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S. Skrochowska

MIGRATIONS OF THE SEA-TROUT (*SALMO TRUTTA* L.), BROWN TROUT (*SALMO TRUTTA M. FARIO* L.) AND THEIR CROSSES
PART I. PROBLEM, METHODS AND RESULTS OF TAGGING

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ABSTRACT

In order to investigate whether the progeny of sea-trout living exclusively in fresh water show a migration instinct, smolt-sized sea-trout of F_2—F_4 pond generations were tagged and released into the River Raba. They were obtained from the artificial spawning of sea-trout caught in the Rivers Dunajec and Rudawa. Besides the "pond" sea-trout, young F_1 sea-trout, brown trout, and their crosses were liberated. The fish were reared in ponds. The results obtained indicate that two-thirds of the fish did not leave the rivers before recapture and one-third descended from the Raba for the sea. The recaptures of migrating fish from the spring stockings were twice as high as those from the autumn stockings. Mature male parr recaptured after descent from the Raba were ten times less numerous than the immature specimens. The recoveries of mature females were thirteen times as high as those of males.

CONTENTS

1. INTRODUCTION

The problem of acquisition of stocking material of the sea-trout *Salmo trutta* L. by rearing spawners in ponds has arisen in connection with the constant deterioration of biological conditions in rivers, the natural environment of spawning of these precious fish.

In order to render this enterprise feasible it has been necessary to solve two problems first, namely, 1) whether sea-trout, when prevented from travelling to the sea, will attain sexual maturity in ponds and reproduce normally, and, in the case of positive results, 2) whether their progeny reared in so different ecological conditions, when released into a river, will show a migration instinct characteristic of their original parents, that is, whether they will descend to the sea and then

return to their native river. This last character of anadromous salmonids or the so-called "homing instinct" was observed for the first time — as quoted by JONES (1959) after I. WALTON — in 1653, when salmon smolts marked with ribbons, tapes etc. tied to their tails were caught on their way back to the same place "usually six months after". MALLOCH (after JONES, 1959) was the first to apply classical tagging (with silver wire), which allowed him to observe the return of salmon (after 1—3 years) for spawning, and together with them, some incidentally marked sea-trout (after 4 years) to the River Tay, into which they had been released as smolts in the spring of 1905.

Good prognoses for the raising of sea-trout were based on the results obtained and published earlier (OTTERSTRÖM, 1933) on the rearing of the salmon *Salmo salar* L., which matured sexually in ponds. An investigation carried out in the Experimental Station of Fisheries, Jagiellonian University, at Mydlniki in 1938—1951 corroborated these suppositions (SKROCHOWSKA, 1951).

The studies reported in the present paper have been initiated to answer the second of the questions posed above. In addition to various generations of the "pond" sea-trout, its crosses with the brown trout *Salmo trutta m. fario* L. have been included to extend the scope of the study and, for comparative purposes, young sea-trout obtained from fish caught in rivers during spawning as well as brown trout were also liberated.

It is obvious that besides its economic importance the problem under study has also an interesting and weighty aspect from the biological point of view. Migrations of fish, especially of salmonids, have been exciting vast curiosity since long ago and they have been the subject of very numerous works [1], which, however, deal exclusively with fish under natural conditions or, at most, their offspring living under artificial conditions for the first years of their lives only. In the face of these facts it seems particularly interesting whether and, if so, to what extent the fish that have been living for generations exclusively in fresh water are fit to transmit the migration instinct to their offspring.

Even the preliminary elaboration of the results of investigation from the first year has shown that the sea-trout of the second pond generation travels to the sea, whereas the specimens of the third generation remain in the river. It appeared that in the second generation of the cross between a female brown trout and a male sea-trout the migration instinct undergoes splitting: part of the fish migrate to the sea and others remain in the river and, in the end, that single specimens of the brown trout may also descend to the sea (SKROCHOWSKA, 1953). However, it was necessary to continue the work both because the material obtained was too scanty to allow generalizations and for need of repetition.

The long duration of such studies, resulting from their very nature, is natural. The best example of this is the fact that DALZIEL and SHILLINGTON (1961) published a preliminary report on migrations in various pond generations of the Atlantic salmon as late as 20 years after the commencement of their study. This is, as far as I know, the only publication on the subject resembling that of the studies carried out at Mydlniki.

2. MATERIAL AND METHODS

The present investigations were carried out in the Experimental Station of Fisheries at Mydlniki [2]. The hatchery and ponds in which experimental fish were bred were supplied with water from the Rudawa, a left tributary of the

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[1] The first studies in which the classical methods of tagging were applied are those by JOHNSTON (1905), CALDERWOOD (1907, 1911), MALLOCH (1910) and others. In Poland the first investigation of migrations of young sea-trout and salmon was carried out by KULMATYCKI (1931, 1932, 1933) in the tributaries of the lower Wisła (stocking of the Brda) and ŻARNECKI (1936) in the tributaries of the upper Wisła (stocking of the Wisłoka). In both cases, experimental material obtained from artificial spawning was reared in ponds.

[2] The Station belonged to the Institute of Ichthyobiology and Fisheries of the Jagiellonian University till 1953 and then to the Department of Fisheries, College of Agriculture in Cracow. The present work was supported partly by a grant from the Hydrobiological Commission, Department II, Polish Academy of Sciences.

upper Wisła (Vistula). The drainage of the hatchery and ponds was directed to the same river. The fish tagged were transported by truck from Mydlniki to a distance of 40—80 km and released into the Raba, a right tributary of the Wisła joining this last river 59 km below the mouth of the Rudawa (the Rudawa joins the Wisła at 75.5th km, the Raba at 134.7th km) and 806 km from the sea. At the time of investigation a large number of sea-trout ascended the Raba for spawning, but only single specimens occurred in the Rudawa [3].

The experiment was started in the autumn of 1951 and from that time for 7 years and a half 1,402—3,764 smolt-sized fish were tagged and released yearly, which makes a total of 21,066 young fish till the spring of 1959. In addition, 56 specimens (the remainder of the batch tagged in 1959) were liberated in March 1960, raising the total to 21,122 specimens.

Fish were released twice a year: late in the autumn — at the end of November and at the beginning of December — and early in the spring (between 12 and 31 March). The time of spring releases depended on the hydro- and meteorological conditions of the given year.

As can be seen from the results of the first year of investigation, the fish released in the autumn of 1951 and in the spring of 1952 arrived in the sea at the same time — not before the spring (SKROCHOWSKA, 1953). For this reason, the results concerning the specimens obtained from the same spawning and released in the two above-mentioned periods are discussed here together, the release of fish in the autumn of 1951 and in the spring of 1952 being designated as the first group, that in the autumn of 1952 and in the spring of 1953 as the second, etc. In this way, 8 batches of tagged fish were released in the years 1951—1959, but in the years 1955, 1956 and 1959 stocking was done only in the spring.

Two- and three-year-old specimens were used for tagging. As a matter of fact, the fish released in the autumn were not exactly 2 or 3 years of age yet, but they were reckoned in these age groups for simplification. In this I am justified by the fact that smolts, both these from the autumn stocking and those released in the spring, migrate downstream together in the spring, autumn descents being regarded as exceptions.

The lower limit length of fish was established at about 16 cm. Two-year fish which had not reached this length by the time of spring tagging, were kept in a pond for another summer or a year and released as three-year-olds. Thus, one fish group derived from the same spawing was divided into specimens with a faster growth rate (2 years old) and a slower growth rate (3 years old).

Silver tags were attached with silver wire (0.3—0.4 mm in diameter) to the back of a fish, beneath the first rays of the dorsal fin. Preliminary experiments, which consisted in keeping sea-trout with tags attached beneath the first rays and those with tags fixed beneath the last rays of the dorsal fin in running water, showed that the first of these two manners is more expedient. This result has been confirmed by experiments carried out by CALHOUN (1953) and explained by Prandtl's theory, which concerns phenomena occurring at the movements of streamlined bodies (such as the body of a smolt) in liquid environment.

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[3] The years 1952 and 1953, when, as a result of the proceeding stocking of this river, 250 sea-thout spawners were caught in the spawning season in the autumn of 1952 and 120 in the autumn of 1953, are exceptional (ŻARNECKI, 1960).

According to this theory, a body at rest or in slow motion in a liquid becomes coated with an adhesive parietal layer, along which the adjoining currents slide. On the other hand, at the time of an increase in the speed or a change in the direction of motion the layer tears away in the place where the streamlined body begins to narrow (in a smolt the region behind the dorsal fin) causing a strong turbulence and a rise in the resisting force in this place.

Fish released in the first four years of the present investigation (1951/ /1952—1954/1955) were marked with hexagonal tags, accepted for Poland at the International Council for the Exploration of the Sea in 1933. Their weight was about 0.2335 g each (the mean weight from 100 tags). In the next years oblong tags with rounded corners (resembling the Swedish tags in shape) and a weight of 0.1360 g were applied. The percentage recoveries of oblong tags were 3 times as great as in the case of hexagonal tags (Table I). This was, above all, due to their smaller weight, though their streamlined shape was probably of some importance, too.

Table I. Recoveries of hexagonal and oblong tags from sea-trout of second pond generation (F_2)

Years	Sort of tag	Number of fish released	Number of fish recaptured					
			In the sea		In the Raba		Total	
			No.	%	No.	%	No.	%
1951/1952 to 1954/1955	Hexagonal	3,027	111	3.67	57	1.88	168	5.55
1956 to 1958/1959	Oblong	2,561	219	8.55	212	8.28	431	16.83
Total		5,588	330	5.91	269	4.81	599	10.72

The number of oblong tags regained in sea catches was 2.3 times and in the catches in the Raba 4.4 times as large as the respective numbers of hexagonal tags, which shows that fish lose far more of the heavier tags, especially when they stay in rivers.

The influence of the sort of tags used on the number of recoveries was demonstrated, for comparability of results, by the example of F_2 sea-trout, for only the fish of this generation were marked with both types of tags in fairly large numbers. The specimens of other forms were released mostly or even exclusively in periods when only one of these tags was used. Anyway, the general result of recapture of experimental fish confirms the opinion that the number of recoveries depends on the sort of tags used, since 10.88% (1073 tags) were recovered from all the specimens marked with hexagonal tags, 9,866 in number, whereas for 10,863 specimens released with oblong tags the recoveries came to 19.25% (2,091 tags).

A slight part of the fish, 393 specimens, were caught in the Raba directly or a short time after they had been released, and so still before the date of recapture of smolts in the Wisła on their way downstream to the sea

(varying from 11 March to 19 April). These fish have not been included in my considerations on the assumption that it was impossible for them to leave the river. In the face of the foregoing the experimental material consisted of 20,729 specimens tagged.

CHARACTERISTICS OF MATERIAL (ORIGIN OF FISH TAGGED)

The following groups of fish were used for tagging experiment:
1. F_1—F_4 sea-trout (St) generations   11,500 specimens
2. Crosses between the sea-trout and the brown trout
   a) female brown trout × male sea-trout (Bt×St), F_1—F_4 generations   4,141 „
   b) female sea-trout × male brown trout (St×Bt), F_1 and F_2 generations   3,411 „
3. Brown trout (Bt), F_3 and F_4 generations   1,677 „

Total   20,729 specimens

1. Experimental specimens of the sea-trout (St) derived from spawners caught in two tributaries of the upper Wisła: the Dunajec and Rudawa. The specimens of the first generation (St F_1) were offspring of the sea-trout from the Rudawa. The release of young F_1 sea-trout is a routine practice of stocking rivers with artificially reared material. It is only by the further rearing of these fish till they attain sexual maturity that a generation called the first generation of the pond sea-trout is obtained.
The next generations of the sea-trout, F_2, F_3 and F_4, were derived from the spawners caught in the Dunajec.
2. Crosses [4] between the sea-trout and the brown trout were produced by fertilizing a) eggs of the brown trout with sperm of the sea-trout (Bt×St) and b) eggs of the sea-trout with sperm of the brown trout. (St×Bt). Sperm of the F_1 sea-trout from the River Dunajec was used for (Bt×St) crosses. In the case of the (St×Bt) F_1 crosses, eggs of the sea-trout from the Rudawa were fertilized with sperm of the brown trout [5]. The (St×Bt) F_2 crossbreed was obtained from the spawning of these fish.
3. All the b r o w n   t r o u t (Bt), and therefore also those whose eggs (F_1 and F_2) or sperm (F_2 and F_3) were used for crossing, as well as the young ones (F_3 and F_4) that were tagged, were derived from the brown trout reared in the Mydlniki ponds from the spring of 1938 and regarded as the first generation (F_1). These last were produced from eggs delivered by the Centre for Fish Stocking at Folusz in the Jasło District, where their rearing was based on local material from the drainage basin of the Wisłoka, which itself is a right tributary of the Wisła and joins it at the 226.9th km.

3. RESULTS

a. Results of tagging in the River Raba and after descent from the Raba for the sea

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[4] In this paper the term "cross" has not its exact genetic meaning but is used for lack of any other short and suitable designation.
[5] Only in one year (St×Bt) F_1 hybrids (288 specimens) were produced from eggs of the F_1 pond sea-trout generation descending from Dunajec spawners.

A total of 20,729 young fish tagged were released into the Raba throughout the experimental period, from November 1951 to March 1960 (Table II).

Up to mid-February 1963 3,164 tags were recovered from recaptured specimens, i.e., 15.26% of the fish released. About two-thirds of these tags (2,102—10.14%) came from fish that had not started on their downstream migration to the sea before catch, the rest of them, 1,062 specimens (5.12%), from those which had taken up this migration.

Table II. Total numbers of tagged fish released and recaptured

| Form and generation | Number of fish released | Number of fish recaptured | | | | | | Ratio of fish-recaptured while migrating to fish taken in the Raba |
| | | In the Raba | | Migrating | | Total | | |
		No.	%	No.	%	No.	%	
St F_1	951	45	4.73	86	9.04	131	13.77	1 : 0.5
St F_2	5,588	269	4.81	330	5.91	599	10.72	1 : 0.8
St F_3	4,093	451	11.02	85	2.08	536	13.10	1 : 5.3
St F_4	868	150	17.28	69	7.95	219	25.23	1 : 2.2
(Bt × St) F_1	1,023	291	28.45	69	6.74	360	35.19	1 : 4.2
(Bt × St) F_2	1,601	79	4.93	70	4.37	149	9.31	1 : 1.1
(Bt × St) F_3	1,417	143	10.09	151	10.66	294	20.75	1 : 0.9
(Bt × St) F_4	100	6	6.00	5	5.00	11	11.00	1 : 1.2
(St × Bt) F_1	1,393	142	10.19	64	4.60	206	14.79	1 : 2.2
(St × Bt) F_2	2,018	188	9.32	110	5.45	298	14.77	1 : 1.7
Bt	1,677	338	20.16	23	1.37	361	21.53	1 : 14.7
Total	20,729	2,102	10.14	1,062	5.12	3,164	15.26	1 : 2.0

In order to make both the tables and the interpretation of the data included in them simple and clear, all the specimens caught that did not undertake a journey to the sea are placed in the column "In the Raba", whereas all those which, exhibiting a migration instinct, left this river for the sea are given under the caption "Migrating". Thus the first group comprises 2,053 specimens caught in the Raba, 45 specimens caught in the tributaries of the Raba, and 4 specimens caught in other rivers, altogether 2,102 specimens that did not leave the rivers.

The group of fish included in the column "Migrating" consists of 23 smolts caught in the Wisła on their way to the sea, 703 specimens caught in the sea, and 336 adult specimens caught in rivers during their spawning migration, altogether 1,062 specimens that descended from the Raba to the sea.

The foregoing remarks on the captions "In the Raba" and "Migrating" refer also to Tables III, IV, V of this Part, Table II of Part II and Table I of Part III.

In particular forms and generations the numbers of fish caught in the Raba (4.73—28.45%) and while migrating (1.37—10.66%) ranged within wide limits. The same is also true of the numerical relation of these two groups to each other, given in the table to illustrate the ability of the

fish to undertake a journey to the sea. This ratio ranges from the value established for F_1 sea-trout (1 : 0.5), which were caught during their migrations in numbers twice as large as those of the same fish recovered in the Raba, to the value found for the brown trout (1 : 14.7), the recaptures of which in the Raba were nearly 15 times as numerous as those during migration. The number of specimens of the successive sea-trout generations, F_1—F_3, caught on migration decreased, whereas the crosses of further pond generations generally increased in number (Table II) [6].

b. Comparison of the results of spring and autumn releases

Observations connected with spring and autumn fish releases allow the statement that spring stackings give much better results, especially as regards catches of migrating specimens which from spring stockings were nearly twice as numerous as those planted in the autumn (Table III). Similar results of stocking rivers with brown trout were obtained by WESTERMAN and HAZZARD (1945) and with respect to the salmon and sea-trout in the sea by CARLIN (1955); CHRZAN (1963); SKROCHOWSKA (1964); BARTEL (1965) and others. The causes of this state of things are, according to our opinion, a higher mortality rate and a poorer progress in the turning of specimens into smolts in autumn batches than in spring ones. This suggestion concerning longer stay in the river of autumn batch before downstream migration is based upon investigations on the behaviour of young salmonids in rivers (GERKING, 1953; MILLER, 1957; KALLEBERG, 1958), on their death as a results of accumulation of lactic acid in the blood (BLACK, 1955, 1957 a,b,c, 1958; MILLER, 1958; WENDT, 1964, 1965, 1967), and on their loss in weight after being released (KLAK, 1941; NEEDHAM and SLATER, 1945; MILLER, 1952 and others).

Table III. Comparison of recoveries of tagged fish released
in spring with those released in autumn

Released		Recaptured		
Season	Number of fish	In the Raba	Migrating	Total
Autumn	9,113	No. 739	313	1,052
		% 8.11	3.43	11.54
Spring	11,616	No. 1,363	749	2,112
		% 11.73	6.45	18.18
Total	20,729	No. 2,102	1,062	3,164
		% 10.14	5.12	15.26
Ratio of recoveries from autumn releases to those from spring releases		1:1.4	1:1.9	1:1.6

c. Migrations of sexually mature parr

The numbers of sexually mature specimens were noted each time the fish were released into the Raba (at spring tagging starting from 1955). Mature

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[6] A detailed discussion of migrations of specimens belonging to particular forms and generations will make the subject of a separate paper dealing with the sea--trout up to 6th pond generation.

males were found among both 2- and 3-year-old fish, mature females only among 3-year-olds. Moreover, a relatively large number of males, especially among the 3-year-olds (8.2%), have still active gonads in the spring (spermatozoa mobile in water and fit to fertilize [7]). Only 7 females with eggs unlaid in the autumn and shed at a slight pressure were found in the spring (March 1957). Their eggs, however, transparent, distended and whitening immediately when immerged in water, were unfit to develop. These females came to sexual maturity in the autumn, but they had not spawned and their eggs had not undergone resorption yet.

Mature males occurred in all the forms of experimental fish in the autumn periods throughout the course of investigation, their total number being 1,106 specimens, that is, 12.14% of the tagged fish (9,113). Among the 3-year-olds they were 3 times as numerous (17.25%) as in the group of 2-year fish (5.85%) [8].

No mature males were found among the 2-year-old F_1 sea-trout during the spring tagging experiments, but they were present in the other forms, though less numerous and less regularly than in the autumnal experiments, and in 1959 they were not found at all. The total of sexually mature males released in the spring periods was 517 specimens (5.15% of the fish marked), i.e., 339 (8.18%) 3-year-olds and 178 (3.01%) 2-year-olds.

Mature females (exclusively 3-year-olds and only in autumn) were 83 in number or 1.65% of the fish tagged (5,027 specimens). In the smallest number they occurred in F_2 sea-trout group (in 2 out of the 5 batches used for stocking, 1 specimen in either), whereas only among F_1 sea-trout they were not found at all. Mature females were present in all the batches of other forms released and they formed from 0.81 to 5.86% of the total of the given group.

The recoveries of the early maturing specimens discussed are presented in Table IV. For comparability of results only these forms of 3-year-old fish released in the autumn are included in it, in which mature females occurred.

In this table both the numbers of fish released and those of tagged fish recaptured are given according to sex and stage of gonad development. Since all the specimens belonging to given forms and generations were always kept under the same conditions (in the ponds, when being tagged, during transportation and in the river when released), the recaptures of sexually mature fish as compared with the results of catch of immature juvenile specimens indicate the influence of the developmental processes of gonads upon the ability of fish to undertake a journey to the sea. Nearly all the males caught same from the River Raba. Only a slight proportion of them were taken while migrating, a tenth of juvenile fish. The proportion of migrating mature females, however, somewhat exceeded that of specimens

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[7] This may be exemplified by the development of roe of the rainbow trout fertilized with sperm of similar young males of the brown trout (spring 1955). The hatching of hybrids was very poor, and the larvae were mostly abnormal. This abnormality most often affected the development of head, especially that of eyes, which were very small or lacking at all. Eggs of the brown trout fertilized with sperm of rainbow trout developed scarcely in few cases and even then only to reach the eyed stage. Similar results as regards direction of crossbreeding are reported by BACKIEL (1964).

[8] The number of fish released during the whole period of investigation included 5,027 3-year-olds, out of which 867 were sexually mature males and 4,086 2-year-olds with 239 mature males.

Table IV. Recoveries of fish sexually mature at the time of release

Released into the Raba			Recaptured		
			In the Raba	Migrating	Total
Mature male parr	No.	716	119	2	121
	%	18.94	16.62	0.28	16.90
Mature female parr	No.	83	10	3	13
	%	2.20	12.05	3.61	15.66
Immature juvenile fish	No.	2,981	296	85	381
	%	78.86	9.93	2.85	12.78
Total	No.	3,780	425	90	515
	%	100.00	11.24	2.38	13.62
Ratio	females to males	1: 8.6	1:1.4	12.9:1	1:1.1
	females to juveniles	1:35.8	1.2:1	1.3:1	1.2:1
	males to juveniles	1:4.2	1.7:1	1:10.2	1.3:1

with undeveloped gonads (the ratio being as 1.3 : 1) and, at the same time, they were 13 times as numerous as the males. It should, besides, be emphasized that all the sexually mature specimens left the Raba in the spring following their autumnal release, as indicated by their measurements and confirmed by an analysis of scales. This was, in addition, supported by the recapture of a female smolt in the Gulf of Gdańsk (Jantar) in the spring, which female was released as completely mature in the preceding autumn and spawned, as proved at a dissection made by me (cross $(Bt \times St)_3$ F_2, tag No. P 5188, released on 9 December 1952, length 21.0 cm, weight 95 g, recaptured on 16 April 1953, weight 63 g).

It is also worth notice that in the Raba (and thus also in general) the recaptures of sexually mature fish are far more numerous (males 16.62%, females 12.05%) than those of immature specimens (9.93%, Table IV). As the fish tagged was caught in the Raba exclusively by rod, these results may be explained by the increased voracity of spawned specimens. Moreover, it appeared that, contrary to the general opinion, males were more voracious than females.

