 were significantly higher than analogous data based on scales of 3-year-old fish (3+) caught with the same fishing gear in the autumn of 1969. Marciak (1977), studying growth of carp bream, *Abramis brama* in warm Konin lakes, concluded that the values of the back readings, based on scales of younger fish were significantly higher. The author explained it by a higher availability of faster-growing, undersized bream for the fishing gear.

Size-selective mortality of fishes may be vary depending on the fishing gear used. Błachuta and Kusznierz (1992) stated that the growth rate of brown trout caught on hook and rod was significantly higher than the growth rate of the fish captured with an electrofishing device. Analogous data were provided by Miranda et al. (1987) for

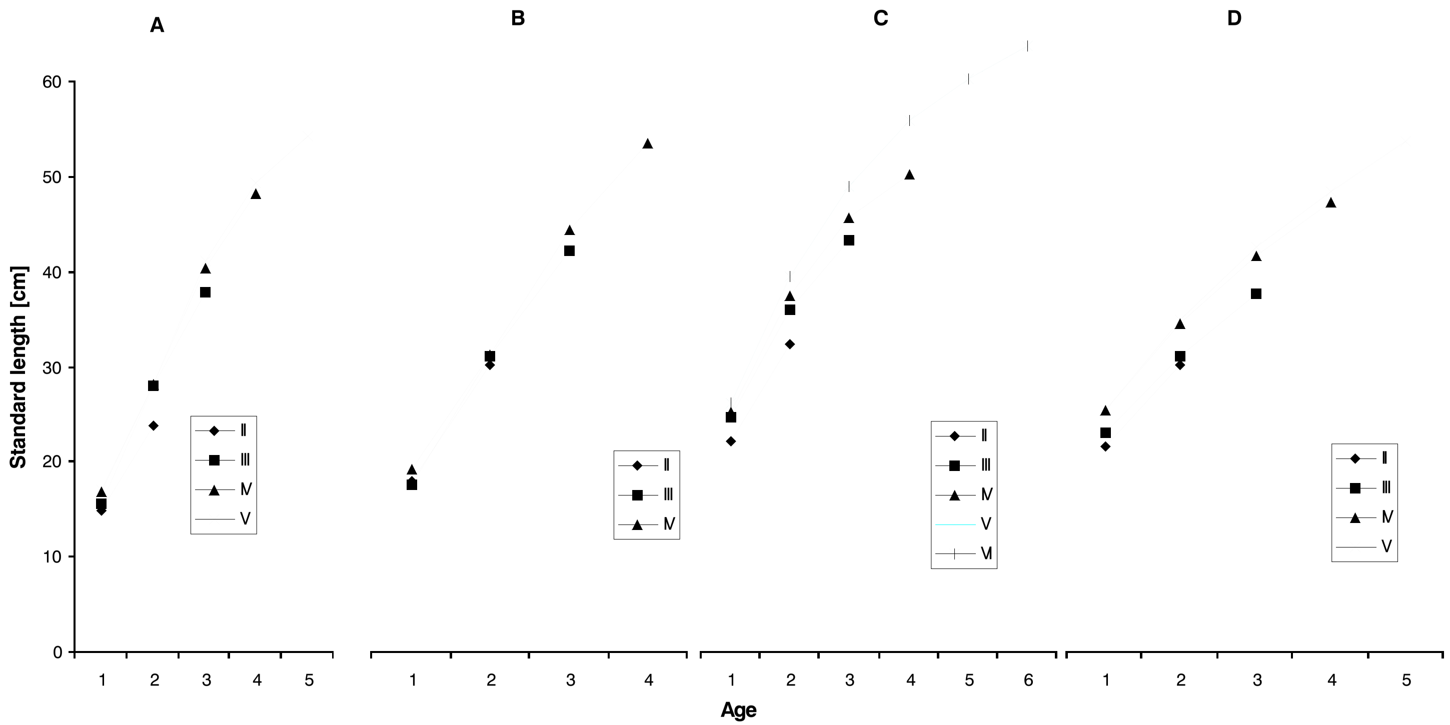


Fig. 8. The growth rate of zander, *Sander lucioperca*, from different water systems: A, Szczecin Lagoon and B, Lake Dąbie (Neja and Turowska 1998); C, Międzyodrze Canal System (Błaszczyk 1999); D, Pomerian Bay (Szypuła 1996); A, C, D examples of *a negative Lee`s phenomenon*; individual curves represent different months denoted by Roman numbers