Because of presence of the abundant material and the possibility to compare the recoveries from autumn and spring releases, the data on all the sexually mature males recaptured are given in Table V, which shows that:

1. the recaptures of migrating male specimens mature at the time of release were markedly less numerous than those of fish released as immature, which were 1.6—8.7 as many;

2. fish released as mature males were recaptured in the Raba in numbers varying with their age and the time of release but from 3.9 to 47 times as large as the number of migrating fish; none of the 3-year-old males released in the spring was caught while migrating and as many as 32.15% of their total number were recaptured in the Raba. The difference between the numbers of immature specimens recaptured were far smaller — the fish caught in the Raba were 1.03—3.9 times as numerous as those taken while migrating;

3) the recaptures of exclusively migrating sexually mature males released

Table V. Recoveries of sexually mature

Released into the Raba					
Season	Stage of gonad development		2-year-olds	3-year-olds	Total
Autumn	Mature male parr	No. %	239 5.85	867 17.54	1,106 12.25
	Immature specimens	No. %	3,847 94.15	4,077 82.46	7,924 87.75
	Total	No. %	4,086 100.00	4,944 100.00	9,030 100.00
Spring	Mature male parr	No. %	178 3.01	339 8.20	517 5.15
	Immature specimens	No. %	5,726 96.99	3,796 91.80	9,522 94.85
	Total	No. %	5,904 100.00	4,135 100.00	10,039 100.00
Percentage ratio of recaptures from autumn and spring releases	mature male parr				
	immature specimens				

in the autumn were always more numerous than the corresponding recaptures of males released in the spring. In all other cases (recaptures of males in the Raba and those of immature specimens in the Raba and while migrating) the spring releases gave about twice as high results as the autumn ones) according to the data from Table II).

4. SUMMARY

An investigation was carried out to determine whether and, if so, to what degree the offspring of the sea-trout *Salmo trutta* L. living exclusively in fresh water for several generations inherit the instinct of seaward migration. Positive results of the investigation would allow the production of stocking material for rivers on the basis of the pond rearing of spawners. In addition to the F_2—F_4 generations of the sea-trout reared in ponds the study material included F_1 sea-trout, brown trout derived from tributaries of the Wisłoka, and crosses of these fish. Experimental sea-trout were obtained by artificial spawning from "migratory" specimens caught in the rivers Dunajec and Rudawa. The fish were reared in ponds supplied with water from and drained to the Rudawa. Tagged specimens were released into the Raba, which opens into the Wisła 59 km below the mouth of the Rudawa and 806 km up the river from the sea. All the above-mentioned rivers are tributaries of the Upper Wisła.

Two- and three-year-old fish were tagged. The lower limit of length was about 16 cm. The fish that at the age of 2 years were not sufficiently long were released later as three-year-olds. Hence the former had a higher growth rate than the latter. A total of 20,729 specimens, 11,505 two-year-olds and 9,224 three-year-olds, were released. The number of fish recaptured formed 15.26% of the total of fish released, the fish (not migrating) caught in rivers (10.14%) being twice as numerous as those caught after they had started on a seaward journey (5.12%).

males released in autumn and spring

Recaptured					
2-year-olds			3-year-olds		
in the Raba	migrating	total	in the Raba	migrating	total
27 11.30	7 2.93	34 14.23	143 16.49	3 0.35	146 16.84
189 4.91	176 4.57	365 9.49	370 9.08	124 3.04	494 12.12
216 5.29	183 4.48	399 9.77	513 10.38	127 2.57	640 12.95
42 23.60	4 2.25	46 25.84	109 32.15	—	109 32.15
524 9.15	511 8.92	1,035 18.07	658 17.33	171 4.50	829 21.84
566 9.59	515 8.72	1,081 18.31	767 18.55	171 4.13	938 22.68
1:2.1	1.3:1	1:1.8	1:2.0	—	1:1.9
1:1.9	1:2.0	1:1.9	1:1.9	1:1.5	1:1.9

Fish were released late in the autumn and early in the spring. The recoveries of the latter fish were altogether 1.6, in the sea 1.9, and in rivers 1.4 times as high as those of the former.

Sexually ripe male and female parr occurred among the fish released. River recoveries of these fish were considerably higher than those of specimens with undeveloped gonads. The males caught after descent from the Raba formed one-tenth of the number of immature fish, whereas mature females were not less numerous than these last and 13 times as numerous as the males.

5. STRESZCZENIE

Badania przeprowadzono w celu stwierdzenia, czy i w jakim stopniu potomstwo troci *Salmo trutta* L., żyjących w ciągu kilku pokoleń wyłącznie w wodzie słodkiej dziedziczy instynkt wędrówki do morza. Pozytywne wyniki badań pozwoliłyby na produkcję materiału zarybieniowego dla rzek w oparciu o stawową hodowlę tarlaków. Badaniami objęto prócz hodowanych w stawach troci pokolenia F_2—F_4 również troć F_1, pstrągi potokowe pochodzące z dorzecza Wisłoki i krzyżówki tych ryb. Materiał doświadczalny troci uzyskano ze sztucznego tarła „wędrownych" osobników złowionych w rzece Dunajec i Rudawa. Wychów przeprowadzano w stawach nawadnianych z Rudawy i odwadnianych do tej samej rzeki. Znakowane osobniki wypuszczano do rzeki Raby uchodzącej do Wisły w odległości 59 km poniżej ujścia Rudawy i 806 km powyżej ujścia Wisły do morza. Wszystkie wymienione rzeki należą do dopływów górnej Wisły.

Znakowano 2- i 3-letnie ryby. Dolna granica długości wahała się około 16 cm. Osobniki nie osiągające w wieku 2 lat wymaganej długości wypuszczano jako 3-letnie. Stąd pierwsze odznaczały się szybszym tempem wzrostu niż drugie. Ryb 2-letnich wypuszczono 11 505, 3-letnich 9224, razem 20 729 osobników. Ogółem odłowiono 15.26⁰/₀ osobników, z czego 2 razy więcej (10.14⁰/₀) w rzekach bez wędrówki do morza niż po podjęciu tej wędrówki (5.12⁰/₀).

Zarybienia przeprowadzano późną jesienią i wczesną wiosną. Z tych ostatnich odłowiono ogółem 1,6, w morzu 1,9 i w rzekach 1,4 razy więcej ryb niż pierwszych.

Wśród wypuszczonych ryb trafiały się samce i samice dojrzałe płciowo. Rzeczne odłowy tych ryb były znacznie wyższe niż osobników o nierozwiniętych gonadach. Po spływie z Raby złowiono 10 razy mniej samców niż ryb niedojrzałych, natomiast dojrzałych samic nie mniej niż tych ostatnich i 13 razy więcej niż samców.

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MIGRATIONS OF THE SEA-TROUT (*SALMO TRUTTA* L.), BROWN TROUT (*SALMO TRUTTA M. FARIO* L.) AND THEIR CROSSES PART II. MIGRATIONS IN THE RIVER RABA

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ABSTRACT

A clear majority of the fish were caught in the rivers in the first year after release, the recaptures being the most numerous in the place of stocking and the least numerous below this place. The specimens caught in small numbers in the next period, up to 3 years and a half after release, travelled steadily up the stream. Very few specimens left the Raba entering its tributaries and only single ones were recovered in other rivers out of the Raba catchment basin. The fish released at the age of 3 years were recaptured in the rivers twice as many as those released at the age of 2 years.

CONTENTS

1. INTRODUCTION

All the tagged fish that had not left the rivers and were recovered in them were caught by rod when the period of descent of smolts to the sea was already over. This fact was determined on the basis of the dates of recaptures of descending smolts in the Wisła and those of the first recoveries of smolts in the sea. Most of the fish caught in the rivers, if not all, may therefore be regarded as devoid of migration instinct.

The specimens of 3-year F_1 sea-trout, 160 in number, released in March 1957 have been omitted in present the Part. As they were selected as smolts from other specimens of that year (397) and therefore quite ready to start on their seaward journey, they were all recaptured, without an exception, after they had left the Raba (not a fish released at the stage of smolts was caught in it). As a result, the total number of experimental fish dealt with in this Part is 20,569, of which 11,505 released as 2-year-olds and 9,064 as 3-year-olds.

The tagged fish were released in 11 places over a distance of 62 km of the Raba course, from 19 to 81 km up from its mouth [1].

The specimens angled were divided into groups according to: a. direction of migration (fish recaptured above, below or in the place of release), b. time of catch (fish recaptured within the first year following the release or in the period from 1 to 3 and a half years after it), and c. place of catch (fish recaptured in the Raba, in its tributaries or in other rivers not joining the Raba).

2. DIRECTION OF MIGRATIONS

The numbers of tagged fish released and the numbers of those recaptured are given according to the direction of their migrations in Table I.

Most both 2- and 3-year-old fish were recaptured in the place of release, i.e., within a distance of 1 km upstream or downstream of the place of stocking. The recoveries of tags from the fish caught upstream of the place of release were somewhat less numerous and the fewest fish were caught downstream of this place (Table I).

Table I. Tagged fish recaptured in rivers according to the direction of their migration

Age of fish	2-year-olds specimens		3-year-olds specimens		Total	
Number of fish released into the Raba	11,505		9,064		20,569	
Number of fish recaptured	No.	%	No.	%	No.	%
Upstream of the place of release	340	2.96	483	5.33	823	4.00
In the place of release	354	3.08	560	6.18	914	4.44
Downstream of the place of release	113	0.98	252	2.78	365	1.78
Total	807	7.01	1,295	14.29	2,102	10.22

The general recoveries of 3-year-olds (14.29%) were in percentage values twice as high as those of 2-year-olds (7.01%). A similar proportion was found among the specimens caught in the place of release; upstream of this place 2-year-old fish were recaptured in somewhat higher proportions, whereas the 3-year-olds prevailed considerably downstream. These differences are characterized best by the numerical relations between the fish released at the age of 2 years and those at the age of 3 years found among the recaptures taken in these places. This ratio was as 1 : 2.04 in general, 1 : 2.01 for recaptures in the place of release, 1 : 1.80 for recaptures upstream of the place of release and 1 : 2.84 for recaptures downstream of the place of release.

[1] The characteristics of the River Raba are given in the paper on the results of the first year of investigation (SKROCHOWSKA, 1953).

The reach of the shortest migrations both up- and downstream in the River Raba was 2—3 km for all the forms under study. The longest upstream journeys ranged from 11.7 km (St_2 F_2) to 56 km (Bt_2), and the downstream journeys from 3.3 km (2-year cross $St \times Bt$ F_1) to 31 km (St_2 F_2, St_2 F_3, Bt_3). It should also be stressed that in the case of stocking carried out in the region situated more than 50 km up the River Raba (domain of the brown trout) the longest journeys of fish in both upstream and downstream directions covered similar distances (about 25 km). When the fish were released downstream of this region, their journeys up the river were the longer and those down the river the shorter, the closer to the mouth of the river the place of release was situated. Regardless of the direction of their migrations some specimens were recaptured many a time at the same distance (up to 35 km upstream and to 28 km downstream) of the place of release after they had stayed in the Raba for several months, a year and even 2 years.

3. TIME OF CATCH OF SPECIMENS TAGGED

Tagged fish were recaptured in the Raba within the period of three years and a half, i.e., 42 months, after release. In the first year after stocking the recoveries were, however, decidedly most abundant. In that period 2,032 tags (9.88%) of the fish released) were recovered. They came from 778 2-year-olds (6.76% of the fish released at this age) and 1,254 3-year-olds (13.83%). The ratio of the former to the latter was, therefore, as 1 : 2.

The catching of fish was started in March or April (according to the time when the smolts descended in the given year; the fish caught earlier, as has been mentioned in Part I of this paper, were not included in these considerations) and ended in September, and thus it lasted for 6 or 7 months. In the second half of the year (from October throughout February of the next year) not a fish was caught.

Only the specimens from autumn stocking, sometimes in fairly large numbers, were caught in this period (they have been left out in the discussion of the results). For example, in the mild winter of 1958/1959 out of the 1,146 marked fish released on 8 and 10 December 1958, 96 specimens were recaptured in December, 23 in January and 2 in February (121 specimens altogether). 76 fish were taken in the place of release and 45 at a distance of 2—8 km upstream; 33 specimens of this last group were recovered in December and 12 in January (34% and 52% of the total of fish recaptured in respective months), which proves that the fish travelled up the river also in winter.

The majority of fish were caught in May, namely, 50% of the total of recoveries of the first year (1,021 specimens), April with 30% (603 fish) and June with 13% (267 fish) come in next. Altogether 93% of the fish (1,891 specimens) were recaptured during these three months. The remaining 7% (141 specimens) were caught within 4 months, when the catch ranged from 0.25% (5 fish) in September to 3.74% (76 specimens) in July. The distribution of the specimens discussed in the river in relation to the places of stocking was as follows: the highest proportion of fish, 44.4% (903 specimens), were caught in the place of release, the fewest of them, 17.0% (345 specimens) downstream of this place, and 38.6% (784 specimens) upstream.

2*

In the next years of the stay of fish in the river, that is, in the second, third and fourth year (from the 13th to the 42nd month) a total of 70 fish were recaptured, which makes 0.34% of those released. A similar low proportion of recoveries of tags, never exceeding 1%, is reported by WESTERMAN and HAZZARD (1945) for standard-sized brown trout recaptured later than a year after stocking.

In the second year, 13 to 18 months after planting fish (2.III.—8.VIII.), 42 specimens were caught (0.20% of the fish released), of which 16 fish released at the age of 2 years (0.14%) and 26 at the age of 3 years (0.29%). As in total recoveries and those of the first year, the ratio of the former to the latter was as 1 : 2.

In the third year (25—29 months after stocking; 30.III.—14.VII.) 26 fish were recovered (0.13% of the fish released). The specimens that were 3 years old at the time of release prevailed (the ratio of 2-year-olds to 3-year-olds was as 1 : 1.6).

In the fourth year of their stay in the river 2 fish released into the Raba at the age of 2 years were recaptured (at the time of catching 5+ years of age). One of them was an F_3 sea-trout, released on 27 November 1951 at the 50th km of the Raba, recovered after nearly 42 months, on 22 May 1955, at a distance of 4 km upstream of the place of release, the other an F_2 sea-trout liberated at the 60th km of the Raba on 20 March 1956 and recaptured at a distance of 10 km upstream after about 40 months and a half, by 7 August 1959.

The pattern of recoveries in particular months in the second and third year after stocking was similar to that in the first year, i.e., they were most numerous in spring months, May and April, and then in June. The distribution of fish in the river had, however, undergone some changes, namely, in the first year a majority of fish were caught in the place of release, in the second and next years upstream of this place. As the time passed, the difference in abundance of recoveries between the places discussed increased, which indicates that the fish which had stayed in the river for a long time moved steadily up the stream, as illustrated by the Table II.

Table II. Percentage recaptures of fish in successive years after release

Places of recapture	In first 12 months	13—18 months	25—29 months	40—42 months
Upstream of the place of planting	38.6	45.2	69.2	100.0
In the place of planting	44.4	19.1	11.6	—
Downstream of the place of planting	17.0	35.7	19.2	—
Total	100.0	100.0	100.0	100.0

4. PLACE OF RECAPTURE OF SPECIMENS TAGGED

Nearly all the specimens tagged that had not descended seawards were recaptured in the Raba, whereas only poor catch was taken in its tributaries and in other rivers. 2,053 tags (9.98% of the fish released) were recovered from the Raba. In the 9 tributaries joining the Raba from about 21st to 88th km up from the mouth and, therefore, nearly coinciding with the range

of the places of stocking (from about 19th to 81st km of the Raba) only 45 fish, i.e., 0.22⁰/₀ of the released specimens, were caught. In both these groups the ratio of 2-year-olds to 3 year-olds was as 1 : 2, in the Raba 788 (6.85⁰/₀) 2-year-olds and 1,265 (13.96⁰/₀) 3-year-olds were recaptured, whereas in its tributaries these values were 17 (0.15⁰/₀) and 28 (0.31⁰/₀), respectively.

Twenty-two specimens, thus nearly half of all the fish taken from the tributaries, were caught in the Krzyworzeka, the second longest right-hand-side tributary of the Raba, joining it at the 55th km. They divided into 8 2-year-olds and 14 3-year-olds, the ratio of the former to the latter being as 1 : 2.

In the Stradomka, the longest (about 35 km) right-hand-side tributary, opening into the Raba ot the 40th km, 11 fish were recovered. In the other 7 tributaries 12 fish were caught altogether, of which 5 in the Babica, which joins the Raba nearest its mouth, 2 in the Świdówka (its mouth is opposite that of the Stradomka) and 1 in each tributary opening into the Raba between its 26th and 88th km. Most of the fish, 41 in number, were recaptured in the first year after planting (5 April—22 July) and 4 specimens in the second year (15 May—8 August). They were taken, for the most part, near the mouths of these tributaries, only in the two longest ones at a distance from the mouth (up to 10 km in the Krzyworzeka and up to 5 km in the Stradomka). In the longest upstream journey the fish covered about 50 km (recapture in the Lubieńka, which joins the Raba at the 88th km) and in their longest downstream migrations they descended 24 km (a stream opening into the Raba at its 26th km).

In general, no F_1 sea-trout were recaptured in the tributaries of the Raba and F_3 specimens were the most numerous of its further pond generations and proportionally they exceeded the F_2 and F_4 sea-trout by two to one. The most abundant catch in the tributaries was that of brown trout, in which the specimens from the stockings carried out above the mouth of the given tributary outnumbered those from the stockings below its mouth by 1.5 to 1. As for the recoveries of fish of the other forms, the relation was reversed, that is, the specimens released below the mouth of the tributary were 5—9 times as numerous as those released above it.

To summarize the results of recaptures in the Raba and its tributaries, one may state, as follows:

1) a very small number of the specimens left the river in which they had been planted and ascended its tributaries (9.98⁰/₀ of the fish released were caught in the Raba, 0.22⁰/₀ in its tributaries);

2) most of these specimens (35 out of 45) entered the tributaries that open into the Raba above the place of planting;

3) the greater part of the fish caught in the tributaries were from the near by places of planting (mostly the nearest ones). Only a few specimens made relatively long journeys (up to 50 km).

Four tagged fish that had not migrated to the sea were caught out of the Raba catchment basin. Having left this river, they swam up the Wisła (Vistula), and 3 of them entered other tributaries, namely, the Rudawa (1 fish caught near its mouth) and the Skawinka (2 fish, recovered 5 km up from the mouth). The distance of the places of recapture of these fish from the Raba mouth ranged from 33 km (in the Wisła at its 102nd km) to about 79 km (in the Skawinka) and, when measured from the place of stocking, from 55 to 130 km.

In the Rudawa and Skawinka the fish were recaptured 16—20 months after stocking and in the Wisła as early as the next spring after autumnal stocking, that is, after the lapse of 5 months (on 26 April 1953). The earlier catch of 9 other specimens released into the Raba in the same place and on the same day, in the Gulf of Gdańsk, up to 70 km E of the mouth of the Wisła (16—26 April 1963), indicates that this fish had stayed in the Wisła in spite of the occurrence of favourable conditions for setting out on the seaward journey.

Among the fish that had not left the Raba there were also 3-year sea-trout of the first generation ($St_3 F_1$). It is worth while to give special attention to 14 of them, namely:

1) 3 specimens recaptured at the age of 5 years, more than 25 months after their release (released at the 57th km of the Raba on 20 March 1956, recaptured 5 and 7 km downstream of the place of release on 16 April and 5 May 1958);

2) 2 specimens caught at the age of 4 years after a stay in the Raba lasting more than a year (one of them was released at the 60th km of the Raba on 20 March 1956 and recovered in the place of release on 2 April 1957 and the other was liberated at the 38th km of this river on 3 December 1957 and caught at a distance of about 22 km upstream of the place of release on 31 May 1959);

3) 9 3-year-old sea-trout caught in the year of release but in the summer months, and therefore at the time when owing to the water temperature, which is too high, smolts do not undertake seaward migrations (EVROPEJCEVA, 1957). Seven of these sea-trout were released on 20 March 1956 and recaptured: 3 specimens from 27 to 30 May 1956, 2 specimens on 10 and 11 June 1956 and 2 specimens on 2 and 10 August 1956. Two fish released on 3 December 1957 were caught 22 km upstream of the place of stocking on 15 July 1958 and 12 km downstream of it in September 1958. All these sea-trout were caught in the river after the season of descent of smolts in the given years. At the time of release their measurements rendered them fit for seaward journey, but they were all at the stage of parr then.

I should also touch on the results of an experiment carried out on F_1 generations of the sea-trout, namely, on 18 May 1955 the then 2-year specimens were divided into smolts and parr. The total number of sea-trout was 454 and

Table III. Release and recovery of 3-year-old F_1 sea-trout

Release (20 March 1956)					Recapture					
Number of fish	Mean weight of specimen, in g	Number of mature males	Stage of fish		in the Raba			migrating		
			8 May 1955	20 March 1956	No.	%	Number of males	No.	%	Number of males
14	115.5	9	smolt	parr	5	1.35	3	—	—	—
123	101.2	—	smolt	smolt	—	—	—	30	8.11	—
52	63.5	—	parr	smolt	—	—	—	7	1.89	—
181	57.9	51	parr	parr	24	6.49	11	9	2.43	—
370	75.3	60	137 smolts, 233 parr	175 smolts, 195 parr	29	7.84	14	46	12.43	—

consisted of 151 smolts having a mean body weight of 53.6 gms and 303 parr with a mean body weight of 32 gms. The smolts had their adipose fin cut off, which made it possible to check the fish again a year later before their release (in March 1956). The results of catch of specimens tagged are given in Table III.

Together with 370 tagged 3-year sea-trout the remainder of the age group, i.e., 28 parr, too small to tag, much below 16 cm in length and with an average weight of 25.0 gms, were also released (a total of 398 specimens, of which 175 were smolts and 223 parr).

As will be seen from Table III, a small number of the largest specimens, which at the age of 2 years reached the stage of smolt, having gone through desmoltification, remained typical parr at the age of 3 years (March 1956). Sexually mature males prevailed among them (9 specimens in 14). The other specimens put on a smolt appearance again after a year. Scarcely 20⁰/₀ of the 2-year parr, the largest ones (52 specimens with a mean weight of 63.5 gms), underwent smoltification in the next year, whereas 209 fish (mean weight — 53.5 gms; 28 small specimens were not tagged) remained parr. Sexually mature males occurred in large numbers among the parr (60 males in the group of 195 parr), but there was none at all among the smolts.

Parr alone were recaptured in the Raba, nearly half of them being sexually mature males at the time of release. The number of sea recoveries of migrating sea-trout (30 specimens) which, showing a more rapid rate of growth, went through the process of smoltification in the second year of life was 1.9 times as large as that of the fish which, growing more slowly, were parr at the same time, at the age of 2 years (16 specimens). Out of these last specimens 7 were smolts at the time of release and 9 were still parr. The former made 13.5⁰/₀ and the latter 5.0⁰/₀ of the fish released at the respective stages. Not a male released in this batch with signs of maturity was recaptured while migrating (Table III).

5. SUMMARY

Most the tagged fish that had not migrated to the sea were recaptured in the place of stocking, the fewest below this place. The longest journeys in the river were 56 km upstream and 31 km downstream. The most abundant catches (2,032 fish) occurred in the first year after release. Later, up to 3 years and a half after release, 70 fish were recovered. These specimens travelled steadily up the stream. Nearly all the fish were caught in the Raba (2,053), only 45 specimens in its tributaries, and 4 in other rivers out of the Raba catchment basin. Most the specimens caught in the tributaries were brown trout, none of them was an F₁ sea-trout. The fish caught in the tributaries, except for the brown trout, were mostly those released below their mouth. The specimens released at the age of 3 years were recaptured in the rivers in twice as large a number as that of specimens released at the age of 2 years. The same proportions were also found for the total catches, the catches of the first and the second year after release, those of the Raba and all its tributaries together and, lastly, the catches in one of the tributaries, i.e. the Krzyworzeka, separately.