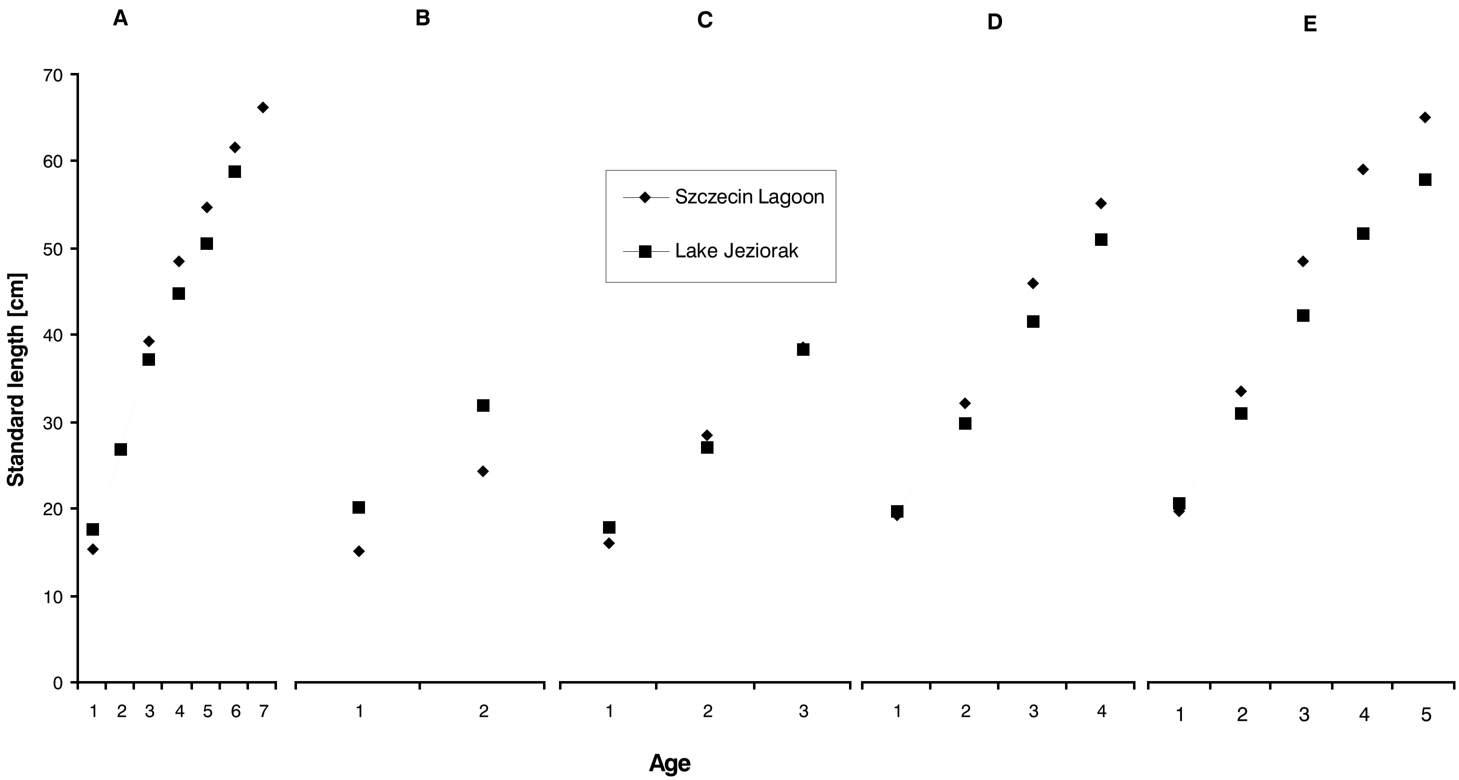


Fig. 9. Growth rate of zander, *Sander lucioperca*, in Szczecin Lagoon (Neja and Turowska 1998) and Lake Jeziorak; A, average growth rate; B, C, D, growth rate of successive age groups