6. STRESZCZENIE

Najwięcej znakowanych ryb, które nie odbyły wędrówki do morza, odłowiono w rzekach w miejscu wypuszczenia, najmniej poniżej tego miejsca. Najdalszy zasięg wędrówek w górę rzeki wynosił 56 km, w dół rzeki 31 km. Najliczniejsze odłowy (2032 ryby) przypadły na pierwszy rok po zarybieniu. W późniejszym czasie do 3

i 1/2 lat po wypuszczeniu odłowiono 70 ryb. Osobniki te wędrowały stale pod prąd. Prawie wszystkie ryby złowiono w Rabie (2053 sztuki), w 9 jej dopływach tylko 45 osobników, a 4 ryby w innych rzekach poza dorzeczem Raby. W dopływach odłowiono, z wyjątkiem pstrągów potokowych, przeważnie ryby wypuszczone poniżej ich ujścia, nie złowiono tu ani jednej troci F_1, natomiast najwięcej pstrągów potokowych. Osobniki wypuszczone w wieku 3 lat zostały 2 razy liczniej odłowione w rzekach niż wypuszczone w wieku 2 lat. Proporcję tę stwierdzono zarówno w odłowach ogólnych jak też wśród ryb odłowionych w pierwszym i w drugim roku po wypuszczeniu, wśród osobników złowionych w Rabie oraz we wszystkich jej dopływach łącznie, w końcu w jednym z nich — Krzyworzece.

S. Skrochowska

MIGRATIONS OF THE SEA-TROUT (*SALMO TRUTTA* L.), BROWN TROUT (*SALMO TRUTTA M. FARIO* L.) AND THEIR CROSSES
PART III. MIGRATIONS TO, IN AND FROM THE SEA

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ABSTRACT

This part deals with all the fish recaptured during their seaward migration, sea-life, and upstream journey for spawning. A mass descent of smolts was observed in the spring and it was sometimes undertaken immediately after the release of fish into the river. Sea migrations of smolts were confined to the littoral zone of the Gulf of Gdańsk and those of grown-up fish covered nearly the whole area of the Baltic and even crossed its western bounds, reaching as far as the Skagerrak. All the adult fish returned for spawning to the Raba, into which they had been released at the size of smolts.

In contrast with the catches in the Raba (see Part II of this paper), in the sea recaptures the specimens released at the age of 2 years were twice as numerous as those released at the age of 3 years.

CONTENTS

1. INTRODUCTION

Sea migrations were not significantly affected by the fact to which form (sea-trout, brown trout, cross) or pond generation particular specimens belonged. After descent to the sea they all behaved like the sea-trout, from which they could not be distinguished in respect of their external appearance, either. Similarly, the specimens that remained in the river did not differ from the brown trout. The age

of fish at the time of release had a bearing on the abundance of recaptures but not on the range of migrations. For this reason, the migrations of fish will be presented on the basis of tag returns from specimens of all groups jointly and the difference in age at release will be taken into account in some cases only.

2. TAGGED SPECIMENS RECAPTURED
AFTER THEIR DESCENT FROM THE RABA

The results of catch in the Raba and its tributaries showed that in rivers the number of recaptures of 3-year-olds was twice as large as that of 2-year-olds. As has already been said, the division into these two age groups was brought about by different rates of growth of the young fish. In connection with the foregoing, in order to examine whether and, if so, to what degree the ability to undertake a seaward journey depends on the rate of growth, the specimens recaptured after their descent from the Raba were divided according to their age at the time of release and the results obtained are presented in Table I, in which the catch in the Raba is also included for comparative purposes. The data tabulated in it show that 1) in contradistinction to the catch in the Raba, the 2-year-olds recaptured while migrating were twice as numerous as the 3-year-olds; 2) the recoveries of migrating 2-year-olds and those in the Raba were almost equal (ratio as 1 : 1.1), whereas the 3-year-old fish taken while migrating formed less than a quarter of the number of specimens caught in the Raba (ratio as 1 : 4.3); 3) the total catch of 3-year-olds exceeded that of 2-year-olds by 4%.

Table I. Number of tagged 2- and 3-year-old fish recaptured in the Raba and while migrating

Age of fish at release	Number of fish released into the Raba		Number of fish recaptured						Ratio of recaptures — migrating: in the Raba
			In the Raba		Migrating		Total		
	No.	%	No.	%	No.	%	No.	%	
2-year-olds	11,505	55.50	807	7.01	759	6.60	1,566	13.61	1:1.1
3-year-olds	9,224	44.50	1,295	14.29	303	3.28	1,598	17.57	1:4.3
Total	20,729	100.00	2,102	10.14	1,062	5.12	3,164	15.26	1:2.0
Ratio of 3-year-olds to 2-year-olds	1:1.2		2.0:1		1:2.0		1.3:1		

The previous findings, that is, the considerably more frequent occurrence of sexually mature specimens among 3-year-olds than among 2-year-olds and the remarkably more numerous recaptures of individuals that were sexually mature at the time of release than immature specimens in the Raba and, in consequence, in general (see Part I Tables IV and V), suggested that the cause of the relatively great difference between the captures of 3-year-old fish and

those of 2-year-olds (Table I) was nothing but the more abundant occurrence of sexually mature specimens in the first of these two age groups. In order to check the righness of this supposition, the general recaptures of exclusively immature fish were compared, and the results of this comparison are given below:

sexually immature fish released into the Raba		total number of immature specimens recaptured	
age	number	number	%
2 years	9,573	1,400	14.62
3 years	7,928	1,326	16.73

The ratio of the former to the latter was in recoveries as 1 : 1.1.

The obtainment of similar results indicates that the more abundant catch of 3-year-olds was due to the fact that more specimens become sexually mature at this age than a year earlier. Therefore, the results of recaptures illustrate the actual presence of fish released at the age of 2 and 3 years in the Raba and after descent from this river (migrating).

Differences characterizing sea migrations of fish which at the time of release differed in age are analysed in Table II. The sea recaptures were, besides, divided according to the distance of the place of catching from the Wisła (Vistula) mouth, namely, into these recovered in the Gulf of Gdańsk and those taken in the open sea (Baltic).

Though the percentage value of catch of 2-year-old fish was in general twice as high as that of 3-year-olds, this ratio was not maintained in all the places of catching. The greatest deviations were found in the catch of smolts in the Wisła (equal numbers) and in that of adult fish in the sea out of the Gulf of Gdańsk, where 2.8 times as many 2-year-olds as 3-year-olds were recaptured. This last fact indicates that the fish which had left the river at a younger age made long journeys in the sea in large numbers, whereas those which owing to the slow rate of growth had stayed in fresh water a year longer were more numerous in the regions situated near the mouth of the Wisła (Gulf of Gdańsk) and also ascended the river in larger numbers (Table II). The catch of smolts will be discussed in the section of their journey to the sea.

A detailed division of all the fish recaptured after their descent from the Raba into groups according to their size (smolts, grown-up fish) and the place and time of catching is presented in Table III. As will be seen from the data collected in this table, 22% of the total recoveries were still specimens of the size of smolts, most fish, however, showed a remarkable increase in size at that time (they had stayed in the sea for more than 6 months). Nearly all the smolts and most of the grown-up fish were caught in the sea, whereas in rivers only very few smolts were taken during their seaward journey and 40% of the total of grown-up fish (833 specimens) were caught when ascending for spawning. All the descending smolts were recaptured in the Wisła, in which nearly all the adult fish that had left the sea were also taken (326 specimens). Nine fish were caught on the spawning grounds in the Raba, and the only sea-trout that had not returned to the Wisła after its stay in the sea was recaptured in the River Ina, which opens into the Szczecin Zalew, about 300 km west of the Wisła mouth as the crow flies (acc. to Ostsee-Handbuch, Vol. IV, the length of the seaway from Gdańsk to Świnoujście is 200 sea-miles, i.e., 370.4 km). As regards sea catch, it was more than 3 times as abundant in

Table II. Numbers of 2- and 3-year-old fish

Age of fish at release		Fish released into Raba	Place of	
			Smolts	
			Wisła (descending)	Sea (after descent)
2-year-olds	No. %	11,505 55.50	13 0.11	152 1.32
3-year-olds	No. %	9,224 44.50	10 0.11	54 0.59
Ratio of 3-year-olds to 2-year-olds		1:1.2	1:1.0	1:2.2

Table III. Experimental fish recaptured in particular areas of

Time of recapture of fish after its descent from the Raba		Stage of fish development					
		Smolts				Total of smolts re-captured	Gulf of Gdańsk
		Wisła (descending fish)	Sea				
Year Months			Gulf of Gdańsk	Out of Gulf of Gdańsk	Total		
I 03—03	No. %	23 0.11	204 0.98	2 0.01	206 0.99	229 1.10	73 0.35
II 04—03	No. %	—	—	—	—	—	176 0.85
III 04—03	No. %	—	—	—	—	—	76 0.37
IV 04—03	No. %	—	—	—	—	—	11 0.05
V 04—03	No. %	—	—	—	—	—	1 0.005
VI 04—03	No. %	—	—	—	—	—	1 0.005
VII 04—03	No. %	—	—	—	—	—	—
Total	No. %	23 0.11	204 0.98	2 0.01	206 0.99	229 1.10	338 1.63

recaptured after the descent from the Raba

catching and number of fish recaptured

Grown-up fish				Total
Gulf of Gdańsk	Open sea	Total in the sea	Rivers after stay in the sea	
237 2.06	124 1.08	361 3.14	233 2.03	759 6.60
101 1.09	35 0.38	136 1.47	103 1.12	303 3.28
1:1.9	1:2.8	1:2.1	1:1.8	1:2.0

fishing in successive years after their descent from the River Raba

and place of recapture

Grown-up fish							Total number of all fish recaptured
Sea		Rivers				Total of grown-up fish recaptured	
Out of Gulf of Gdańsk	Total	Wisła	Raba	Ina	Total		
35 0.17	108 0.52	12 0.06	—	—	12 0.06	120 0.58	349 1.68
98 0.47	274 1.32	136 0.66	—	1 0.005	137 0.66	411 1.98	411 1.98
24 0.12	100 0.48	145 0.70	8 0.04	—	153 0.74	253 1.22	253 1.22
2 0.01	13 0.06	32 0.15	1 0.005	—	33 0.16	46 0.22	46 0.22
—	1 0.005	—	—	—	—	1 0.005	1 0.005
—	1 0.005	—	—	—	—	1 0.005	1 0.005
—	—	1 0.005	—	—	1 0.005	1 0.005	1 0.005
159 0.77	497 2.40	326 1.57	9 0.04	1 0.005	336 1.62	833 4.02	1,062 5.12

the Gulf of Gdańsk (542 fish, of which 204 were smolts) as out of it (161 fish, of which 2 were smolts). On the other hand, in the Gulf of Gdańsk twice as many grown-up fish were caught as in the open sea.

The recaptures, as a rule, came to an end in the fourth year after the descent of the fish from the river. In the next three years only single specimens were recaptured, in the Gulf of Gdańsk in the 5th and 6th years and in the Wisła in the 7th year. In determining the time of catch of the sea-trout April was assumed to be the first month of the sea period in their life, which is supported by the following facts: 1) smolts descending to the sea were recovered in the Wisła during the 8 years of investigation and in 5 of these years their first specimens were caught in March and 2) most of the smolts recaptured in the sea were taken by the end of April.

The most abundant catch of the tagged fish occurred in the second year after descent, when in the Gulf of Gdańsk more than a half of the total number of specimens recaptured in that region (52%) were caught, this proportion being still higher for the open-sea catch (62%). In the rivers (Wisła, Ina), 41%c of the total number of the fish returning from the sea for spawning were caught in the second year after descent.

The first year after descent comes in second in respect of number of recaptures. Nearly two-thirds of the fish caught in this year were smolts.

Sixty per cent of the fish recovered in the third year were caught in rivers. It was the best year for recaptures of fish coming upstream for spawning (46% of their total number, of which 8 fish were caught in the Raba). On the other hand, there was a great decrease in the sea catch of that year as compared with the previous year. This decrease was particularly pronounced as regards the catch in the open sea, which catch equalled a quarter of that from the second year after descent, in the Gulf of Gdańsk it was less than a half. Most of the fish, therefore, left the sea, especially its farther regions, in the third year and migrated up the river for spawning.

Only a very small number of fish, scarcely 4.3% of the total (1,062) were caught in the fourth year. In the preceding 3 years the annual catch was successively 32.9, 38.7 and 23.8% (95.4% all together) of the total catch. As in the third year, most of the fish were recaptured in rivers, forming 72% of the total annual catch (in the Gulf of Gdańsk — 24%, in the open sea — 4%, i.e., 2 specimens). In the next three years, as has already been said, 1 fish was recovered in each (0.3% of the total catch in all). Thus, the relatively small number of fish that had stayed in the sea as long as 4 years, undertook a journey for spawning in this year, and so appeared in the sea only exceptionally (Table III).

3. MIGRATIONS OF SMOLTS

a. Downstream migration

River recaptures show that the fish tagged may still stay downstream of the place of planting in the Raba as late as 2 years after release and that some of them, having left the Raba, turn upstream in the Wisła, not downstream. For this reason, in the discussion of the downstream migration of smolts only these specimens were taken into account, in which the circumstances of catch (place and time) did not raise any doubt as to their being on

the way to the sea. They were, therefore, fish caught in the Wisła at a great distance below the mouth of the Raba (where the brown trout does not occur) and at the usual time of descent of smolts, i.e., in the spring or autumn. Twenty-three of them were caught. Most of them, 18 specimens, had been released a short time before catch in the spring (0.15% of the fish tagged at that time; out of the autumnal stockings, 5 smolts, 0.05%, were recaptured).

Recaptures of smolts on their way downstream to the sea were casual, and their number depended, above all, on the water level at the time of descent. The higher the water level, the fewer smolts were caught. The casualness of recaptures is indicated by the lack of any correlations between the number of smolts caught in the Wisła in the particular years of study and the number of fish released in these years on the one hand and, on the other hand, which is still more important, by the number of fish from the same stockings recovered after their descent to the sea (Table IV, e.g., season 1957/1958: the largest number of fish released, the highest per cent of recoveries after descent and at the same time the second lowest per cent of smolts captured during the descent). This lack of correlation is also confirmed by the percentage ratio of the 3-year-old smolts to the 2-year-olds recaptured in the Wisła (1 : 1, Table II), which ratio differs fundamentally from that characterizing the recoveries of all the fish that reached the sea (from 1 : 1.8 to 1 : 2.8, Table II).

Table IV. Number of fish released in the successive years of experriment and those of smolts taken in the Wisła and fish recaptured after their descent to the sea

Year of release	No. of fish released	Number of			
		smolts recaptured in the Wisła		fish recaptured after their descent to the sea	
		No.	%	No.	%
1951/1952	2,551 (4)*	2**	0.08	100	3.92
1952/1953	1,573 (19)	—	—	56	3.56
1953/1954	2,041 (34)	2	0.10	45	2.20
1954/1955	3,701 (30)	1	0.03	44	1.19
1956	3,028 (—)	3	0.10	224	7.40
1957	2,814 (105)	9	0.32	211	7.50
1957/1958	3,725 (39)	2	0.05	321	8.62
1958/1959	1,241 (161)	3	0.24	37	2.98
1960	55 (1)	1	1.82	1	1.82
Total	20,729 (393)	23	0.11	1.039	5.01

* The number of fish recaptured immediately after release and omitted in the calculation of results is given in brackets
** In 1952 two smolts, one dead and other injured and weak were found, and not caught, at the bank of the Wisła (descent with spring highlevel water, SKROCHOWSKA, 1953).

Smolts were captured in the Wisła during their seaward migrations over a distance of 497 km, from 161st to 640th km downstream of the mouth of the Raba (correspondingly from 645th to 166th km up from the mouth of the Wisła, Fig. 1).

A single smolt was taken in the autumn (22 September 1957), 177 km downstream of the mouth of the Raba and 237 km downstream of the place

of release. All the other smolts (22 specimens) were recaptured in the spring, in March and April. IVLEV and GALKIN (1958) found similar relations in descending salmon smolts, of which less than 10⁰/₀ descended in the autumn and over 90⁰/₀ in the spring. The findings presented by ŻARNECKI (1936) show similar proportions in the Dunajec sea-trout released in the Wisłoka and migrating seawards in the autumn (3 specimens, 8.8⁰/₀) and in the spring (31 specimens, 91.2⁰/₀).
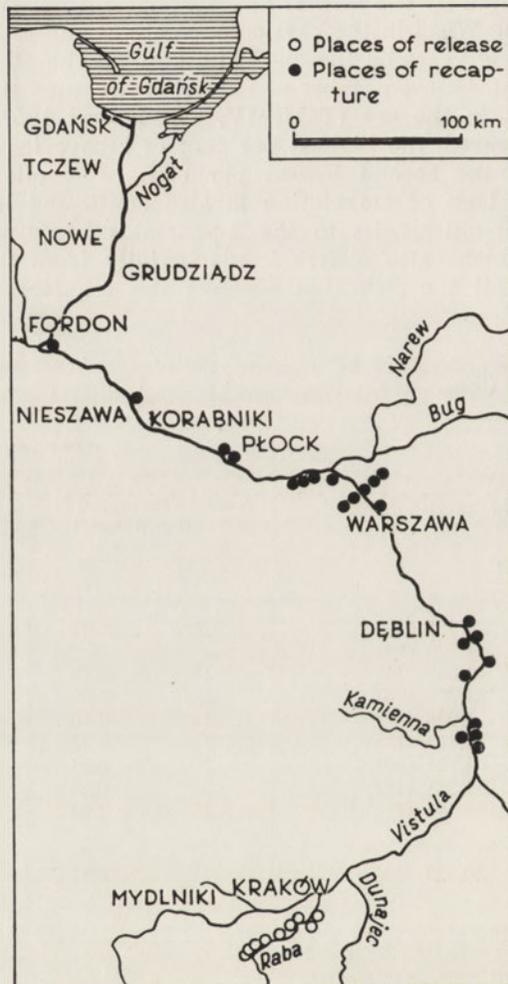

Fig. 1. Release and recapture sites of smolts descending to the sea in the Wisła

These results agree thoroughly with the observations made while the fish were being tagged before releasing, namely, a large number of fish were found to be in the stage of smolt or parr-smolt at the time of spring taggings

(2030 specimens, i.e., 19.94⁰/₀ of the 10,181 fish tagged [1]), whereas the specimens with the appearance of parr-smolts occurred only exceptionally (44 parr-smolts, which forms 0.94⁰/₀ of the 4,663 fish tagged) during the autumn taggings. Both the results of catch in the Wisła and the differences in the numbers of smolts among the fish tagged in the autumn and in the spring are corroborated by the studies on the process of smoltification, in which the authors state that the proper season of this process is the spring months (EVROPEJCEVA, 1957, 1960; FONTAINE, 1960).

Other phenomena that accompany the descent of young fish to the sea could also be traced on the basis of the results of recaptures of smolts and observations made simultaneously. Thus, it was found that the time when they start their migration depends closely on 1) external environmental factors, which are in turn controlled by the hydro- and meteorological conditions of the year and 2) the internal factors induced by smoltification, that is, a process preparing the animal for the change of fresh-water environment for the marine one. The dependence on the external factors was indicated by the simultaneous or separate descents of fish released in the autumn and in the spring in particular years of the study, that is to say, the fish from the stockings carried out in both these periods descended simultaneously when owing to a prolonged cold weather the first sudden rise in temperature and in water level — the most important stimuli releasing the downstream migration of smolts (EVROPEJCEVA, 1957, 1960; SWAN, 1957; FONTAINE, 1960) — occurred late in spring, not before the spring stockings (1952 — SKROCHOWSKA, 1953). If, however, thanks to an early spell of warm weather the above-mentioned conditions occurred in the pre-vernal period, then the fish released in the autumn started their journey still before the spring batch of fish had been released. This is true of the year 1954, in which a smolt released on 30 November 1953 was recaptured in the Wisła (224 km below the mouth of the Raba) on 11 March, whereas the spring stockings were carried out as late as 27 March and the first smolts from these stockings were recovered in the Wisła (209 km below the mouth of the Raba) on 19 April.

The dependence of the time of seaward migrations on internal factors is exemplified by the earlier recaptures of specimens released at the same time and belonging to the same form and generation in the sea than in the Wisła or by their simultaneous recaptures in the Wisła, in places fairly distant from each other. Despite the fact that they spent their juvenile periods of life together (from the moment of fertilization of eggs to that when the first of them left the Raba), and therefore under the same conditions, they started their seaward journey at different times. Such specimens were represented by 2 St_3 F_1 sea-trout released at the stage of smolts at the 50th km of the Raba on 16 March 1957. The first of them was recovered in the sea at a distance of 858 km from the place of release on 29 March 1957 and the other in the Wisła, 528 km downstream of the place of release, on 30 March 1957. The capture of 2 specimens of St_2 F_2 sea-trout was another example. The fish released without any signs of smoltification at the 60th km of the Raba on 16 March 1957 were recaptured in the Wisła, at distance of 310 and 453 km downstream of the place of planting on 30 March 1957, and so 143 km apart.

The date of release of fish into the Raba and that of recapture of the first smolts in the sea were used to calculate the minimum speed of their journey,

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[1] The number of smolts was recorded from the autumn of 1954.

assuming that under favourable conditions the fish started their downstream journey immediately after release, and otherwise, as soon as such conditions (temperature, water level) ensued, and were recaptured just after they had reached the sea.

In 1952 the minimum speed of migrating smolts, calculated in this manner, was 65 km per day (SKROCHOWSKA, 1953). A still higher speed has been obtained on the basis of the results from 1957:

1. An $St_3 F_1$ sea-trout, being a typical smolt, was released at the 50th km of the Raba at 12 o'clock on 16 March and recaptured in the sea, 2 km from the mouth of the Wisła and 858 km from the place of release 13 days later (at 6 o'clock A.M. on 29 March). The thermal and hydrological conditions on the day of release suggest that the sea-trout could not start its journey to the sea until 18 March (the first simultaneous rise in temperature by 2.9°C and in water level by 15 cm, whereas the previous changes in these conditions were reverse). The time of migration was therefore 11 days, its average speed being 78 km per day [2].

2. Another $St_3 F_1$ sea-trout released at the same place and on the same day and also in the stage of smolt, was recovered off the southern coast of the Wiślany Zalew (Św. Kamień between Tolkmicko and Frombork) about 108 km from the mouth of the Wisła on 2 April. The distance of the place of catching from that of release was 964 km, the time of migration 15 days (starting from 18 March), the lowest average speed over the whole distance 64 km per day. Since the smolt undoubtedly moved more slowly in the sea, its speed in the river must have been higher. If we assume that this sea-trout, like the first one, reached the sea on 29 March, then its speed in the sea was 27 km per day.

3. The recapture of two 3-year-old F_2 sea-trout in the Wisła released without symptoms of smoltification at the 35th km of the Raba on 26 March 1957 permits the computation of the speed of their migration on the assumption that they set out at the same time and migrated downstream together. The first of them was captured at the 528th km of the Wisła on 13 April, he other at the 703rd km on 15 April. If they journeyed downstream together, then the fish captured on 15 April covered a distance of 175 km in 2 days and its speed was 87.5 km per day.

Further data concerning the speed of the downstream migration of smolts were obtained in 1963 (the study is still being continued). Three fish released in the Raba (50th km) on 8 April were recaptured in the Gulf of Gdańsk 4 km W of the mouth of the Wisła on 17 or 18 April (on 18 April they were taken out of a net set on 17 April). The distance between the place of release and that of capture was 860 km, and the fish covered it in 10 or 9 days, the speed of their journey being, therefore, 86—95.5 km ped day. Two other fish planted in the Raba (at the 50th and 38th km) on 8 April were caught in the Gulf of Gdańsk, at 54°50 N latitude and 19°35′E. longitude, that is, about 68 km to the north-east of the mouth of the Wisła (25 km W of the nearest eastern coast of the Gulf) 15 days later (on 23 April 1963). The places of release of these fish were 912 and 924 km away from the place of recapture and thus the minimum average speed of migration over the whole distance was about

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[2] If the descent had begun directly after the release of the sea-trout, it would have reached the sea in 306 hours (12 days and 18 hours) at a speed of 67 km per day.

61 and 62 km per day. If we assume, as in the case of the St_3 F_1 sea-trout released in 1957, that the smolts captured on 17 (18) April and on 23 April 1963 migrated seawards together and reached the mouth of the Wisła simultaneously, then their speed in the sea was about 11—14 km per day. The recaptures of smolts in 1963 indicate the mass descent of these fish (3 specimens in one net) and, at the same time, that having finished their river journey, they are immediately able to swim in the sea, fairly far from the shore.

b. Sea recaptures of smolts

The smolts recaptured in the sea soon after they had reached it, from 25 March to 4 June, showed no, or only very slight, increase in size. Their total number was 206 (Table III, Fig. 2), most of which were taken in April (the number of specimens captured in particular months was as follows: March — 2, April — 111, May — 84, June — 1; no detailed date of catch, (April or May, was given in 8 cases).

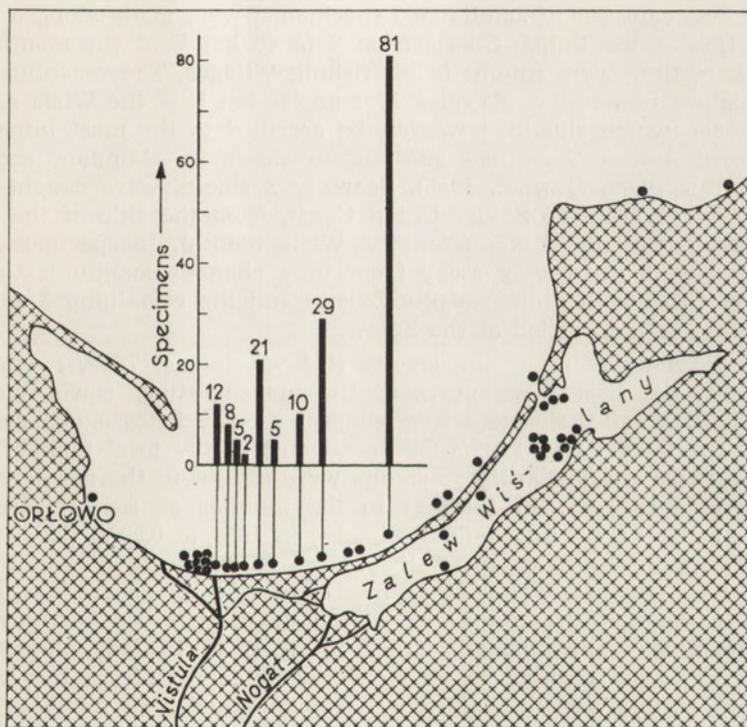Fig. 2. Recapture sites of smolts in the sea

Nearly all these smolts (204 specimens) were recaptured in the Gulf of Gdańsk, including 16 smolts taken in the Wiślany Zalew separated from the Gulf by the Wiślany Sand-bar and communicating with it through the Baltic Channel about 72 km NE of the mouth of the Wisła. Out of the Gulf of Gdańsk, two 3-year F_1 sea-trout smolts released into the Raba on 20

March 1956 were recaptured off the southern coast of the Kurskiy Bay on 15 and 23 May 1956. The distance of the place of recapture of the first of these fish (Zelenogradsk) was about 131 km NE of the mouth of the Wisła measured in the straight line (about 150 km along the coast-line), the other was caught 17 km nearer (Pionerskiy).

The places of recapture of smolts extended along the southern coast of the Baltic over a distance of 183 km, from Orłowo, 33 km NW of the Wisła mouth (29 km, as the crow flies) to Zelenogradsk, 150 km NE of that place. Nine smolts (4.4% of the total of fish recaptured at this stage) were taken west of the mouth; eight of them at a very small distance (1.5—6 km) in 1957 and only 1 somewhat father (29 km) in 1959. Twelve smolts (5.8%) were captured at the very mouth of the Wisła and 185 (89.8%) to the east, in the Gulf of Gdańsk, Wiślany Zalew and Kurskiy Bay. Having left the Wisła, most of the smolts migrate decidedly in the direction of the east. ŻARNECKI (1936) found the same direction of migration in sea-trout smolts coming from the Wisła and ŻARNECKI et al. (1964) in those from the rivers of Pomerania.

The richest captures of smolts (165 specimens) were made along a 44-kilometre portion of the Polish Coast (from 2 to 46 km E of the mouth of the Wisła), where they were caught in all fishing villages. The recaptures attained the highest numbers at Krynica Morska (34 km E of the Wisła mouth — 81 specimens), which should, however, be ascribed to the most intensive fishing carried out at that time and not to the most abundant occurrence of fish in this place (JOKIEL, 1955). Scarcely 2 smolts were caught further to the north-east, off the Soviet Union Coast, from the side of the Gulf of Gdańsk (about 57 and 72 km from the Wisła mouth), 13 specimens in the Wiślany Zalew, a short way away from they channel communicating with the Gulf of Gdańsk (Kaliningradskiy Zalew) and the remaining 3 specimens in the south-western portion of the Zalew.

Nearly three-quarters of the smolts (151 specimens, 73.3%) were recovered within the first three years of the present study (springs of 1952, 1953 and 1954), when their successive recaptures formed 2.39% (61 specimens), 3.24% (51 specimens) and 1.91% (39 specimens) of the total number of fish released in those years. Hardly 55 smolts were caught in the next five years, i.e., from 1955 to 1959. In relation to the number of fish released their recaptures ranged from 0.16% (2 specimens) in 1959 to 0.59% (18 specimens) in 1956. The main cause of these differences seems to have been the technics of fishing, that is, smolts were mostly caught in inshore herring drift nets during the spring catch or at trial casts of nets for herrings, which in the spawning season (usually from 10 April to 15 May, JOKIEL, 1955) appear in the same regions as young sea-trout coming from the Wisła (in the vicinity of the Wiślana Sand-bar). The unprecedented numbers of herrings caught in 1950 and especially in 1951 caused a great intensification of fishing (a larger number of fisherman and drag-nets) in the years 1952 and 1953. In these years, however, herrings occurred in small numbers, the catch was poor, whereas smolts were taken in abundance (after JOKIEL, 1955). When herrings continued occurring in small numbers, intensive fishing was given up and, as a result, the number of smolts recaptured decreased. The places of their captures situated to the east of the Wisła mouth lay in the same area as previously, but smolts were also found towards the west

of the mouth of the Wisła, where they had never been recorded from before (ŻARNECKI, 1936; KULMATYCKI, 1940a,b). Besides, though not very numerous here, they formed a half of the total number of smolts recaptured in the sea in the given years.

4. MIGRATIONS OF GROWN-UP FISH

a. General characteristic of the course of recaptures

There were no tagged fish in catch from the moment when the recaptures of smolts had finished, which practically took place in the first half of May (only 5 smolts were captured after 16 May). They did not appear in it again until the autumn months, October and November, when they already showed considerable increases in size [3].

Throughout the whole period of study there were 3 exceptions, i.e., specimens caught in August (relatively small, 34 and 35 cm in length and 0.34 and 0. 45 kg in weight, but exceeding smolts in size considerably and so reckoned among grown-up fish).

The detailed course of monthly catches of grown-up fish in the three regions of fishing, namely, in the sea out of the Gulf of Gdańsk, in the Gulf of Gdańsk and in the Wisła is presented in Table Va, b and c, and the general results of monthly recaptures in Fig. 3.

Except for the specimens caught in August (2 of them in the Gulf of Gdańsk, 34 and 44 km E of the Wisła mouth and one near Klaipeda), the recaptures of grown-up fish began in the seventh month after their descent from the river (October), at a great distance from the Gulf of Gdańsk, in the open sea. One of the tagged fish was caught off the eastern coast of Sweden, near the island of Brämö, about 890 km N of the Wisła mouth on 10 October and another fish 75 sea-miles (139 km) SW of Liepaja, i.e., about 210 km N of the Wisła mouth on 27 October (Fig. 4A). The thus commenced catches out of the Gulf of Gdańsk, increased in the autumn-winter months, then only slightly in the spring-summer period and ended in catching 2 tagged specimens in the fourth year after their descent: in April (37th month after descent) in the northern portion of Kattegat and at the beginning of August (41st month after descent) presumably in the vicinity of the Gulf of Gdańsk (the tag returned from the GDR without the exact place of catching, Table Va).

The first fish (2 specimens) in the Gulf of Gdańsk were caught in November in the year of descent and the last one at the beginning of April in the

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[3] A similar but far longer (from the descent of smolts to March of the next year) absence of salmon in catch round the British Isles was observed by MENZIES (1925) and JONES (1959) and in the Baltic Sea by ALM (1928) who explains it, according to Dahl, by the supposedly pelagic ways of living of the fish at that time. The same results were obtained by CARLIN (1955) for salmon from the River Lagan in the sea off the western coast of Sweden. The lack of sea-trout tagged in Baltic catches (after smolts had ceased appearing in them) till the autumn was reported by CHRZAN (1963). The complete lack of post-smolt stage sea-trout in the catch from the Baltic Sea (or only single recaptures in July or August) and appearance of specimens tagged in the catches of the autumn months were indicated by the data given by ŻARNECKI (1936, 1964c), PACKIEL and BARTEL (1963) and ŻARNECKI at al. (1964). The same phenomenon with respect to the salmon from tributaries of the Wisła is shown by the finding of ŻARNECKI (1964b).

Table V. Monthly recaptures of grown-up fish

a. In the sea out of the Gulf of Gdańsk

Successive year of stay in the sea	Month of recapture												Total	
	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	No.	%
I	—	—	—	—	1	—	2	10	9	4	5	4	35	22.0
II	2	—	—	2	2	5	17	20	19	11	11	9	98	61.0
III	6	3	—	2	1	—	2	5	4	1	—	1	24	15.7
IV	1	—	—	—	—	—	—	—	—	—	—	—	2	1.3
Total No.	9	3	—	4	4	5	21	35	32	16	16	14	159	100.0
%	5.7	1.9	—	2.5	2.5	3.1	13.2	22.0	20.1	10.1	10.1	8.8	100.0	

b. In the Gulf of Gdańsk

Successive year of stay in the sea	Month of recapture												Total	
	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	No.	%
I	—	—	—	—	2	—	—	2	11	13	9	36	73	21.7
II	27	8	2	—	2	1	—	9	32	29	15	50	175	52.1
III	29	14	2	—	3	1	—	5	7	4	3	7	75	22.3
IV	4	1	1	—	—	—	—	—	3	—	—	2	11	3.3
V	—	—	—	—	—	—	—	—	—	—	1	—	1	0.3
VI	1	—	—	—	—	—	—	—	—	—	—	—	1	0.3
Total No.	61	23	5	—	7	2	—	16	53	46	28	95	336	100.0
%	18.2	6.8	1.5	—	2.1	0.6	—	4.8	15.8	13.7	8.3	28.3	100.0	

c. In the Wisła (Vistula)

Successive year of stay in the sea	Month of recapture												Total	
	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	No.	%
I	—	—	—	—	—	—	—	2	1	—	—	8	11	3.4
II	7	2	—	3	23	12	11	22	15	6	7	27	135	42.2
III	22	6	15	20	24	13	5	7	13	6	2	9	142	44.4
IV	9	4	2	4	5	5	1	—	—	—	—	1	31	9.7
VII	—	—	—	—	—	1	—	—	—	—	—	—	1	0.3
Total No.	38	12	17	27	52	31	17	31	29	12	9	45	320	100.0
%	11.9	3.7	5.3	8.4	16.3	9.7	5.3	9.7	9.1	3.7	2.8	14.1	100.0	

Remarks:
Exact date (month and day) of recapture not given for 2 specimens in the Gulf of Gdańsk and for 6 ones in the Wisła.

6th year after descent (61st month), all of them in the neighbourhood of the Wisła mouth. These fish stayed in the sea from 8 to 60 months (Table Vb).
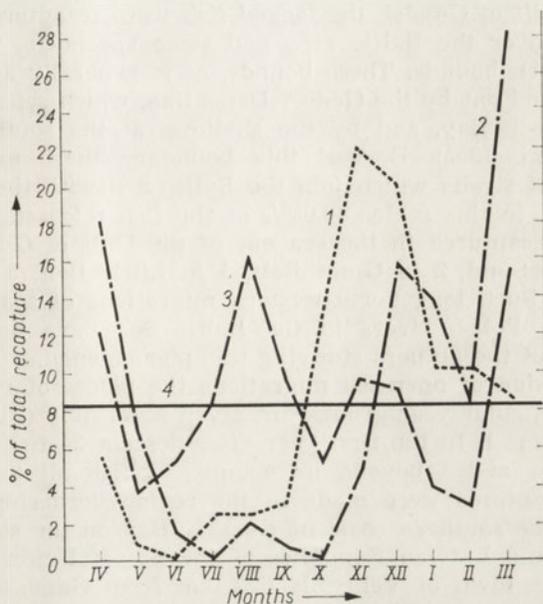

Fig. 3. Monthly recaptures of grown-up fish in the
1 — open Baltic Sea, 2 — Gulf of Gdańsk, 3 — Wisła, 4 — average recapture of the year

In the Wisła 12 grown-up fish were captured in the first year after release, the first two in November, i.e., 8 months after their release in the spring, 1 in December, 8 in March (12th month of the stay in the sea) and 1 fish, for which no exact date of catching has been given. Most of these fish were recaptured at the very mouth of the Wisła (4 specimens) or hardly 2 km above it (5 fish). Only 3 specimens were caught away from the mouth of the Wisła, namely, 2 fish at a distance of 8 (933rd km of the Wisła) and 88 km (Nowe on Wisła) from the sea in March and one about 34 km from the sea (Tczew) without the date. Another specimen was caught at the same distance from the sea; its stay in the sea, the longest on the record and determined on the basis of the dates of release (27 March 1957) and recapture (27 September 1962), was 78 months (recovery in the 7th year after release.) However, since the tag was returned without scales and data concerning its measurements, it was impossible to check whether this fish had already spawned before or whether it had not lingered in the river for a year before descending downstream (it was released at the age of 2 years, 14.9 cm in length and 33 gms in weight — Table Vc).

A comparison of the general course of annual catches of tagged fish in the open sea and in the Gulf of Gdańsk (Fig. 3) with the annual course of commercial catches made in these regions in more or less the same years

showed their essential correspondence with each other in both cases [4]. This fact indicates that the material discussed was sufficiently rich to avoid casual elements in results.

b. Migrations in the open Baltic Sea and out of its bounds

Out of the Gulf of Gdańsk the tagged fish were recaptured in large numbers nearly all over the Baltic area and some specimens were even taken beyond its western bounds. These bounds, as is generally assumed in Polish papers, are marked out by the Gedser-Darss line, which separates the Arcona Basin from Lubeck Bay, and by the shollows at the southern end of Ore Sund (Mańkowski, 1955). Beyond this boundary there extends an intermediate region of straits which join the Baltic Sea with the North Sea. Ten fish were caught in this region (0.05% of the fish released and 6.3% of the grown-up fish recaptured in the sea out of the Gulf of Gdańsk), namely, 1 specimen in Ore Sund, 2 in Great Belt, 1 in Little Belt, 5 in Kattegat and 1 in Skagerrak. Such long north-western migrations of sea-trout or salmon descending from Polish rivers to the Baltic Sea have not been recorded hitherto by any of the authors studying this phenomenon.

In the discussion of open-sea migrations the places of recaptures of fish belonging to particular year-groups are given separately (Figs 4A, B, C).

Year-group I. In the first year after descent 34 fish were recaptured in the Baltic Sea and 1 beyond its bounds, 35 fish all together (Fig. 4A). Most of the recaptures were made in the region bordering upon the Gulf of Gdańsk and the southern coast of Kurskiy Bay on the south, the coast of the Lithuanian and Latvian Republics of the Soviet Union on the east and the region of the town of Ventspils (394 km from Gdańsk [5]) on the north. On the west this region is bounded by a straight line drawn from Rozewie northwards beyond which, about 25 km to the west, only 1 fish was recaptured. Inclusive of this specimen in the area described 28 fish were captured, of which 21 up to 50 km from the shore and, in turn, 11 out of these last in the region between Sambian Cape (Brüster ort) and Ventspils. The distance of the places of recapture of 11 specimens did not exceed 50 km from the boundary of the Gulf of Gdańsk either. The captures were made in all the consecutive months of the year from October till March. The remaining 7 fish were caught in ahe region of Bornholm (4 fish, 3 in Decembre and 1 in February) and 1 in each of the following localities: off the northern coast of Gotland (Hallshuk, March), in the Gulf of Bothnia in the neighbourhood of the islet of Brämö (the above-mentioned first grown-up fish caught in the sea in October) and out of the Baltic Sea in Great Belt off the eastern coast of the Danish island of Fyn, near the town of Nyborg (652 km from Gdańsk). In the neighbourhood of Bornholm 3 fish were recaptured west of this island (26 km NW of Hammeren and 33 km NW of Rönne) and 1 on the eastern side (at a distance of 46 km).

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[4] Christensen (1961) presented the average monthly catches in the Baltic in the period 1952/1953—1959/1960 and Kändler (1963) for the period 1954—1961, whereas Romański (1964) offered these values for the Gulf of Gdańsk in the years 1955, 1959 and 1960.

[5] All the distances from Gdańsk are given after Ostsee-Handbuch, Vol. IV. No. 2003, 1959, sea miles being converted into kilometres. The distance of the mouth of the Wisła from Gdańsk is 6 sea miles or 11 km in the eastern direction.
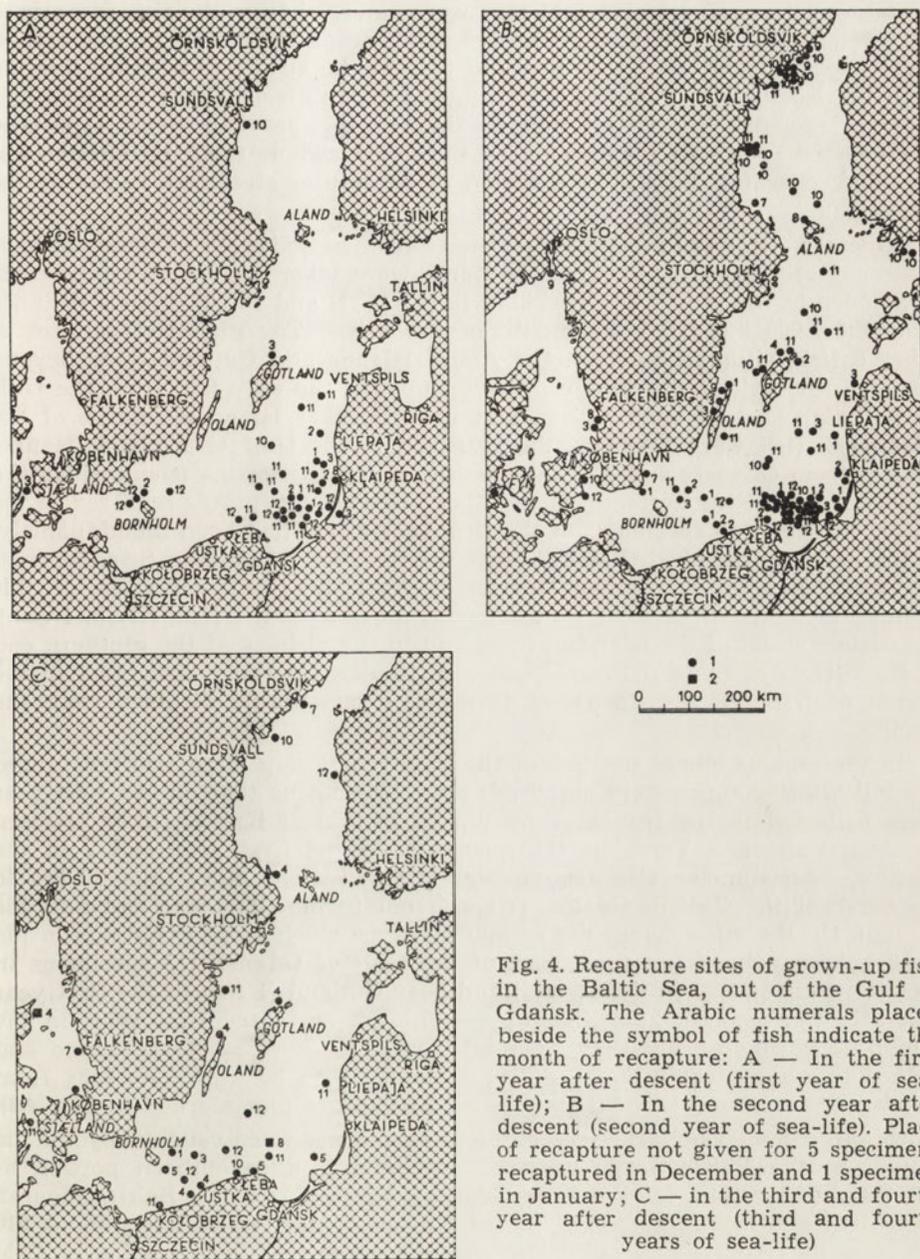
Fig. 4. Recapture sites of grown-up fish in the Baltic Sea, out of the Gulf of Gdańsk. The Arabic numerals placed beside the symbol of fish indicate the month of recapture: A — In the first year after descent (first year of sea-life); B — In the second year after descent (second year of sea-life). Place of recapture not given for 5 specimens recaptured in December and 1 specimen in January; C — in the third and fourth year after descent (third and fourth years of sea-life)

Y e a r - g r o u p II. Ninety-eight tags were returned from the fish recaptured out of the Gulf of Gdańsk in the second year of their stay in the sea; of these tags 93 from the Baltic Sea and 5 from the straits connecting this sea with the North Sea (Fig. 4B). The range of recaptures in both these regions extended remarkably in relation to that in the previous year, especially towards the north. In the Baltic Sea the nearly whole Gulf of Bothnia was included, out of the Baltic the region of recaptures stretched as far as the Skagerrak.

Nineteen fish were recaptured in the Gulf of Bothnia; out of these, 3 specimens captured farthest towards the north were taken near the eastern coast of Sweden in the region of Örnsköldsvik (63°16′ N and 18°50′ E), at a distance of about 1,000 km from the mouth of the Wisła. The places of capture of other 6 fish, situated between the Aland Islands and Gotland were beyond the range of fish of the first year-group (except the only fish from the Gulf of Bothnia). One of them was caught near Bogskär Island (26 km S of the Alands), 2 fish were taken at the entrance to the Gulf of Finland (Hanko, 659 km from Gdańsk) and 3 to the north-east and east of the island of Gotska Sandön (37 km N of Gotland). Some other places of recaptures occurred in the region in which no specimens of the first year-group had been found, namely, in the neighbourhood of Öland (4 fish), off the eastern coast of Sweden, west of Öland (Skäggnäs, Kalmar District, 1 fish), the southern coast of this country to the north-west of Bornholm (Sandhammeren, 1 fish, Kivik, 1 fish), the eastern coast of the island of Sjaelland in the vicinity of the southern end of the Straits of Sund (Klint, 1 fish) and, finally, off the Polish coast in the region of Ustka (4 fish, some of them at a remarkable distance from the land).