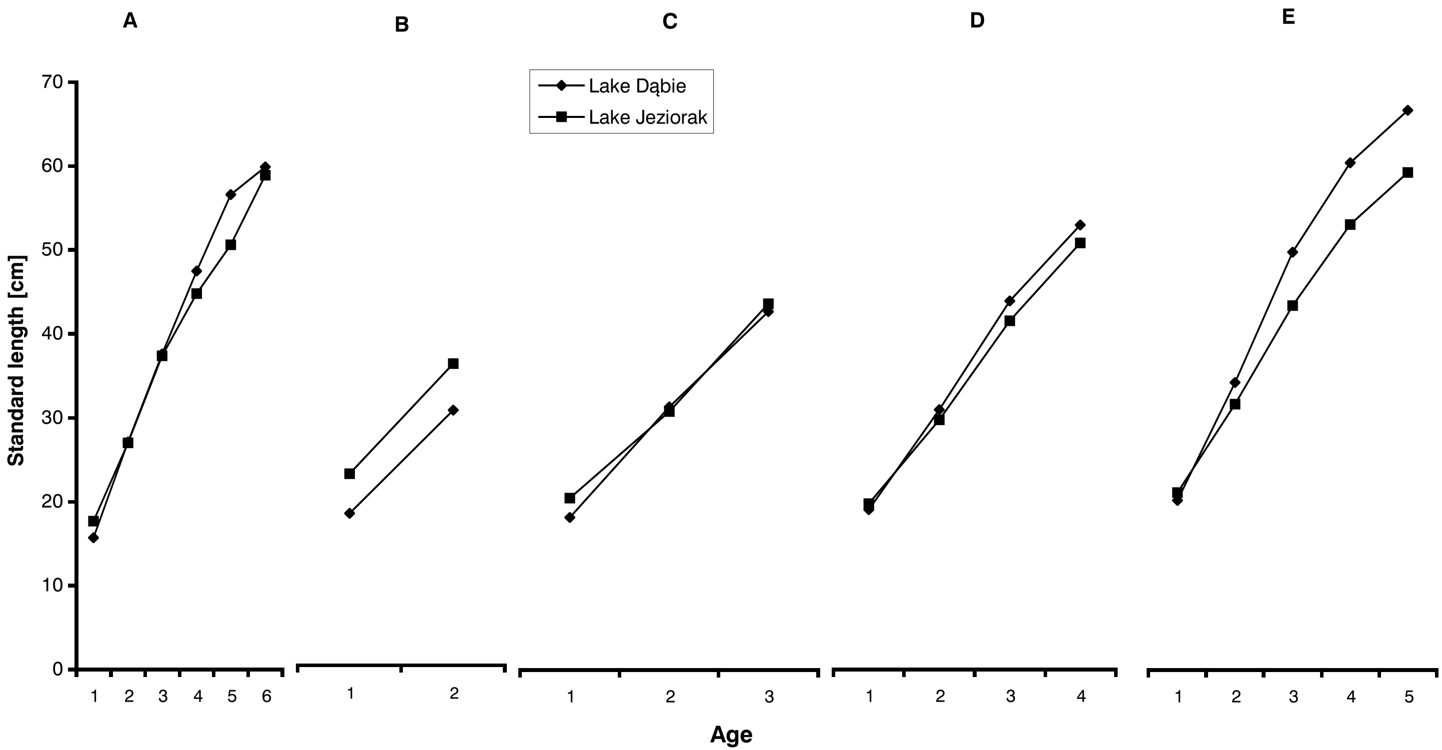


Fig. 10. Growth rate of zander, *Sander lucioperca*, in Lake Dąbie (Neja and Turowska 1998) and Lake Jeziorak; A, average growth rate; B, C, D, E, growth rate of successive age groups

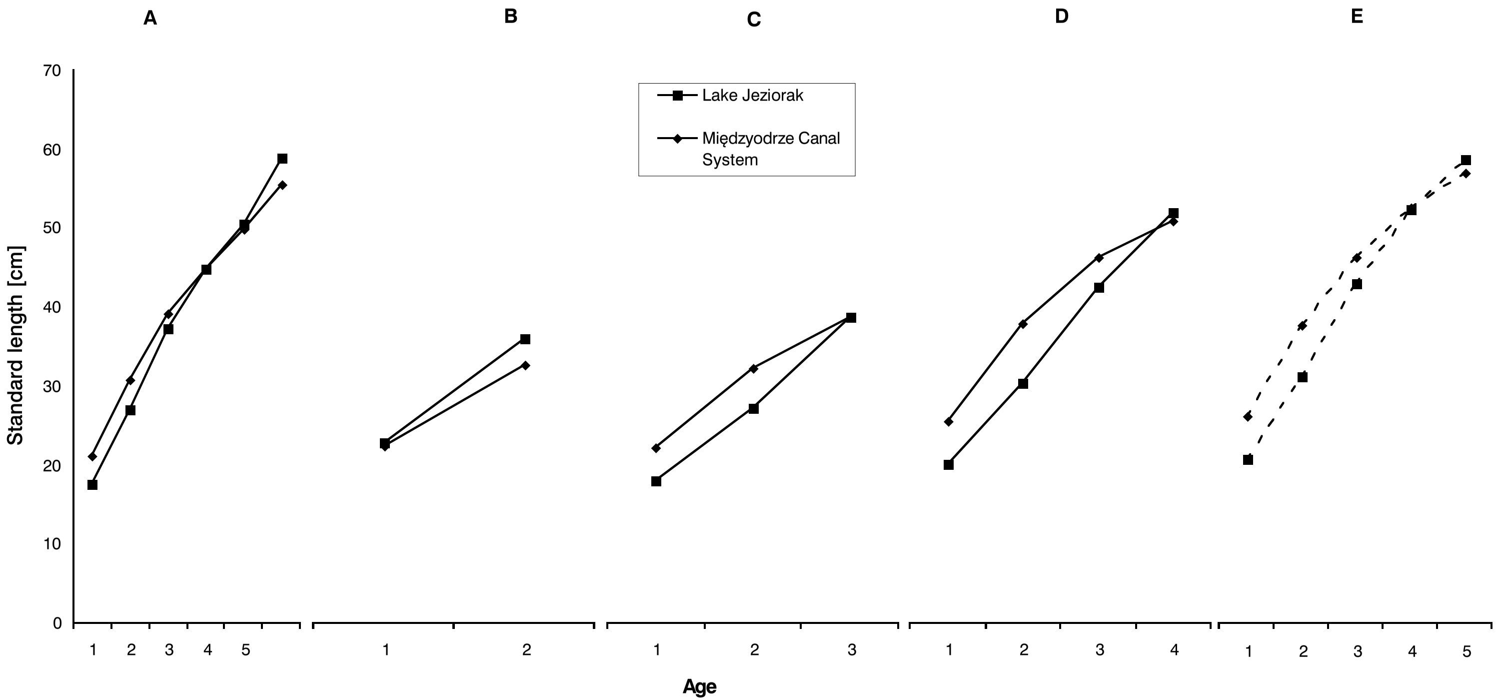


Fig. 11. Growth rate of zander, *Sander lucioperca*, in the Międzyodrze Canal System (Błaszczyk 1999) and Lake Jeziorak; A, average growth rate; B, C, D, E, growth rate of successive age groups