In the regions where the fish of the first year-group were also recaptured the following changes were observed: fewer specimens than in the first year were collected in the inshore zone (up to 50 km) of Kurskiy Bay between Sambian Cape and Ventspils (11 specimens in the first year and 7 in the second), their number was also smaller in the regions more than 50 km to the north of the Gulf of Gdańsk (7 specimens in the first year and 5 in the second). On the other hand, the recaptures were much more numerous in the close neighbourhood (up to 50 km) of the Gulf of Gdańsk (11 specimens in the first year and 29 in the second) and near Gotland (1 fish in the first year and 5 in the second). Four fish were captured, as in the first year, in the region of Bornholm, but they were all caught to the east of the island and at a somewhat greater distance (from about 37 to 80 km). The tags from 6 fish were returned without the place of recapture (not marked in Fig. 4B).

In the second year after descent five specimens were caught beyond the bounds of the Baltic Sea, namely, 1 specimen in the southern portion of Ore Sund (Köge Bay, 427 km from Gdańsk), one fish in Little Belt (Aabenraa Fiord, 694 km from Gdańsk), 2 in the Kattegat (Gulf of Laholm, about 610 km from the Wisła mouth) and 1 in the Skagerrak (southern portion of Oslo Fiord, about 950 km from the Wisła mouth), which is the farthest locality to the northwest of the Gulf of Gdańsk. Captures were made from August to March (17th—24th month after descent), the first and the last fish being caught in the Gulf of Laholm (Fig. 4B).

Y e a r - g r o u p III. Twenty-four fish were captured out of the Gulf of Gdańsk in the third year of their stay in the sea, 21 of them in the Baltic

and 3 in the straits connecting the Baltic with the North Sea (Fig. 4C). The picture of recaptures in the southern portion of the sea in the third year after descent haa undergone a thorough change as compared with the two preceding years. Only 3 specimens were caught close to the Gulf of Gdańsk and off the coast of the Lithuanian and Latvian Soviet Republics (N of Rozewie, N of Sambian Cape and W of Liepaja), whereas in the previous years the captures were most abundant in this region. New localities of catches, however, appeared along the Polish coast west of Rozewie (Łeba, Darłowo, Dąbki, Mrzeżyno), where 5 specimens were taken at distances ranging from 25 km (OP-7 fishing—ground) to 213 km (Mrzeżyno). The other places of recaptures lay within the range of year-group II, but were less numerous and except for the region of Bornholm only single specimens were caught in them. Thus, starting at the north, 4 fish were recaptured in the Gulf of Bothnia, 3 off the eastern coast of Sweden from Örnsköldsvik to the southern end of this gulf, and 1 off the western Finnish coast (Skaftung). Three fish were taken in the region between the Aland Islands and Gotland and Öland, one off the northern coasts of either of these last islands and a third one off the Swedish coast, to the north of Öland (Harstena). Four specimens were captured up to 63 km E and SE of Bornholm, one north of Łeba and one north of Ustka, these last two at a considerable distance from the shore (74 and above 130 km).

Three fish were caught in the straits joining the Baltic Sea with the North Sea, 2 in the Kattegat, of which one in its southern part, off the morthern coast of the island of Sjaelland (Gilleleje) in April and the other farther to the north, off the western coast of Sweden) Falkenberg, 657 km from the Wisła mouth) in July; the third fish was captured in the Great Belt, off the western coast of Sjaelland (Asnaes Peninsula, about 730 km from the Wisła mouth) in November.

Year-group IV. Only 2 tags have been returned from the fish recaptured in the fourth year after descent. In April 1 fish was caught in the northern part of the Kattegat, in Aalbaek Bay (about 760 km from the mouth of the Wisła). The locality of catch of the second fish, taken in the Baltic in August, was not given (the tag was returned by the G.D.R., whose fishermen fished in the vicinity of the Gulf of Gdańsk, Fig. 4C).

The results of recaptures of tagged fish in the sea out of the Gulf of Gdańsk discussed above make it possible to establish the following presumable course of their migrations:

The greater part of the fish, carrying on the migrations of most of the smolts, leave the Gulf of Gdańsk along its eastern coast (some of them still at the smolt stage) and travel a relatively short distance towards the north without moving too far from the shore, as evidenced by the recaptures of tagged fish in the area between the Gulf of Gdańsk and Ventspils (394 km from Gdańsk) in the period from August till March or till the end of the first year of their sea life. Only a few specimens take up a further journey to the north immediately and reach remote regions of the Gulf of Bothnia (Brämö, about 900 km from the mouth of the Wisła) before winter.

Smaller numbers of fish, having left the Gulf of Gdańsk, direct themself at once towards the north-west and come to the region of Bornholm; before the year has elapsed, some of them migrate on to the region of straits between the Danish islands.

It the second year after descent the fish which up to that time have stayed in the littoral zone of the Lithuanian and Latvian Soviet Republics and in the region to the west of this zone journey to the north and are captured in large numbers throughout the part of the Baltic Sea stretching in that direction from the Gulf of Gdańsk. The farthest portion of the Gulf of Bothnia (beyond 64°N. latitude), where they have not been found, is an exception. From the region of Bornholm the fish, whose number is constantly completed (uniform catches in the three successive years after descent), scatter towards the southern coast of Sweden and in fairly large numbers swim out of the Baltic Sea to reach the Skagerrak.

In the second year many fish also leave the Gulf of Gdańsk and swim out into the open sea neighbouring upon the gulf. These fish, recaptured in large numbers in the winter (25 specimens of the total of 29 were taken from November to February, Fig. 4B), belong to those which are the first to return to the Gulf of Gdańsk, as shown by their slight occurrence (2 fish, Fig. 4C) in catches of this region in the third year after descent.

In the third year after descent only a small number of the fish remain in the open sea, where relatively many of them (9 specimens out of the 24, i.e., 37.5%) were recaptured at the beginning of that year, namely, in the spring months, April and May (in the previous, second, year only 2 fish were captured in this period, Table Va). The occurrence of numerous fish off he Polish coast, between Świnoujście and Rozewie, suggests that many of them return this way from the western regions of the sea to the Gulf of Gdańsk, lingering longest in the region of Bornholm (still captured in January and March, i.e., in the 34th and 36th months after descent).

In the fourth year all the fish leave the open sea, for only 2 specimens were caught there in this period, both in the first part of the year (April and August, Fig. 4C), and not a fish was caught out of the Gulf in the next, fifth, year of their sea life.

To conclude this description of the open sea migrations of the sea-trout, it should also be mentioned that the share of Polish fisheries in the catches out of the Gulf of Gdańsk, in which all the Baltic countries took part, was slight. Polish fishermen caught 1 fish in the Deep of Gdańsk and 7 off the western Polish coast (Rozewie — Świnoujście), 8 fish in all, i.e., 5% of the total catch in the open sea (159 specimens). The units of Swedish fisheries caught the most, namely 87 fish, 54.7%. The recaptures made by other states are as follows: G.F.R. — 35 fish (22.0%), Denmark — 22 fish (13.8%), U.S.S.R. — 3 fish (1.9%), Finland — 2 fish (1.3%) and G.D.R. — 2 fish (1.3%). All these countries but Finland caught fish also in the Gulf of Gdańsk, however only in small numers except for the G.F.R., whose recaptures (40 fish) in the Gulf of Gdańsk outnumbered those in the open sea. These last were, besides, made for the most part in the close vicinity of the Gulf of Gdańsk, mainly in the Deep of Gdańsk, and the fishing grounds of this region are reckoned among the richest in the Baltic Sea in so far as salmonid fish are concerned (Thurow, 1960).

c. Migrations in the Gulf of Gdańsk

A total of 338 grown-up fish (1.63% of the fish released, Table III, Fig. 5) were caught in the Gulf of Gdańsk. A great many fish were taken near the shore in all localities in which smolts were caught (the most numerous recap-
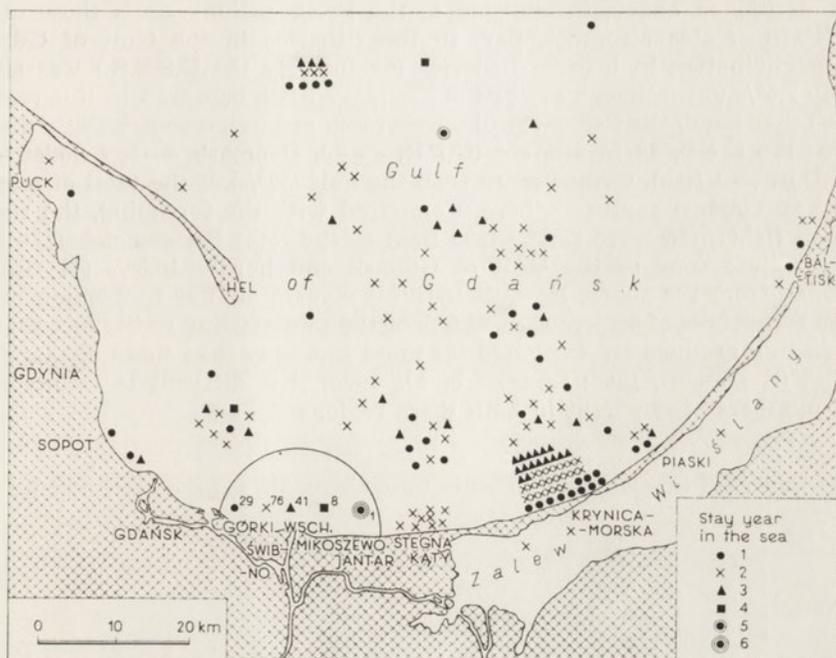
Fig. 5. Recapture sites of grown-up fish in the Gulf of Gdańsk. All the fish of a particular year-group recaptured up to 11 km from the mouth of the Wisła are marked with only one symbol their number being given beside the symbol. In the remaining area each fish is given a separate symbol. Place of recapture not given for 2 specimens after 1 year in the sea and for 12 specimens after 2 years in the sea

tures were made at the mouth of the Wisła — 52 specimens, then at Krynica Morska — 49 specimens where the number of smolts captured was also the highest), and there were less abundant catches at a distance from the land [6] (Table VI).

The figures presented in Table VI show that near the shore 2.5 times as many specimens were recaptured as at a distance from it and that their proportions in the catches made in both these regions varied with age of fish. These changes proceeded in quite opposite directions, since the inshore catches became relatively more and more aboundant, while the number of fish of older age-groups recaptured at a distance from the shore decreased gradually (this concerns year-groups I—III; the number of fish of the fourth year-group captured was too small, 11 specimens, for the results to be fully reliable). These differences in the age composition of catches were undoubtedly due to the more and more numerous returns of older fish to the inshore waters in connection with their migrations for spawning.

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[6] This batch of fish contains 10 specimens whose tags have been returned from abroad without a mention about the exact place of capture. Owing to this fact, in Fig. 5 all these fish are marked together in the area adjacent to the boundary of the Gulf of Gdańsk, to the north of the mouth of the Wisła.

As mentioned above, in addition to the Polish fishing units those of the other Baltic states also took part in the fisheries in the Gulf of Gdańsk. Their participation in inshore fisheries (exclusively the U.S.S.R.) was slight, scarcely 2.6% (6 specimens out of the 232 tagged fish captured in this region). On the other hand, the fish caught by fishermen of foreign coutries at a distance from the shore, 48 in number (G.F.R. — 40, Denmark — 5, Sweden — 2 and G.D.R. — 1 fish), formed more than the half (52%) of the total of marked fish (92 specimens) captured there. Compared with the foregoing, the results of Polish fishermen were 83.7% (226 fish) of the total Polish catch (270 fish) in the inshore zone of the Gulf of Gdańsk and hardly 16.3% (44 fish) at a distance from the shore. Romański (1964) gives a similar proportion of the inshore recaptures of sea-trout — 81.6% of the total. Owing to the fact that inshore fishing grounds are exploited far more intensely than those distant from the land (Romański, 1964; Chrzan et al., 1965) it is difficult to estimate the actual numbers of sea-trout in both these regions.

Table VI. Adult fish recaptured in the Gulf of Gdańsk according to the distance from the coast

Place of recapture		Number of fish recaptured						
		Successive year after descent						
		1	2	3	4	5	6	Total
Close to the coast	No.	47	117	59	8	—	1	232
	%	66.2	71.3	77.6	72.7	—	100.0	71.6
Far from the coast	No.	24	47	17	3	1	—	92
	%	33.8	28.7	22.4	27.3	100.0	—	28.4
Total	No.	71	164	76	11	1	1	324

The dependence of both the abundance and the age composition of the catches on upstream migration becomes very distinct when the fish recaptured in the Gulf of Gdańsk have been divided into groups according to the distance of the places of recapture from the mouth of the Wisła (Table VII).

Assuming that the estuarial region of fishing covers an area within a radius of 11 km from the mouth of the Wisła [7], one will find that in this small part of the Gulf of Gdańsk (about 190 km²), which forms hardly 3.5% of the surface area of the whole Gulf (exclusive of Wiślany Zalew), nearly the half

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[7] Places of recapture: Górki Wschodnie and Górki Zachodnie, about 10—11 km W of the mouth of the Wisła — 31 fish, 6 km W of the mouth of the Wisła — 1 fish, the region of the mouth of the Wisła as far as 2 km to the east (Świbno, Mikoszewo from the side of the sea) — 52 fish, 3—5 km E of the mouth of the Wisła — 9 fish, Jantar, about 7 km E of the mouth of the Wisła — 32 fish and Stegna, 10—11 km E of the mouth of the Wisła — 30 fish.

Table VII. Adult fish recaptured in the Gulf of Gdańsk according to the distance from the mouth of the Wisla

Place of recapture	Area in km	Fish per km		Number of fish recaptured — Successive year after descent						Total
				1	2	3	4	5	6	
0—11 km from the mouth of the Wisla	190	1.2	No.	29	76	41	8	—	1	155
			%	40.8	47.2	53.9	72.7	—	100.0	48.3
More than 11 km from the mouth of the Wisla	5,290	31.9	No.	42	85	35	3	1	—	166
			%	59.2	52.8	46.1	27.3	100.0	—	51.7
Total	5,480	17.1	No.	71	161	76	11	1	1	321
Zalew Wiślany	838	279.3	No.	—	3	—	—	—	—	3
Unknown places			No.	2	12	—	—	—	—	14
Grand total	6,318	18.7	No.	73	176	76	11	1	1	338

Table VIII. Adult fish recaptured in the Wisla

Section of the Wisla — Place	Upper limit — km of the Wisla	Upper limit — Distance from the sea, in km	Length in km		Number of fish recaptured — Successive year after descent (sea-age)					Total	Length of Wisla riverbed per fish, in km
					1. .0+	2. .1+	3. .2+	4. .3+	7. .6+		
Świbno	939	2	2	No.	9	87	74	16	—	186	0.011
				%	2.8	26.7	22.7	4.9	—	57.1	
Mikoszewo	907	34	32	No.	2	33	35	4	1	75	0.427
				%	0.6	10.1	10.7	1.2	0.3	23.0	
Tczew	771	170	136	No.	1	7	11	3	—	22	6.182
				%	0.3	2.2	3.4	0.9	—	6.7	
Mouth of Brda River	550	391	221	No.	—	6	17	7	—	30	7.367
				%	—	1.8	5.2	2.2	—	9.2	
Mouth of Bug River	324	617	226	No.	—	3	7	1	—	11	20.545
				%	—	0.9	2.2	0.3	—	3.4	
Mouth of Kamienna River											
Mouth of Raba River	135	806	189	No.	—	—	1	1	—	2	94.500
				%	—	—	0.3	0.3	—	0.6	
Mouth of Wisla to mouth of Raba River	941 135	806	806	No.	12	136	145	32	1	326	2.472
				%	3.7	41.7	44.5	9.8	0.3	100.0	

(48.3%) of all the fish were caught. In this region 1 fish fell to 1.2 km², whereas in the whole remaining area (5,290 km²) to 27 times as large an area, i.e., 31.9 km².

In the estuarial portion of the Gulf of Gdańsk the number of fish in successive year-groups (from first to fourth) increased steadily, while out of this region it decreased. More than the half of the younger fish (year-group I and II) were captured at a distance of more than 11 km, whereas the greater half of the older specimens (year-groups III and IV) were caught less than 11 km from the mouth of the Wisła (Table VII).

Three fish were taken in Wiślany Zalew, 2 of them in its south-western Polish portion and one in the Sowiet portion, near the Polish frontier (Fig. 5). Those fish have been counted in the inshore zone. No places of catching have been given for 14 fish from the Gulf of Gdańsk (they have not been included in Table VI and Fig. 5, and in Table VII are given at the end).

d. Upstream migration of adult specimens

A total of 336 grown-up fish tagged (1.62% of the fish released) were recaptured in three rivers, the Wisła, Raba and Ina. The number and time of captures in particular rivers have been discussed before (Table III), now I shall deal with the places of captures.

Fish recaptured in the Wisła. In order to discuss the catches of fish in the Wisła on their way for spawning, the river bed was divided into 6 sections, taking into account the concentration of specimens captured at particular places as well as the hydrological conditions of the river.

The estuarial portion of the Wisła to Świbno and Mikoszewo, hardly 2 km long, was regarded as the first section. It shows a great influence of the sea just as the inshore portion of the gulf is, in turn, influenced by the Wisła waters and they both constitute a transitional zone between the river and the sea. It is hard to establish whether all the fish recaptured here had already started on their journey for spawning (this is particularly true of the 37 specimens caught at the very mouth of the Wisła), but the course of recaptures in this sections is undoubtedly characteristic of the beginning of this migration.

The second section extends over a length of 32 km from Świbno to Tczew (907th km of the Wisła). The influence of the sea upon the water height in the river at its low or medium levels can be observed also for a considerable distance, about 22 km (to the 917th km of the Wisła — Palczewo), in this section.

The upper boundary of the third section with a length of 136 km is marked out by the mouth of the Brda (771.4th km of the Wisła).

The fourth section, 221 km long, stretches between the mouth of the Brda and that of the Bug (550.5th km of the Wisła). This last place is situated more or less in the middle between the mouth of the Raba and the sea and divides this distance into two parts, a lower part 390.5 km long and an upper part 415.8 km in length.

The first three sections form the Lower Wisła, the fourth section covers a part of the lower and a part of the middle course of the river (the boundary between the Lower and Middle Wisła — Korabniki at the 684th km of the river is merely an administrative division, and for this reason has been omitted here).

The fifth section, which is 226 km long, reaches to the mouth of the Ka-

mienna (demarcating the Middle Wisła from the Upper, 324th km). In this place the Wisła leaves the Sandomierz Uplands and its current slackens considerably (from about 84 km per day at an average water level to about 50 km per day).
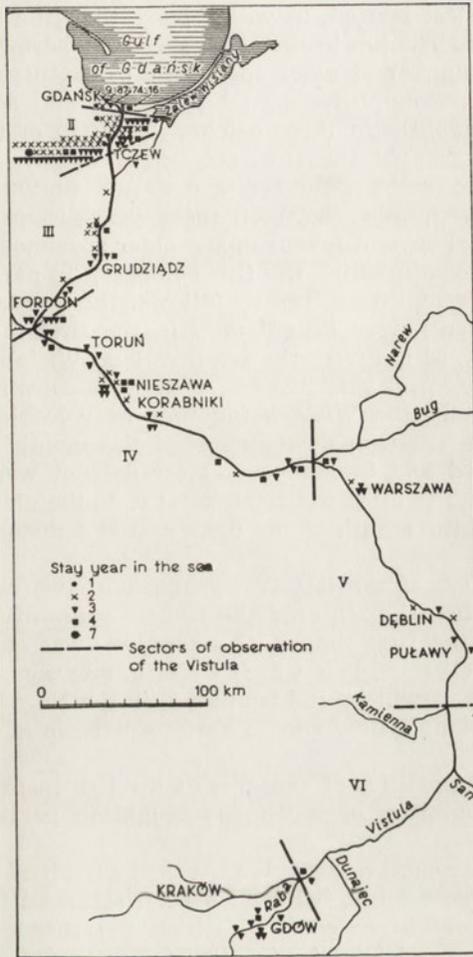
Fig. 6. Recapture sites of adult fish returning for spawning in the Wisła and Raba. In the first section of the Wisła all the fish of a particular year-group are marked with only one symbol, their number being given for each symbol. In the further sections each fish is given a separate symbol

The sixth section, 189 km in length, covers the greater part of the upper course of the Wisła, from the mouth of the Kamienna to that of the Raba (134.7th km of the Wisła).

The fish recaptured in particular sections of the Wisła are analysed in Table VIII and presented in Fig. 6. Both their number and the age composition are characteristic, namely, as the distance from the sea became longer the number of the fish captured decreased markedly (this should also be ascribed, to some extent, to a smaller intensity of fishing in the further sections of the

Wisła), and at the same time the proportion of fish of the younger year-groups diminished in the captures in favour of the older year-groups. The abundance of captures is best characterized by the length of river-bed falling to one fish recaptured; it increased steadily with the distance from the sea (from 11 m in the first and shortest section, in which more than the half of the total of fish were captured, to 94.5 km in the sixth section, where 2 fish were caugth). An increase in the number of older specimens in captures at the cost of the younger ones can be exemplified best by the 2nd and 3rd year-groups, represented most abundantly in these catches. The fish of the 2nd year-group prevailed in the catches in the first section of the Wisła, whereas in the second section the specimens of the 3rd year-group outnumbered them a little, and the difference in number between these year-groups increased steadily in the next sections, always in favour of the older specimens (Table VIII).

The ranges of places in which the fish belonging to particular year-groups were recaptured present themselves as follows: the youngest specimens (the first year after descent) were caught only in the first three sections of the Wisła, at the farthest, 88 km from the sea (Nowe on Wisła). The fish returning for spawning in the second year after descent were captured in five sections, the farthest locality up the Wisła being that near Dęblin at a distance of 547 km from the sea (259 km downstream of the mouth of Raba). The fish returning in the third and fourth years after descent were caught over the whole length of the Wisła up to the 140th km, i.e., to the place situated scarcely 5 km downstream of the mouth of the Raba and at a distance of 801 km from the sea.

Exclusively the fish of the last two year-groups were also recaptured in the Raba. The only fish that entered the river 7 years after release, it is not known whether for the first time (lack of scales), was caught in the second section of the Wisła (Tczew). It is worth while to mention that one of the fish from this section was caught by rod (spinning) in the Nogat, about 30 km from its mouth to the Wiślany Zalew and 15 km downstream of the ramification of the Wisła.

A detailed list of localities of captures of the fish in particular sections of the Wisła and the numbers of specimens caught in particular localities are given in Table IX.

Fish recaptured in the Raba after their return from the sea. Tags from 9 adult fish[8] have been returned from the Raba, and they relate exclusively to females, of which 8 returned from the sea for spawning in the third and 1 in the fourth year after descent (Fig. 6).

The places of capture of 3 fish were at a distance ranging from 19 to 48 km upstream of the places of release, 3 fish were caught in the neighbourhood of the place of release and 3 others from 10 to 31 km downstream of this place.

Only 2 fish were captured in summer, in June and August (acc. to the stage of development of their gonads they were to spawn in the autumn), and 7 during the spawning season, in October and November; 2 of these fish were taken after they had shed eggs in the river. Catching was done by means of

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[8] Two other tagged fish, a male and a female, were caught in the autumn of 1960; these were, however, lost among the sea-trout spawning in masses. Neither were the numbers of their tags read off, and so they have been left out in the discussion of the results. In fact, the total catch in the Raba consisted of 11 specimens.

Table IX. Places of recapture of adult fish in the Wisła

Section of the Wisła	Place			Fish recaptured			
	Name	km of the Wisła	Distance from the sea in km	Distance from the sea in km from to		Number of fish	Total
I	Mouth of the Wisła	941	0			37	
	Świbno, Mikoszewo	939	2	0	2	149	186
II	Drewnica	932	9	7	11	10	
	Ostaszewo	925	16	14	17	5	
	Palczewo	917	24	20	23	7	
	Km of the Wisła	912	29	27	31	4	75
	Tczew	907	34	32	35	45	
	Ostaszewo—Tczew*			16	34	3	
	the River Nogat	15	30	30		1	
III	Gniew	877	64	64		1	
	Nowe on the Wisła	853	88	85	95	6	
	Grudziądz	835	106	102	112	5	22
	Chełmno	806	135	125	135	3	
	Km of the Wisła	790	151	151		1	
	Fordon	775	166	163	167	6	
IV	Solec Kujawski	763	178	176	179	4	
	Toruń	737	204	204		1	
	Złotoryja	728	213	213		2	
	Siarzewo	709	232	231	233	3	
	Nieszawa	704	237	237	239	8	
	Bógdopomóż	690	251	251		1	30
	Włocławek	679	262	268	274	4	
	Ośnica	627	314	314		1	
	Pieczynki Łowickie	597	344	344		1	
	Czerwińsk	578	363	360	366	2	
	Miączynek	567	374	374		3	
V	Nowy Dwór Mazow.	549	392	392		1	
	Suchocin	541	400	397		1	
	Warszawa Cytadela	516	425	412	431	4	11
	Kozienice	412	529	529		1	
	Dęblin	393	548	544	547	2	
	Puławy	372	569	568	570	2	
VI	Dąbrówka Morska	140	801	801		2	2
	Total			0	801	326	326

* The exact place of recapture not given.

electric equipment except for 1 specimen, which was caught by rod in August (spinning; Table X).

E x p e r i m e n t a l   r e a r i n g   o f   s p a w n e d   f e m a l e s   i n   p o n d s. Four of the 5 unspawned females (Table X; Ser. No. 4, 5, 8 and 9) were transported to Mydlniki and spawned there. Their coefficients of condition ranged from 0.95 to 1.07 before spawning and from 0.71 to 0.86 after spawning. Attempts of further rearing of these females in trout ponds failed. One of them,

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Table X. Adult fish recaptured in the

Ser. No.	No. of tag P ...	Form and age	Release				Date	Distance from the mouth of the Raba in km
			Length in cm	Weight in g	Date	Distance from the mouth of the Raba in km		
1	2 503	$(Bt \times St)_2 F_2$	22.0	114	8.12.51	19	8.11.54	38
2	4 573	$St_2 F_3$	19.5	65	29.11.52	22	9.11.55	65—75
3	17 022	$St_3 F_2$	25.2	157	3.12.54	50	28.10.58	50
4	619	$(Bt \times St)_2 F_1$	17.5	57	20.03.56	62	4.11.58	50
5	2 742	$(Bt \times St)_2 F_3$	15.8	39	27.03.56	81	4.11.58	50
6	8 023	$(St \times Bt)_2 F_2$	20.0	77	10.12.57	60	20.06.60	50
7	8 495	$(Bt \times St)_2 F_3$	17.1	60	15.03.58	38	22.08.60	70
8	8 260	$(St \times Bt)_2 F_2$	18.7	62	10.12.57	50	before 22.10.60	ca 50
9	8 824	$St_2 F_3$	17.0	40	15.03.58	50	4.11.60	ca 50

Remarks:

Ser. no. 1 recaptured after spawning, weight of gutted fish; Ser. no. 2 recaptured after spawning, weight estimated Mydlniki on November 5; Ser. no. 6 eggs developed; Ser. no. 7 recaptured by rod (spinning), eggs developed; Ser. no. 8 on November 7.

Table XI. Fish recaptured in the Wisła

Ser. No.	No. of tag P ...	Form and age	Release				Date	km of the Wisła
			Length in cm	Weight in g	Date	Distance from the mouth of the Raba in km		
10	2 851	$(Bt \times St)_2 F_3$	17.9	62	27.03.56	81	23.09.58	775
11	1 088	$St_2 F_2$	16.0	42	20.03.56	50	9.09.59	704
12	4 590	$(Bt \times St)_2 F_3$	18.0	60	16.03.57	57	7.09.59	703
13	18 938	$St_2 F_2$	18.1	50	31.03.55	38	5.08.58	140
14	2 470	$(Bt \times St)_2 F_2$	16.1	43	3.12.51	19	9.11.54	371

Remarks:

Ser. no. 10 spawning on November 7, 1958; Ser. no. 11 spawning on October 26, 1959; Ser. no. 12 spawning on Octo-downstream of the mouth of the Raba.

which we managed to keep alive longest (No. 8), lived out the winter, during which its brown mating colour changed into silver. However, a fortnight after the spring draining of the pond on 13 April 1961, it died too. It appeared that this female had lost 20% of its weight in the period from 27 October 1960 to 13 April 1961 (its weight was 3.0 kg on 27 October 1960, after spawning, and 2.40 kg on 13 April 1961), and then it had not taken any food, though it was offered artificial food and there were large numbers of small crucian in the pond (nearly a half of them — 24 kg — survived till the spring). Other, mostly 11-year-old, spawners of the pond sea-trout, hibernating in the same pond, put on weight on the average by 13.3% during the winter (mean weight of 1 specimen in the autumn — 705.8 gms, in the spring — 800.0 gms, increment in weight — 94.2 gms).

Raba after their return from the sea

			Recapture						
Distance from the place of release in km	Sex	Length in cm	Weight in kg before after spawning		Coefficient of condition before after spawning		Successive year after descent	Scale	
								Number of sea increments	Presence of close rings at the edge
+19	♀	70.0	—	2.40	—	—	3	2	present
ca +48	♀	71.5	—	2.20	—	—	3	3	absent
± 0	♀	81.3	—	4.00	—	0.74	4	3	absent
−12	♀	73.9	4.30	3.45	1.07	0.86	3	3	absent
−31	♀	75.0	4.00	3.00	0.95	0.71	3	2	present
−10	♀	68.0	3.95	—	1.26	—	3	2	present
+32	♀	71.0	3.50— 3.75	—	0.96— 1.05	—	3	2	present
± 0	♀	71.5	3.50	3.00	0.96	0.82	3	—	—
± 0	♀	68.2	3.12	2.42	0.98	0.76	3	—	—

three days after death; Ser. no. 3 recaptured adult, spawned at Gdów; Ser. no. 4 and 5 recaptured adult, spawned at recaptured immature, spawn at Mydlniki on October 26; Ser. no. 9 recaptured immature, spawned at Mydlniki

(Vistula) during their migration for spawning

			Recapture						
Distance from the sea in km	Sex	Length in cm	Weight in kg before after spawning		Coefficient of condition before after spawning		Successive year after descent	Scale	
								Number of sea increments	Presence of close rings at the edge
166	♀	79.0	5.50	4.10	1.12	0.83	3	3	absent
237	♀	76.0	4.80	3.80	1.09	0.87	4	3	absent
238	♀	76.0	5.00	3.90	1.14	0.89	3	2	present
801	♂	86.0	—	—	—	—	4	4	absent
570	♀	73.1	—	3.09	—	0.79	3	2	present

ber 26, 1959; Ser. no. 13 recaptured 5 km downstream of the mouth of the Raba; Ser. no. 14 kelt, recaptured 236 km

The data concerning the release and recapture of females in the Raba are given in Table X, whereas Table XI offers the same data for the 5 fish taken in the Wisła during their upstream journey.

It will be seen from Table XI that 3 still immature females (stage V acc. to Maier's scale) returning for spawning, were caught in the lower Wisła, 166, 237 and 238 km from the sea in September 1958 and 1959. These females (Nos. 10, 11 and 12) were kept for 45—49 days till they attained sexual maturity and then were stripped.

Female No. 10 caught at the 775th km of the Wisła (Fordon) on 23 September 1958 was released into the Raba in March 1956 together with 2 other females (Table X, Ser. Nos 4 and 5), which were captured in the Raba at a distance

of 50 km up from the mouth (Gdów). Had not the spawning migration of female No. 10 been interrupted by its capture in the Wisła, it would probably have spawned in the Raba, as indicated by the results of investigations carried out so far, especially these of HASLER and WISBY (1951), HASLER (1954), and WISBY and HASLER (1954). All the 3 females would have spawned at more or less the same time, because when caught in the Raba (4 November) they were sexually quite ripe and the female recaptured in the Wisła was stripped on the spot on 7 November (it may have attained maturity somewhat earlier). Thus, on the basis of the distance between their recapture sites, equal to 690 km, and the time that elapsed between the recapture dates, 42 days, it can be easily calculated that the mean speed of the upstream migration could not be smaller than 16 km per day. This lies within the limits of 10—20 km per day, given by Lindroth (1952) for salmon travelling up a river to spawn. The speed given concerns remarkably smaller distances, mostly below 100 km. Besides, the author did not find any differences in speed of travelling between fish covering smaller distances and those making longer journeys. JOKIEL (1953) determined the average rate of spawning run for the sea-trout in the lower Wisła (over a distance of 147 km from the mouth) at 20 km per day. On account of the narrowness of the river-bed the current in this part of the Wisła is remarkable.

Another fish was caught in the Wisła near Puławy, 236 km below the mouth of the Raba (5th section of the Wisła — Table IX) on 9 November 1954 (Table XI, Ser. No. 14), which had spawned, as may be presumed, also in the Raba. The uncommon emaciation of this specimen — its coefficient of condition being 0.79[9] is low even in spawned females (Tables X and XI), and the appearance of the head — lack of the kype on the lower jaw — suggest that it was a female returning to the sea after spawning, which is confirmed by the vast erosion of its scale. The day before the capture of this fish in the Wisła another female, which had also spawned already, was caught in the Raba (Table X, Ser. No. 1). The data concerning the recapture of these two females show that the downstream migration was undertaken immediately after spawning.

It is also worth notice that 2 females caught in the Lower Wisła (237 and 238 km from the sea) in September 1959 and artificially spawned there after being kept for about 7 weeks exhibited no growth in the last year before spawning (scales of female No. 11 captured in the fourth year after descent had 3 sea increments and these of female No. 12 caught in the third year only 2 increments). This indicates that the fish had left the sea long before it attained sexual maturity (up to a year) and had stayed in the Lower Wisła ever since. If they had not been captured on 9 and 7 September, they would have made the further journey to the spawning-grounds with their gonads approximating to the state of complete ripeness, covering a distance of more than 600 km a short time before spawning. This fact contradicts

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[9] The coefficient of condition for other specimens caught in the fifth section of the Wisła in the months approximating to the date of recapture of fish No. 14 were as follows: 1.46 and 1.41 for 2 fish captured on 14 and 30 September and 1.13 for a fish caught on 11 December. The lowest condition coefficients were found in 2 fish taken on 7 and 15 June and they were 1.00 and 0.95. All these specimens, as indicated by the recapture dates and condition indices, were on their way to spawning-grounds, and those caught in June had set out on the journey in the preceding year, as is also evidenced by the look of their scales.

the statement that the maturation of gonads of sea-trout from the tributaries of the Upper Wisła demands favourable conditions of mountainous rivers (CHRZAN et al., 1965).

It also must be mentioned that not an adult specimen was recaptured in any other tributaries of the Wisła but in the Raba.

Recapture in the River Ina. The only adult fish captured outside the catchment basin of the Wisła after their stay in the sea was an F_2 sea-trout released in the Raba at the age of 2 years on 20 March 1956. The recapture was made 17 months later (stay in the sea — .1+) on 3 August 1957 in the River Ina, which opens into the Szczeciński Zalew, about 40 km upstream from the mouth, at Stargard (no measurements of the fish were given). This recapture corroborates the phenomenon, recorded in literature, of the dispersal of some anadromous salmonids from their places of origin, which allows for new populations in rivers devoid of them previously. This phenomenon is regarded as one of the adaptations ensuring the preservation of species.

e. Specimens migrating to the sea after a year's stay in the river

Only 5 fish, i.e., 0.5⁰/₀ of the total of 1,062 specimens recaptured after the descent from the Raba (0.02⁰/₀ of the fish released) remained in the river for a year and did not undertake a journey to the sea till the next year after its release. This fact was suggested by their measurements at the time of recapture and confirmed by an analysis of scales. Four of these fish were released at the age of 2 years and one at the age of 3 years. The length of 2-year-olds ranged from 17.7 to 18.5 cm (weights 50—57 gms), the length of the 3-year-old fish was 21.3 cm (weight 90 gms). None of them was therefore too small to start on a journey to the sea at once, as other young fish tagged did, of which many were much smaller in size (the smallest of the fish tagged by me was a 2-year-old Pomeranian sea-trout liberated in the Raba on 17 March 1960; it was 13.6 cm long and weighed 30 gms). All these fish were released in spring (1956—1958). Moreover, it must be mentioned that the descent of a 4-year-old smolt to the sea from the tributaries of the Upper Wisła should be regarded as an exceptional occurrence.

5. SUMMARY

The recaptures of the fish that had descended from the Raba were as follows: 23 descending smolts in the Wisła, 703 fish in the sea, and 336 fish in the rivers during their spawning migrations. Descending smolts were recaptured at distances from 161 to 640 km downstream of the mouth of the Raba. The calculated rate of their downstream journey was at lest 65—95 km per day. 206 smolts and 497 grown-ups were caught in the sea. Nearly all the smolts were recaptured in the littoral zone of the Gulf of Gdańsk, chiefly to the east of the mouth of the Wisła, and in greatest numbers in April. More than twice as many grown-up fish were caught in the Gulf of Gdańsk (338) as out of it (159). In both the regions the fish were recaptured in greatest numbers in the second year after descent, whereas in the rivers the most abundant recaptures of adult fish occurred in the third year. Out of the Gulf of Gdańsk the sites of recaptures were scattered nearly all over the Baltic, reaching beyond its western bounds as far as the Skagerrak. The most fish were caught at a short distance N and NE of the Gulf of Gdańsk.

In the Gulf of Gdańsk 72⁰/₀ of the fish were recovered close to the shore, the rest of them all over its area. As to the distance of the recapture sites from

the mouth of the Wisła, it has been established that 48% of the fish were caught 11 km or less from the mouth.

Fish returning for spawning were taken in three rivers: 326 in the Wisła, 9 in the Raba, and 1 fish in the River Ina, the mouth of which is about 300 km W of the mouth of the Wisła.

Nearly all the fish (1,057) descended from the Raba to the sea in the year of release, only 5 specimens did it a year later.

Unlike the river catches (see Part II), the sea catches comprised twice as many fish released at the age of 2 years as those released at the age of 3 years.

6. STRESZCZENIE

Ryby, które opuściły Rabę, zostały odłowione: 23 spływające smolty w Wiśle, 703 ryby w morzu i 336 w rzekach w czasie wędrówki rozrodczej. Spływające smolty odłowiono w odległości 161—640 km poniżej ujścia Raby. Najmniejsza wyliczona szybkość ich wędrówki wynosiła 65—95 km/dobę. W morzu odłowiono 206 smoltów i 497 wyrośniętych osobników. Prawie wszystkie smolty złowiono w przybrzeżnej strefie Zatoki Gdańskiej, głównie po wschodniej stronie ujścia Wisły, najliczniej w kwietniu. W Zatoce Gdańskiej odłowiono przeszło 2 razy więcej wyrośniętych ryb (338 sztuk) niż poza jej granicami (159 ryb). W obydwu rejonach najwyższe połowy przypadły na drugi rok po spływie, w rzekach najwięcej dorosłych ryb złowiono w trzecim roku. Miejsca odłowu ryb poza Zatoką Gdańską obejmowały niemal cały Bałtyk, przekraczając na zachodzie jego granice, aż po Skagerrak. Najwięcej ryb złowiono w niewielkiej odległości na północ i północny wschód od Zatoki Gdańskiej.

W Zatoce Gdańskiej 72% ryb odłowiono w pobliżu brzegów, resztę na całym jej obszarze. Biorąc pod uwagę odległość miejsc odłowu od ujścia Wisły stwierdzono, że 48% ryb złowiono w odległości do 11 km od ujścia.

Ryby wracające na tarło odłowiono w 3 rzekach: 326 ryb w Wiśle, 9 ryb w Rabie i 1 rybę w rzece Ina (ujście około 300 km W od ujścia Wisły). Obraz łusek ryb, które odbyły tarło w Rabie i tych, które sztucznie wytarto po odłowie w dolnej Wiśle wskazywał, że rozpoczęły one wędrówkę rozrodczą w czasie od kilku miesięcy do roku przed okresem tarła.

Prawie wszystkie ryby (1057 osobników) spłynęły z Raby do morza w roku wypuszczenia, tylko 5 osobników o rok później.

W przeciwieństwie do odłowów w rzekach (patrz Part II) w morzu odłowiono 2 razy więcej ryb wypuszczonych w wieku 2 lat niż wypuszczonych w wieku 3 lat.

S. Skrochowska

MIGRATIONS OF THE SEA-TROUT (*SALMO TRUTTA* L.), BROWN TROUT (*SALMO TRUTTA M. FARIO* L.) AND THEIR CROSSES
PART IV. GENERAL DISCUSSION OF RESULTS

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ABSTRACT

The failure of the downstream migration instinct occurs, above all, in specimens showing a slow rate of growth during their life in fresh water. The attainment of sexual maturity does not impair the action of the downstream migration instinct in female parr, whereas it eliminates this instinct almost completely in males. Sea-migrations of specimens from the River Raba cover the area of the whole Baltic, extending in the west beyond its bounds as far as the Skagerrak. A chemical memory is established in the period directly preceding the downstream migration of smolts.

CONTENTS

1. INTRODUCTION

The results of investigations presented in the three preceding parts of this paper show the importance of choice of the appropriate season (spring) for the stocking of rivers and the influence of the attainment of sexual maturity by male and female parr in fresh water on their ability to undertake a seaward journey (Part I). River migrations of the fish that had not left the rivers till their recapture were discussed in Part II, and Part III dealt with the migrations of the fish that had descended from the Raba to the sea. Now I come to the discussion of the results obtained and their comparison with the data from literature.

2. DISCUSSION AND CONCLUSIONS

The loss of the instinct of seaward migration in the sea-trout and, what follows, the shift of this fish from migratory to stationary ways of living occur mainly in specimens which show a slow rate of growth in the juvenile period.

The connection between the growth rate of young sea-trout and salmon and the age at which they start their migration to the sea was found by MENZIES (1925), NCRDQUIST and ALM (1927) and NALL (1930) long ago. The results obtained by them showed that specimens characterized by a fast growth rate leave the rivers at a younger age than the ones which grow slowly. This dependence has also been confirmed by studies of other authors (FFONTAINE, 1954, EVROPEJCEVA, 1957; VLADYMIRSKAYA, 1958; JONES, 1959; SKROCHOWSKA, 1961, and others). However, the investigations of these authors, based mostly on retrogressive scale reading, could not precisely establish the correlations between the manifestation of the instinct of seaward migration and the rate of growth and the age, closely associated with it, when young fish leave the rivers. It was not before the tagging of whole groups of fish released had been introduced into this study that it become possible to grasp the above-mentioned dependencies. The 16-centimetre length of specimens tagged was assumed as a criterion for their release and, consequently, each group derived from the same spawning consisted of both 2- and 3-year-old fish, the first of which were marked by the same, faster, rate of growth. As a result, it has been found that these very fish were recaptured in the sea twice as numerously as the 3-year-olds. These last specimens, instead, reaching the required size (on the average somewhat larger than in 2-year-old fish, which agrees with the data given by NALL, 1930, for the sea-trout and Jones, 1959, for the salmon) only after spending another year in the ponds, were recaptured in rivers in twice as large numbers. The numerical relation given here and characterizing the share of fish groups which differed in age at the time of their release was obtained repeatedly in the sea and river catches. Three-year-old fish were twice as abundant in the river recaptures as 2-year-olds both in the first and in the second year after release and both in the Raba itself and in all its tributaries together, as well as in one of them, namely, in the Krzyworzeka (in subsequent years and other tributaries of the Raba the recaptures were so scanty that their results could not be regarded as fully or even partly conclusive). A similar but inversed ratio of 2-year-old fish to 3-year-old ones (2 : 1), found in the total of sea catches, repeated with slight deviations in the catch of smolts in the sea and in the catches of grown-up fish both in the open Baltic Sea and in the Gulf of Gdańsk and, finally, in rivers after their stay in the sea. The repeated occurrence of the same ratio indicates that the results of recaptures reflect the actual proportions of fish which had the instinct of migration and those deprived of it in both these environments. In my experiments the loss of faculty for leading a migratory life was, therefore, found, above all, in specimens with a slow rate of growth, their share in the river recaptures being twice as large as that of fast-growing specimens.

Another interesting question is whether and, if so, how many of the sea-trout or salmon living under natural conditions stay in the river permanently.

IVLEV and GALKIN (1958) obtained negative results in so far as the salmon (*Salmo salar* L.) is concerned, that is, they ascertained on the basis of their control catches that not a specimen of the fry and fingerlings stocked before two years had remained in the river Peterupe, 45 km long joining the Gulf of Riga (Baltic Sea). The results presented here might be considered to be contradictory to the well-known fact that the male salmon which mature at the stage of parr remain in rivers (FRITSCH, 1893; BERG, 1948; EVROPEJCEVA,

1957, 1958, 1959; VLADIMIRSKAYA, 1957; FONTAINE, 1960 and others [1]). It should, however, be taken into consideration that the conditions for the sexual maturation of parr may have been unfavourable in the given year or river, which was the case in 1959 during my studies of the sea-trout.

In literature I have found no reports of investigations on the sea-trout similar to those carried out on the salmon by IVLEV and GALKIN (1958). The study discussed, see Part II of this paper, suggests that part of the sea-trout living under natural conditions do not migrate to the sea, which possibility is also mentioned by ŻARNECKI (1936). This fact is indicated by the recaptures of 3-year F_1 sea-trout [2], namely, some of them were caught in the Raba as 4-year and 5-year specimens after staying in the river for one year or two. They were also recaptured in fairly large numbers in the summer of the year of their release, when they were prevented from seaward migration by the water temperature which was too high (EVROPEJCEVA, 1957, 1959). At the same time, the complete lack of F_1 sea-trout whose descent would have taken place later than in the year of their release in the sea catches allows the statement that part of them shows no instinct of seaward migration and spend all their lives in freshwater. This statement is also supported by the results of recaptures of the two groups of F_1 sea-trout, differing in growth rate during the juvenile period of 3 years spent in ponds, for it has been found that in the sea catches the proportion of fast-growing specimens, which reached the smolt stage at the age of 2 years and having an average weigth of 53.6 gms then, was nearly twice as large as that of the slow-growing sea-trout, which at the age of 2 years were at the parr stage (average weight of one specimen — 32.0 g). At the time of release the 3-year-old sea-trout of the first group were also considerably larger than the specimens of the second group. It is characteristic that the specimens released as smolts are completely missing in river catches, though fish at this stage show an increased voracity as compared with parr (HOAR, 1942) and take nearly each bait in the river, without excepting the period of descent (JONES, 1959; this statement refers to the salmon, it may, however, be supposed that the same is true of the sea-trout). The exclusive recaptures of sea-trout, released at the parr stage, in the Raba indicates that they had not gone through smolitification in the river either. As a result, they remained in it, though in the meantime favourable conditions for starting seaward migration had occurred and all the smolts had descended.