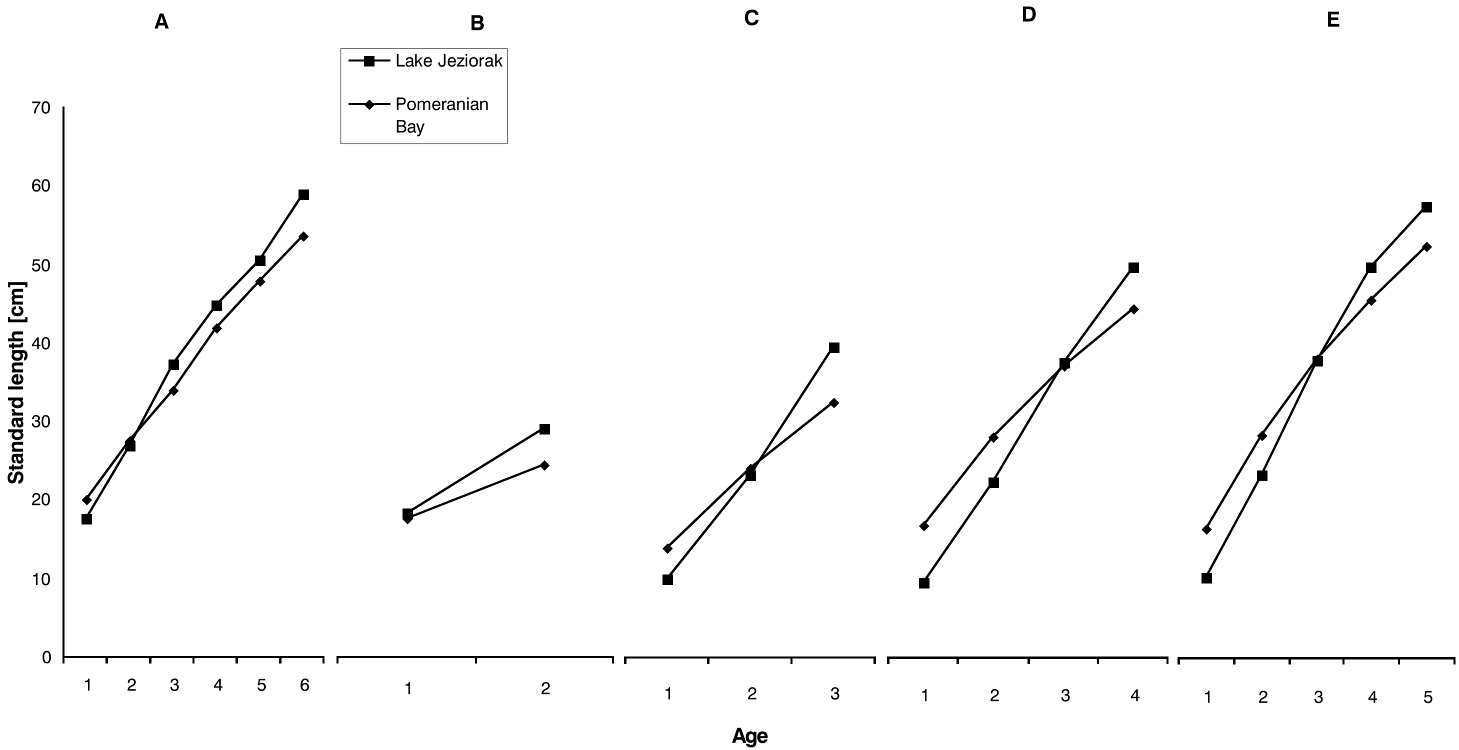


Fig. 12. Growth rate of zander, *Sander lucioperca*, in the Pomeranian Bay (Szypuła, 1996) and Lake Jeziorak; A, average growth rate; B, C, D, E, growth rate of successive age groups

largemouth bass, *Micropterus salmoides* (Lacepède, 1802) and they compared the growth of fish caught on with and rod with the growth of those poisoned with rotenone.

The present paper emphasises that within a single species, different populations, living in the same climatic zone and under similar biocoenotic conditions exhibit either a *positive Lee's phenomenon* (Lake Jeziorak), a *negative Lee's phenomenon* (Międzyodrze canals, Szczecin Lagoon, Pomeranian Bay), or they do not show sighs of size selective mortality (Lake Dąbie). Studying reasons of such diversified intrapopulational relationships may substantially extend the knowledge on the biology of zander populations. One of the methods for explaining those reasons should be examination of growth variability in individual year-classes.

CONCLUSIONS

Zander catches carried out in Lake Jeziorak (Mazurian Lake District) with the aid of summer seine consisted of four age groups: 2+, 3+, 4+, and 5+.

Growth indices computed separately for individual age groups show significant reciprocal differences. Despite of assuming the increase of empirical relationship between the scale radius and the fish length, the older the fish the lower growth indices they show. The above regularity has been described as a *positive Lee's phenomenon in inclusive sense.*

The above-mentioned phenomenon can be most clearly observed within individual year-classes captured within sequential years. It can be also detected through age comparing of a few year-classes caught at the same time.

The growth analysis of zander living in four bodies of water within the Odra River estuary demonstrated that in three cases (Szczecin Lagoon, Międzyodrze canal system, and the Pomeranian Bay) a *negative Lee's phenomenon in inclusive sense* and in one case—absence of size-selective mortality (Lake Dąbie).

Different zander populations, living in the same climatic zone and under similar biocoenotic conditions show either *positive*- or *negative Lee's phenomenon* or they do not show selective mortality. Studying reasons of such diversified intrapopulational relationships may substantially extend the knowledge on the biology of zander populations.

Zander growth curves depend on the age structure of the sample.

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