The foregoing data support the statement that not only some "pond" sea-trout but, in the same numerical relation, those living under natural conditions, for the most part specimens with a slow rate of growth, display no migration behaviour and are exclusively freshwater fish. Observations made in ponds reveal that such specimens, as a rule, differ in nothing from the brown trout. DAHL (1910, 1913, after NALL, 1930) observed the same in the sea-trout which stayed in the inland lakes of Norway all their lives. That all

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[1] Some authors think that mature males do not descend to the sea at all, others that their descent is postponed till the next year.

[2] This evidence may, true enough, be objected to, as the specimens in question, produced by artificial spawning and kept in ponds till the time of their release, did not live in natural conditions all their lives. However, all the mass experiments consisting in tagging young sea-trout and salmon were and are carried out on such material, not excepting the above, mentioned study of IVLEV and GALKIN (1958).

salmon (except for sexually mature males) but only part of sea-trout descend
to the sea is certainly associated with the occurrence of a non-migratory form
of the latter, *Salmo trutta* L., in rivers and the lack of a corresponding form
of the salmon (*Salmo salar* L.) in them.

The attainment of sexual maturity before the descent from the river does
not inhibit the instinct of seaward migration in the female parr and eliminates
it nearly completely in males, as evidenced by sea recaptures of fish which
at the time of release were sexually ripe.

An abundant group of 3-year fish (3,780 specimens) was distinguished
among the fish tagged in the autumn. Besides mature males (716 specimens
or 18.9%) it also included sexually ripe females (83 specimens or 2.2%). The
sea catches reveal that the number of females recovered (3.61%) exceeds that
of fish with undeveloped gonads (2.85%), whereas the males (0.28%) constitute
one-tenth of the latter and one-thirteenth of the former. Another evidence
of the inhibitory effect of sexual maturity on the faculty for seaward migra-
tion in males is provided by the fact that in contradistinction to the results
obtained in all the other cases[3], only the ripe males released in the spring
(normal period of smoltification and descent from the rivers) were recaptured
in the sea still more rarely than those released in the autumn (some of these
last may have had their gonads resorbed during the winter).

The results presented above allow the statement that only the male parr
were deprived of the instinct of seaward migration owing the their attainment
of sexual maturity, whereas in the females this instinct subsisted.

Investigators started to deal with the problem of occurrence of mature
male parr, chiefly those of the salmon, in rivers (mature sea-trout parr cannot
be distinguished from the brown trout in rivers) as early as 1837 (Shaw, 1840;
after Jones, 1959). No females mature before the descent were met with
(Szmidt, 1950), and for this reason all the papers concerned with the influence
of the maturation processes of the gonads on the later behaviour of young
fish refer to males. The authors differ in opinion in this respect. Some of them,
e.g., Jones (1959), believe that "sexual maturity has nothing directly to do"
(p. 31) with the capability to start seaward migration. Other authors however
claim that the attainment of sexual maturity, as a process biologically an-
tagonistic to smoltification, prevents fish from starting on a donwstream jour-
ney (Evropejceva, 1957, 1958, 1959, 1960; Fontaine, 1960). This antagonism
consists in the fact that physiologically both these processes have the same
source, namely, both at smoltification (Lovern, 1934a, b; Fontaine and Hatey,
1950, 1953; Malikowa, 1957; Fontaine, 1960) and during maturation of the
testes (Swift, 1955; Brown, 1957; Fontaine, 1960; Kukucz, 1960) the stores of
glycogen and fat in the organism undergo a reduction.

The results of our investigations support this last opinion. Mature males did
not migrate to the sea. However, it appeared that sexual maturity did not
inhibit the descent of females. Numerous studies (Swift, 1955; Brown, 1957;
Kukucz, 1960; Zahnd and Clavert, 1960, Byczkowska-Smyk — personal
communication — investigation carried out on sea-trout from Mydlniki) showed
that at oogenesis, just as at spermatogenesis, the stores of glycogen and fat,

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[3] The recaptures of ripe males in the Raba and those of unripe specimens in the
Raba and sea were in the case of springs stockings twice as numerous as the
corresponding recoveries from the autumn stockings.

and so the substances that constitute also the source of energy for the processes of smoltification, are utilized. The difference in behaviour between specimens of either sex cannot therefore be elucidated by the fact that different substances have been used for sexual products. Instead, it can be explained by the difference in time at which the function of the gonads stops, for ZAHND and CLAVERT (1960) found that at the moment when the free eggs have been shed into the body-cavity, even before they have been passed out, the ovaries return to their resting state. This thus occurs in females no later than in the autumn and, consequently their smoltification runs uninhibited. On the other hand, the activity of the testes [4], lasting long into the winter, often till the spring (which I also found to be true of young salmon reared in the Mydlniki ponds), inhibits smoltification in males and, consequently, makes them stay in the river. It should be added that, having attained maturity for the first time, the males of the sea-trout, brown trout, and their crosses rematured in the ponds also in the next years, which proves that they were quite unable to live a migratory life. BERG (1948) shares this opinion when he states that dwarfish males never descend from rivers to the sea and remain dwarfish for ever.

JONES's (1959) opinion denying the inhibitory effect of maturation on the occurrence of the instinct of seaward migration in males can be explained in a similar manner to that applied for the explanation of the difference in behaviour between specimens of either sex. He based his statement on the results of studies in which about 3,000 salmon parr and smolts from 12 British rivers were examined for gonads (ORTEN et al. 1938; JONES and ORTON, 1940). Nearly half the fish examined were females, of which all with non-developed gonads. Out of the males, 75% were mature, and 60% of the male smolts examined were completely spent, which indicates that the males which went through smoltification were those whose gonads had undergone resorption early enough to become inactive by that time. When determining the sex of fish being tagged, in the category of adult males I could count only those individuals which at that time were "running-ripe", but I found no such specimens among the smolts or parr-smolts.

The antagonistic nature of the processes of maturation of the male gonads and those of smoltification also seems to account for the remarkable numerical advantage of females over males among migratory adult salmonids. This situation was very often observed among the spawners in rivers (easiest to grasp), but it was also found in the sea and at the mouths of rivers, among the specimens starting their spawning journey.

Among the sea-trout spawners in the river Ava (joining the Baltic Sea 30 km south of Stockholm) ALM (1950) found 1037 males (36.6%) and 1795 females (63.4%). He stated at the same time that the predomination of females is generally characteristic of the sea-trout from other regions and the same is also true of the Atlantic salmon (ALM, 1934 — in the Baltic) and the Pacific salmon (FOERSTER, 1936). Gustafson writes that at the time of spawning migration from Lake Storsjön to the river Damman (Jämtland Province of Sweden) there were 229 females for each 100 males of the large form of the brown trout (Salmo trutta L.). These values converted to percentages give 30.4% (226 specimens) males and 69.6% (603 specimens) females. LINDROTH

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[4] The gonads of adult (older) males often contained no sperm already towards the end of the spawning season.

(1952) counted no more than 70 males among the 315 salmon (*Salmo salar* L.) caught in the Gulf of Sundsvall (Baltic Sea), which forms hardly 22.2% of the whole catch. BARACZ (1952) found that in the Caucasian rivers opening into the Black Sea females of the sea-trout (*Salmo trutta labrax* Pallas) formed on the average 85% of the specimens caught in a period of many years. LAGUNOV and AZBELEV (1958) obtained varying results for the Atlantic salmon in two rivers of the Kola Peninsula, namely, the females predominated largely, forming 80% of the total, in the river Kolviza, which opens into the White Sea above 67° N, whereas still farther to the north, in the river Tuloma, reaching the Barents Sea above 69° N, both sexes occurred in equal proportions or even the males prevailed. The females outnumbered the males remarkably in the catches from the spawning grounds of the tributaries of the upper Wisła /Vistula/ (CHRZAN, 1947; KOŁDER, 1946, 1947, 1948, 1949, 1953, 1954, 1955, 1956, 1957; JUSZCZYK, 1949; ŻARNECKI, 1959). In 1955, of the total of spawners received from the Dunajec (337 specimens, after KOŁDER, 1956) 92.6% (312 specimens) were females. Among the sea-trout and salmon starting their spawning migration ŻARNECKI (1956, 1963a, 1964a), too, found remarkably more females than males in the estuarial section of the Wisła.

Only some of the above-mentioned authors try to explain this disproportion of the sexes. Assuming that the average sex ratio of descending young fish is as 50:50 [5], Alm (1950) puts forward the supposition that in some cases the predominance of females may be due to a higher mortality rate of males in the sea owing to their being caught in comparatively larger number. However, he makes the qualification that no direct explanation of the sex ratio of the sea-trout in the river Ava can be given as yet. Although LAGUNOV and AZBELEV (1958) cannot elucidate the predominance of females in the river Kolviza, they write that some data allow the supposition that precociously mature males occur in this river oftener than in the Tuloma and therefore they are more liable to death. BARACZ (1952, 1957), who found the predominance of females among the sea-trout returning from the sea and, on the other hand, that the male brown trout prevailed in rivers, put forward a theory on the unity of shoals of sea-trout and brown trout, of which most females migrate to the sea and most of the males stay in the river.

However, a comparison of the sex ratio of the sea-trout spawners received from the tributaries of the upper Wisła with that of young fish at the smolt stage (typical silveriness, body slenderness, shedding of scales and other external signs) from the basin of the same rivers shows that in both cases, i.e., for adult and young specimens, the sex ratio is the same, as 1:3 in favour of females. During 13 years (1941—1948 and 1952—1956) 9,834 sea-trout were caught and spawned in the upper Wisła and its tributaries, 7,502 (76.3%) females and 2,332 (23.7%) males. Of the 649 two- and three-year smolts dissected, 482 (74.3%) were females and 167 (25.7%) males (SKROCHOWSKA, 1961). The fish returned to spawn in the same sex ratio as that in which they had descended to the sea.

At the examination of smolts for gonads (May 1960) 816 parr were also dissected. All the fish examined belonged to the same year groups. They were

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[5] The author does not specify what he has based this assumption on; in all probability, on the sex ratio before the descent. On the contrary, BARADUC and FONTAINE (1955) ascertained that the greater part of the salmon smolts caught for study during their migration to the sea were females.

divided, according to their appearance and size, into smolts, already mentioned, and large (resembling smolts in size) and small parr. Of the 398 large parr, 71.1% (283 specimens) were males, which, for the most part, had still large and incompletely absorbed gonads. In the group of 418 small parr the sex ratio was as 1 : 1 (210 females and 208 males). The fact that the sex ratio in the group of smolts is reversed in relation to that for large parr emphasizes the negative influence of the maturation of the testis upon smoltification.

To sum up the results obtained from literature and those of my own studies I venture the following conclusions:

a) As a rule, females predominate among adult migratory salmonids, the sex ratio of the fish returning to a river for spawning being the same as that of the smolts leaving it. The equal numbers of males and females, e.g., in the river Tuloma, should be ascribed to the climatic conditions, which are unfavourable for the early maturation of salmon at the parr stage in the area situated far to the north. This fact is indicated by the small numbers of precociously mature males appearing in the Tuloma (LAGUNOV and AZBELEV, 1958). The numerical predominance of males observed in some years at spawning places in the rivers in which generally females predominate (River Ava) has been explained by ALM (1950), namely, as a mark characteristic of the years abounding in fry owing to the earlier maturation and return of males than females.

b) The predominance of females over males is caused, on the one hand, by a delay in their sexual maturation (no ripe 2-year females are encountered and only few 3-year-olds) and, on the other hand, by the fact that even the attainment of maturity at the parr stage does not inhibit their instinct of seaward migration. It is so because the processes of maturation of the ovaries and those of smoltification do not occur at the same time.

c) Most of the males which mature in the river before descent lose their capability to live a migratory life, for the gonad activity in male parr, drawn out long into the winter and often even up to the spring, prevents their smoltification.

It is worth while to mention that the theory of unity of sea-trout and brown trout shoals, advanced by BARACZ (1952, 1957), has not found support in the results of our investigations. Very poor catches of brown trout in the sea (1.37% — 23 specimens) and very abundant in the Raba (20.16% — 338 specimens) were to each other as 1 : 14.7. The corresponding ratio for the F_1 generation of the sea-trout is as 1 : 0.5, the sea-trout — brown trout hybrids showing a migration instinct, inherited from one of the parents, to a considerably greater extent than the brown trout. Thus both the biological varieties of the species *Salmo trutta* L. keep distinct, though they are both fit to change their habitats. The results of tagging reveal that the sea-trout remains in the river oftener than the brown trout descends to the sea (the ratio of F_1 sea-trout to brown trout in the river catches was as 1 : 4.26, whereas that of brown trout to sea-trout in the sea catches as 1 : 6.60).

Sea migrations of the sea-trout from the River Raba cover not only the whole area of the Baltic Sea but also reach beyond its bounds, as far to the west as the Skagerrak.

The recoveries of the fish tagged revealed that, having left the Gulf of Gdańsk, the sea-trout, its crosses with the brown trout, and the brown trout (caught in the Gulf of Bothnia, about 1000 km from the mouth of the Wisła),

coming from the Raba, travelled a long way. The migrations differed in direction and their range covered nearly the whole area of the Baltic Sea and even stretched out of it on the west. Through the Danish straits the fish reached the Kattegat and the eastern part of the Skagerrak. These far migrations show that the sea-trout from the tributaries of the upper Wisła adapts well to the living conditions in waters showing great differences in salinity. It travels to the Gulf of Bothnia, the salinity of which ranges from 5.5‰ in the south to 3‰ (in May even 1‰) in the north, there being only slight variation with depth (an increase of hardly 0.5—1.0‰), as well as to all the other parts of the Baltic with the salinity of superficial water layers equal to 6‰ south of the Åland Is., to 7‰ south of Gotland and to 8‰ in the whole southern part of the Baltic Sea. The highest salinity 10‰, occurs in a small area near the western bound of the sea. A relatively poorly marked layer of rapid change in the salinity (at a depth of 30—50 m in the Arkona Basin and 60—80 m in the Bornholm and Gotland Basins) shows differences in salt concentration, which varies with region from 4 to 8‰. The salinity of the Baltic Sea does not, besides, undergo any distinct cyclic seasonal changes. Thus, in the Baltic the fish stay in water with a low and, as a rule, steady salt content. It is not before they cross its bounds that they meet with a sudden and marked rise in the salt concentration, which changes with depth and shows cyclic seasonal variation. In the Belts the salinity of the surface waters ranges between 14 and 15‰ from south to morth in the summer and between 17 and 20‰ in the winter and, in addition, the layer of rapid change in the salinity is well defined in the summer and shows a difference of 10—15‰ in concentration, delimiting the lower, intensely salty (26—32‰), layers of water at a depth of about 20 m. The salinity of the surface layers of water of the Kattegat, also increasing towards the north, varies from 15 to 30‰ in the summer (August) and from 20 to 32‰ in the winter (February), being still higher in the deeper layers [6].

In connection with the above-presented picture of conditions in which the sea-trout lives the problem whether and, if so, what influence the water salinity exerts upon the rate of growth of the fish seems to be of interest. Taking into consideration the results of Murisier's experiment (1918; after CEGIELSKI, 1939), which manifested the huge voracity of brown trout placed in a 35‰ solution of NaCl (this voracity disappeared after the fish were moved back to fresh water) and twice as great length increments as those in control fish in fresh water, one might suppose that the sea-trout staying in the regions with higher salinites show a faster rate of growth. In addition to the salinity, one must naturally take into account also the effect of the water temperature, which is much lower lor a longer time in less salty regions in the north of the Baltic Sea.

A comparison of the sea migrations of sea-trout and salmon descending to the Baltic from different rivers or released directly into the sea shows that all these fish gather in common feeding grounds. The sea-trout from the Wisłoka (ŻARNECKI, 1936) and those from the rivers of West Pomerania (ŻARNECKI et al., 1961, 1962, 1964) and from the Bałda, which opens into the Wiślany Zalew (CHRZAN, 1963), were recaptured at the same places as the sea-trout from the Raba. The migrations of the sea-trout from the tributaries

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[6] The data concerning the salinity of the Baltic Sea have been taken from the Ostsee-Handbuch, Volumes I and IV.

of the lower Wisła released in the region of its mouth covered the whole Baltic (BACKIEL and BARTEL, 1963). The lake trout (*Salmo trutta lacustris* L. releaesed into the Gulf of Gdańsk had a similar range of migrations only that it was not found in the western Baltic regions with higher salinities, which seems to be characteristic. Its growth was also somewhat slower (BACKIEL et al., 1962; BACKIEL and BARTEL, 1963). Salmon descending from the Swedish rivers (ALM, 1928, 1934; MENZIES, 1947) were encountered in the same areas as the sea-trout from the Polish rivers. The same is also true of the salmon derived from Swedish eggs and released into the tributaries of the upper Wisła (ŻARNECKI, 1964b, 1966), but their migrations showed a considerably smaller range as compared with that of the sea-trout.

The results presented in this paper confirm the earlier statements (DONALDSON and ALLEN, 1958; SKROCHOWSKA, 1959, 1964; CZAPLICKI 1962; CHRZAN, 1963; ŻARNECKI 1963b, 1964b and c, 1965, 1966) that the return of anadromous salmonids to a river is conditioned by their stay as young fish in this river in the period preceding the descent to the sea and not, as was believed till not long ago, by their stay in it in the first years of life. Thus, the specific smell of each river becomes fixed in the "memory" of young fish in the period preceding their descent. This smell, as has been demonstrated by WISHY and HASLER (1954), enables the adult specimens leaving the sea to find their way to the given river.

The investigations mentioned above show that tagged fish transferred to another river, often to another drainage area, when they had already reached the smolt age and size, returned or were on their way to the very places where they had been released. This was the case with all the fish recovered in rivers except for a small number of "stray" specimens and, on the other hand, not an adult fish was found in the rivers from which the spawners came and also in which it had spent its juvenile period before being released. This last refers to the cases in which eggs were moved from the place where they had been obtained to the hatcheries situated on another river. In the ponds near these hatcheries specimens making up experimental material were also reared.

The results of the papers quoted are summarized in Table I and they quite agree with the findings of my present study (see Part I and III of this paper).

The papers of authors mentioned do not give the stage at which the fish were released. However, all (or nearly all [7]) the specimens released in autumn were in the parr stage. Their stay in the river preceding the descent fluctuated between 4 and 6 months and towards the end of that period the fish underwent smoltification.

The specimens released in the spring represented unquestionably various stages and spent in the river, to which they returned for spawning, different periods of time. According to DONALDSON and ALLEN (1958) they stayed in pools situated in the upper and lover course of the river (places of return of spawners from the sea) for 2 months. In the experiments carried out by ŻARNECKI (1964b, 1966) the fish remained in the river up to a month. This period may, however, have been shorter (one of the fish was caught in the sea 28 days after its release).

The specimens released by me in the spring remained in the Raba from

[7] At autumn tagging hardly 0.94% of the fish were at parr-smolt stage (see Part III of this paper).

Table I

Author	Species	River from which eggs were derived	River in the water of which fish were reared	River into which tagged fish were released	Time of release	River in which adult fish were recaptured
Donaldson, Allen, 1958	O. kisutch Walb.	Soos Creek	Soos Creek	Issaquah Creek	18—19.3.1952	Issaquah Creek, exactly in both places of release
Skrochowska, 1959	S. trutta L.	Dunajec, Rudawa, tributaries of the upper Wisła	Rudawa, tributary of the upper Wisła	Raba, tributary of the upper Wisła	27.11.—10.12. and 12—31.3. 1951—1959	Raba
Czaplicki, 1962	S. trutta L.	Parsenta, Grabowa, West Pomerania	Drwęca, tributary of the lower Wisła	Drwęca	November 1958, 1959	Drwęca
Chrzan, 1963	S. trutta L.	Słupia, West Pomerania	Słupia ponds at Suchacz on Wiślany Zalew	Bałda flowing into Wiślany Zalew	mid-October 1957, 1958, 1959, a few November	Bałda
Skrochowska, 1964	S. trutta L.	West Pomeranian rivers (eggs from Słupsk)	Prądnik, tributary of the upper Wisła	Raba, tributary of the upper Wisła	7.1, 17.3. 1960	Raba
Żarnecki, 1964b, 1966	S. salar L.	Indalsälven Sweden	Rudawa, tributary of the upper Wisła Łopuszanka, tributary of the Dunajec	Dunajec, tributary of the upper Wisła	4.4.1962 (2-year fish) 20.4.1963 (3-year fish)	Wisła
Żarnecki, 1964c	S. trutta L.	Słupia, West Pomerania	Bętkówka, tributary of the Rudawa	Dunajec. tributary of the upper Wisła	30.11, 1.12. 1961	Wisła

several days to a month, as indicated by the dates of recaptures of descending smolts in the Wisła and the earliest dates of recaptures of smolts in the sea. As I found while tagging, the fish were in different stages at the time of release. Part of them were parr, whose smoltification, as in the fish released in the autumn, occurred in the Raba. According to EVROFEJCEVA (1958) the peak of intensity of this process takes place 15—16 days after the appearance of the first symptoms. Part of the fish were released as parr-smolts and part as typical smolts. These last specimens had gone the whole process of smoltification in a foreign environment (water from the Rudawa) and frequently left the Raba a very short time after their release, as indicated by their recaptures in the sea (the distance of about 860 km) as early as 10 and 13 days later.

To be sure, no fish tagged at the smolt or parr-smolt stage were recaptured in the Raba (at spring taggings such specimens formed no more than 20% of the total of fish released), but there are other evidences that they were able to return there. As to F_1 sea-trout the Wisła recaptures of fish returning for spawning showed no differences between the numbers of fish released in the stage of parr and those released as smolts. These last fish recaptured during their upstream migration formed 46.4% (13 fish out of 28) and 47.1% (8 out of 17) of the total, i.e., sea and river catch of grown-up specimens released in 1956 and 1957, respectively. The same value for the parr liberated together with smolts in 1956 was 55.5% (5 fish out of 9). Since the number of the parr recaptured is very small, 1 specimen constitutes 11.1% and, as a result, the difference is not significant. In 1957 only smolts were released.

It also appeared that 2 F_2 sea-trout, the first released at the smolt stage (31 March 1955) and the second at the parr-smolt stage (16 March 1956), returned to the region of the mouth of the Raba (recaptured 5 km downstream of the mouth). In addition to all the external signs of the smolt, the coefficient of condition of the former was 0.84 at the time of release and that of the latter fish 0.96 (smoltification had not been completed). This coefficient, according to FONTAINE (1954, 1960) fluctuates about 0.8 for salmon smolts and exceeds 1 for parr.

Presented results indicate that the "smell" and perhaps some other properties of water become fixed in the "memory" of young fish directly before they start their downstream migration. Thus the phenomenon called "imprinting" by HASLER and WISBY (1951) and the "chemical impregnation of memory" by ŻARNECKI (1965) does not take a long time nor demands a long stay of the fish in the river. A decisive part is played by the last impression. It is enough for young fish to be present in a given river before its departure at the smolt stage to recognize it and return to it after a several-year stay in the sea (lake). In connection with the foregoing the generally used term "return to the parent river" should rather be replaced by the term "return to the river of starting on downstream migration".

3. SUMMARY

Having considered the results of recaptures of tagged fish in the sea and rivers, the observations made in the course of tagging and concerning the growth rate of specimens released, the state of their gonads, and the stage (smolt, parr) in which they were at the time of release, and on the basis of my own results with the data

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from literature, I arrived at the following conclusions: 1. Instinct of seaward migration declines, above all, in specimens showing a low growth rate. 2. The attainment of sexual maturity before descent to the sea does not inhibit the migration instinct in females but eliminates it in males. 3. Sea migrations of the sea-trout coming from the tributaries of the upper Wisła cover the whole area of the Baltic and reach in the west beyond its bounds as far as the Skagerrak. 4. Chemical memory of the fish develops immediately before descent from the river and not in an earlier period.

4. STRESZCZENIE

Biorąc pod uwagę wyniki odłowu znakowanych ryb w rzekach i w morzu, obserwacje zebrane w czasie znakowania dotyczące tempa wzrostu wypuszczonych osobników, stanu ich gonad, stadium w chwili wypuszczenia (smolt, parr), następnie w oparciu o zestawienie wyników własnych z danymi z literatury wyciągnięto następujące wnioski: 1 Instynkt wędrówki do morza zanika przede wszystkim u osobników wykazujących wolne tempo wzrostu. 2. Osiągnięcie dojrzałości płciowej przed spływem do morza nie hamuje wystąpienia instynktu wędrówki u samic, eliminuje go natomiast u samców. 3. Morskie wędrówki troci z dorzecza górnej Wisły obejmując cały Bałtyk sięgają na zachodzie poza jego granice aż do Skagerraku. 4. Pamięć chemiczna powstaje bezpośrednio przed spływem z rzeki, a nie w okresie wcześniejszym.

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THE PRODUCTION AND STANDING CROP OF PLANKTONIC LARVAE OF *DREISSENA POLYMORPHA* PALL. IN TWO MAZURIAN LAKES

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ABSTRACT

The period of occurrence, abundance and seasonal fluctuations of *Dreissena polymorpha* larvae in the plankton were different in two investigated lakes and two successive years. The mean standing crop of the larvae for the period of occurrence was about 0,02 g/m³. The production was estimated assuming that the life duration of larvae in plankton is 8 days. The mean daily (24 — hourly) P/B coefficient was 0,24 to 0,27 which is very similar to that obtained for crustaceans. Both the standing crop and production of planktonic larvae of *Dreissena polymorpha represent* a very small proportion (few per cent only) of the total zooplankton production in summer period.

CONTENTS

1. INTRODUCTION

The zebra mussel *Dreissena polymorpha* Pall. occurs in large numbers in most Mazurian lakes as well as in the two lakes investigated, Lake Tałtowisko (mesotrophic, holomictic) and Lake Śniardwy (eutrophic, pleomictic [1]). In these lakes the numbers, distribution and production of adult *D. polymorpha* have been the subject of long-term investigations (Stańczykowska 1961, 1963, 1964, 1966); some data on the production of adults in Lake Tałtowisko is also given in Kajak and Rybak (1966) and Kajak (1967).

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[1] Information about the morphometry and trophic typology of these lakes can be found in Olszewski, Paschalski (1952) and Paschalski (1964).

The biology and ecology of the larvae is not well known compared with the adults (LIMANOVA 1964). The early papers were concerned mainly with the anatomy and general biology of larvae (KORSCHELT 1891, WELTNER 1891, KORSCHELT and WELTNER 1892, MEISENHEIMER 1901). More recently, there were investigations on changes in numbers and biomass of the larvae (KAČANOVA 1961, KIRPIČENKO 1964, 1965).

The aim of the present work was an attempt to estimate the production and standing crop of planktonic larvae *D. polymorpha* as veliger stage (according to KIRPIČENKO'S 1965, classification) appearing abundantly in the plankton. At the same time, investigations were being carried out on the other components of the zooplankton, the rotifers and crustaceans (HILLBRICHT-ILKOWSKA, GLIWICZ, SPODNIEWSKA 1966; WARDA 1968; HILLBRICHT-ILKOWSKA, WĘGLEŃSKA 1969). This investigation on the production of larvae *D. polymorpha* completed the general picture of plankton production in the two lakes.

2. METHODS

The production of larvae was estimated by the method developed by WINBERG, PEČEN and SUŠKINA (1965)[2] which is basically identical with that of Greze (1965) and by which the adult production was estimated also (STAŃCZYKOWSKA 1966; KAJAK 1967). According to this method, the production of the investigated population is the product of number of individuals and their daily (24 — hourly) growth rate in weight. The daily growth in weight of an individual is in turn estimated by division of the total growth in weight by the number of days during which this growth took place; for Dreissena larva by the number of days of its planktonic life.

The investigation was carried out in Lake Tałtowisko in 1963 and 1964 and in Lake Śniardwy in 1966. Samples were taken weekly from beginning of May to the end of October by means of a 5-litre volume Bernatowicz sampler. The samples were filtered through a plankton net with a mesh-hole size of about 55 μ. In both lakes the larvae were found mostly in the epilimnion, that is, down to 7 m depth, so that all the data in this work refers to this layer of water.

3. RESULTS

a. The period of occurrence and the numbers of larvae

In both lakes, the numbers of settled adult *D. polymorpha* were very great; in the zone where the mussel occurs, that is the littoral and sublittoral, there were several thousands individuals per 1 m². STAŃCZYKOWSKA (1964) includes both lakes among those Mazurian lakes charakterised by their very great numbers of zebra mussels.

Figure 1 shows that both the numbers and the period of occurrence of the larvae in the plankton of both lakes had a distinct character in successive years.

In Lake Tałtowisko in 1963, the larvae occurred in the plankton from the beginning of June to the end of August, a period of about three months. The mean number for this period was about 77 individuals/litre, the maximum about 400 individuals/litre and there were two periods of peak abun-

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[2] For a detailed description of this method, see HILLBIRCHT-ILKOWSKA and PATALAS (1967) and KAJAK (1967).

dance. During the following year 1964, the period of occurrence of the larvae in Lake Tałtowisko was about twice as short, from the end of June to the beginning of August. The mean number however, for the total period of their occurrence was 92 individuals/litre, higher than in the previous year but the maximum numbers were lower, about 250 individuals/litre. There was
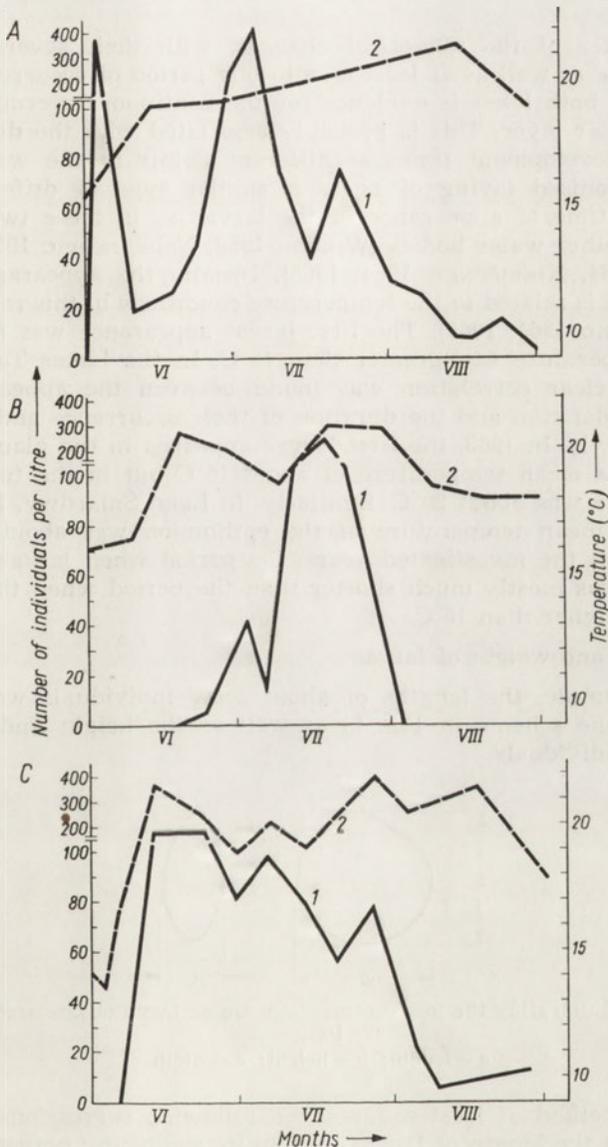

Fig. 1. Changes in the numbers of larvae of *Dreissena polymorpha* Pall. in the plankton of the lakes investigated. A. Lake Tałtowisko 1963, B. Lake Tałtowisko 1964, C. Lake Śniardwy 1966.

1 — number of larvae; 2 — mean water temperature of the epilimnion

only one period of peak abundance during the second half of July. As early
as August, no larvae were found. In Lake Śniardwy in 1966, the larvae occur-
red in the plankton from the beginning of June to the end of August. Maxi-
mal numbers were about 100 individuals/litre, the mean number about 70
individuals/litre. The numbers of larvae were rather high in both June and
July and showed rather little changes. During the rest of the period numbers
were very low.

The character of the numerical changes, with their several periods of
peak abundance as well as at least month-long period of occurrence of larvae
in plankton of both lakes is evidence for the continuous recruitment of lar-
vae in this water layer. This is probably associated with the different dura-
tions of egg development times at different points in the water body, or
with unsynchronised laying of eggs. A similar type of difference in the
character and time of appearance of the larvae as in these two lakes were
found also in other water bodies (WIKTOR 1958, NEDELJKOVIC 1959, KAČALOVA
and SLOKA 1964, KIRPIČENKO 1964, 1965). Usually the appearance of larvae
in the plankton is related to the temperature conditions in this region (BREITIG
1961, KIRPIČENKO 1964, 1965). The first larval appearance was found usually
when the temperature was greater than 16°C. In the Lakes Tałtowisko and
Śniardwy, no clear correlation was found between the appearance of the
larvae in the plankton and the duration of their occurrence and temperature
conditions (Fig. 1). In 1963, the first larvae appeared in the plankton of Lake
Tałtowisko at a mean temperature of about 16°C but in the following year,
the temperature was about 20°C. Similarly, in Lake Śniardwy, larvae appea-
red when the mean temperature of the epilimnion was about 21°C. Apart
from this, in all the investigated years, the period when larvae appeared in
the plankton was mostly much shorter than the period when the mean tem-
perature was higher than 16°C.

b. The size and weight of larvae

For each sample, the lengths of about forty individuals were measured
(according to the scheme in Fig. 2) as well as the height and width of at
least twenty individuals.
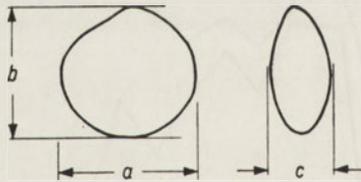
Fig. 2. Diagram illustrating the measurements made on larva of *Dreissena polymorpha*
Pall.

a — length; b — height; c — width

Using the method of least squares, the following regressions were deter-
mined: between the length of larvae (a) and its height (b); between the larval
length (a) and width (c). All measurements were in microns. These relation-
ships are expressed in the following formulae (Fig. 3):

$$b = 0,58 \, a \, 1.08 \quad \text{(mean standard deviation} \sim 13\%)$$
$$c = 1,12 \, a \, 0.74 \quad \text{(mean standard deviation} \sim 8\%)$$

From these measurements of length, hight and width, the larval volume was calculated for each size (length) class (Fig. 4). Different methods of calculating volume were employed as follows:
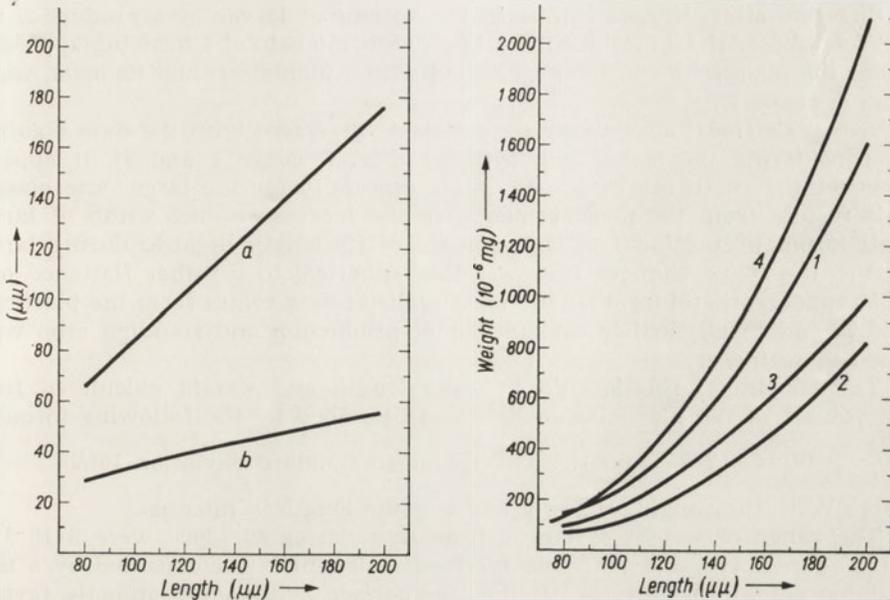
Fig. 3. Regressions between the various body measurements of larvae of *Dreissena polymorpha* Pall.

a — height $(0.58 \cdot a^{1.08})$; b — width $(1.12 \cdot a^{0.74})$

Fig. 4. Regression between length and volume (weight) estimated by different methods

1 — by comparison with a cylinder; 2 — by comparison with a spheroid; 3 — from measured volume plasticine models; 4 — from the data of Kosova, 1961

1. By approximating the larval shape to some geometric solid of similar length, height and width.

    a. A cylinder with a base equal to the surface area of the plain projection of larval shell and with a height equal to half the measured width of the larva (Fig. 4, curve 1).

    b. A solid consisting of two parts of a spheroid which simulates better the shape of the larva than a cylinder (Fig. 4, curve 2). The volume of this solid was calculated according to the following equation:

$$V = 2\pi \, ab \left\{ \frac{2 r^3}{3 b^2} \left[1 - \left(\sqrt{1 - \frac{b^2}{r^2}} \right)^3 \right] - r + c \right\}$$

where V = volume in μ^3, a = half of the larval length in μ, b = half the larval height in μ, c = half the larval width in μ, $r = \frac{1}{2} \cdot \frac{b^2 + c^2}{c}$.

2. The measurement of the volume of a plasticine models (Fig. 4, curve 3). The volume of each model was measured by the volume of water it displaced. This method was used by Sebestyén (1958) for determining the volume of

planktonic organisms. About tweny plasticine models of different length, height and width were made in a scale 1 : 2000, trying to produce the most realistic shape corresponding to different size classes.

3. The application of the data by Kosova (1961) on the weights of larvae of different sizes. Kosova estimated the volume of larvae as a product of the surface area of the larval outline (drawn with the help of a drawing apparatus under the microscop and later measured with a planimetr) and its mean width (Fig. 4, curve 4).

Kosova's (1961) data shows the greatest agreement with the data obtained by considering the larva as a cylinder (Fig. 4, curve 1 and 4). It appears however that both results are too high, especially for the larger size classes. This results from the measurements, as the increase of the width of larval shell is not proportional to the increase of its length because during larval growth the shape changes from a rather spherical to a rather flattened one.

It appears, therefore, that the most realistic data comes from the plasticine models and so all further calculations of production and standing crop were based upon these.

The functional relationship between length and weight calculated from the volume of the plasticine models was described by the following formula:

$$W = 58.207 - 2.636 \cdot l + 0.037 \cdot l^2 \text{ (mean standard deviation 16%)}$$

where W = the weight, 10^{-6} mg and l = the length in microns.

The range of weight of larvae from size classes 80—200μ were $9 \cdot 10^{-5}$ to $1 \cdot 10^{-3}$ gm. A two and half fold increase in lenght is accompanied by a ten-fold increase in weight. A similar comparison with adult animals reveals that a two and half increase in length is accompanied by a five-fold in weight (Stańczykowska 1965).

Knowing the mean length of larvae from each sample, their mean individual weight was estimated from the above formula. Knowing also the numbers of larvae present, then the larval standing crop for each successive sample could be assessed as a product of numbers and mean individual weight. The arithmetic mean of the standing crop values from particular samples was taken to the mean larval standing crop for the period of their occurrence in the plankton.

In Lake Tałtowisko, the mean larval standing crop was 0.0199 mg/l, that is about 0.02 g/m³ in 1963 and in the following year was 0.0193 mg/l or 0.02 mg/m³. The mean larval standing crop for Lake Śniardwy was also very similar, 0.020 g/m³.

c. The growth rate in weight, the population production and daily P/B coefficient of larvae

The growth rate i.e. the values of the daily weight increments of larvae are obtained by dividing the total larval increase in weight during their planktonic life by the number of days they spent in plankton. According to previous workers (Thiel, 1928, Wesenberg-Lund 1939, Žadin 1952), the larvae live in the plankton for about eight days. The total increase in larval weight during their planktonic life is estimated from the difference in the mean weight of the smallest and largest size classes of larvae. The daily weight increments of a larva during its planktonic life estimated in this way, comes to 60—70·10⁻⁶ mg per day (Table 1). These values differed very little

between years or between lakes. However, it was greater in Lake Tałtowisko for the year 1964 than 1963 and this difference originated from differences in the size structure of larval populations.

The total production of larvae population during their occurrence in plankton can be computed from above data on daily weight increments and their number (Table II). The calculation was made separately for particular time intervals between successive samples and the total production for the whole period of occurrence of larvae was obtained by summing the productions for these particular periods.

Table I. Daily (24-hourly) weight increments of larvae of *Dreissena polymorpha* Pall. during their eight day planktonic life

| Lake | Year | Total weight increase for the larval period | | | Daily weight increments |
		length (μ)	weight (mg 10⁻⁶)	weight difference (mg 10⁻⁶)	(mg 10⁻⁶)
Tałtowisko	1963	85—170	110—685	570	71.9
Tałtowisko	1964	90—160	125—590	465	58.1
Śniardwy	1966	90—170	125—685	560	70.0

Table II. Standing crop, production and indicators of production for planktonic larvae of *Dreissena polymorpha* Pall.

| Lake | Year | Number of days larvae occurred in plankton | For the period of occurrence: | | | Mean daily P/B coefficient (for 24 hours) | $\tilde{T}_B$** turn-over (in days) |
			total production (g/m³)	mean standing-crop (g/m³)	P/B*		
Tałtowisko	1963	86	0.470	0.0199	23.6	0.27	3.7
Tałtowisko	1964	33	0.184	0.0193	9.5	0.29	3.4
Śniardwy	1966	78	0.367	0.020	17.5	0.23	4.3

* P/B coefficient = the ratio of production to standing crop.
** turn-over time of biomass — estimated on the basis of the mean daily P/B coefficient.

In 1963, the total production in Lake Tałtowisko from the end of June to the end of September was about twice as large as in the following year (Table II). The P/B coefficient, that is the ratio of production to standing crop for this period, was about 24 for 1963 and 10 for 1964. This result was associated with the much shorter (about twice) period of larval occurrence in plankton in 1964 compared with 1963. In Lake Śniardwy the P/B coefficient was about 18 (Table II). On the other hand, the mean daily value of the P/B coefficient was very similar in both years and for both lakes and was 0,23—0.29; moreover the biomass turnover time ($\tilde{T}_B$) was 3—4 days (Table II [3]).

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[3] $\tilde{T}_B$ represents the turn-over time for biomass. This is the period of time in which the amount of produced matter equals the mean biomass (standing crop) for period T. Detailed explanations of the term may be found in HILLBRICHT-ILKOWSKA and PATALAS (1967).

Independently from the method of computing daily larval weight incre-
ments and larval production described above (that is based upon an eight-day
duration of planktonic life) an attempt was made to determine the actual
life duration of planktonic larvae in Lake Tałtowisko. Analysis of the apparent
changes in the distribution of larval sizes in each weekly sample revealed
a regular increase in the mean larval size during a certain period. This period
of time may be taken to represent the planktonic period of life of one "gene-
ration" or "cohort" of larvae. In Lake Tałtowisko this period was 10—12 days,
that is not much longer than that given in the literature. For each period
of planktonic life distinguised in such a way, the larval growth rate and
production was estimated. The results did not differ greatly, about 10⁰/₀,
from the previous ones which were based upon the assumption that the dura-
tion of larval planktonic life is constant and lasted eight days.

4. CONCLUSIONS

The production rate of larval *D.polymorpha* is several times greater than
that of adult animals. The daily P/B coefficient for planktonic larvae is about
150 times that of the adults. The daily P/B coefficient for larvae is approxi-
mately equal to the annual P/B coefficient for adults, assuming that the
adult mussels grow for 150 days during the year (Stańczykowska 1966).
The daily P/B coefficient for larval *D. polymorpha* is 0.2—0.3 which is
very close to the values for planktonic crustaceans. Suskina (1966) gives the
values for the daily P/B coefficient for Cladocera (mean value for eutrophic
lake) about 0.2; for Diaptomidae 0.16; for predatory Cyclopidae 0.12. Hillbricht-
Ilkowska, Węgleńska (un-published results) and Warda (1969) also obtained
a P/B coefficient of about 0.2 for Cladocera and Copepoda (summer period)
in the lakes Tałtowisko and Śniardwy.
In spite of this similarity in the daily P/B coefficient which reveals that
the rate of production of larval *D. polymorpha* is similar to that of planktonic
crustaceans, the contribution of larval production to the total zooplankton
production during the summer period is very small, because of their short
period of occurrence and their small size. It represented only 4⁰/₀ of the
zooplankton production in Lake Tałtowisko in 1963 (rotifers and crustaceans
together, Hillbricht-Ilkowska, Węgleńska un-published results) and in
Lake Śniardwy was only 2⁰/₀. The contribution of larval standing crop to that
of the whole zooplankton in summer period is also very small, only a few
per cent.

5. SUMMARY

Investigations were carried out in two lakes characterised by the great abundance
of adult *D. polymorpha,* namely. Lake Tałtowisko (mesotrophic and holomictic) and
Lake Śniardwy (eutrophic and pleomictic). The larvae were almost entirely confined
to the epilimnion (0—7 m depth).
The time and duration of occurrence of the larvae in plankton of the two lakes
and the two years of the investigation varied from one to three months during June,
July and August (Fig. 1). There was no correlation between the appearance of
larvae and changes in the temperature of the surface layers of the lakes (Fig. 1).

Changes in the numbers of larvae showed one or several peaks. The maximal numbers were 300—400 individuals/litre (Fig. 1) and the average fluctuated from 70—90 individuals/litre.

From actual measurements of larvae (according to the scheme given in Fig. 2), regressions were obtained between length (a) and height (b) which was $b = 0.58 \, a^{1.08}$ and between length (a) and width (c) which was $c = 1.12 \, a^{0.74}$ (Fig. 3) where a, b, c were in microns.

The individual weight of larvae was computed by several methods (Fig. 4). It is considered that the best estimate of larval weight was obtained from the method based upon plasticine models. The estimated functional depedence between larval weight (W) and length (l) (Fig. 4, curve 3) is:

$$W = 58.207 - 2.636 \cdot l + 0.037 \cdot l^2$$

where W = the weight, 10^{-6} mg and l = the length in microns.

The growth rate of larvae was estimated on the basis of the assumption that the duration of the larval planktonic life lasted eight days (Table 1). The total production for the whole period of occurrence of larvae in plankton was different in both lakes and in both investigated years; on the other hand, the mean standing crop for this period was very similar (Table II).

The indicators of production rates, namely, the mean daily P/B coefficient and the mean turn-over time, $\tilde{T}_B$; are similar and were 0.23—0.29 and 3—4 days, respectively (Table II). The relative production rate of the planktonic larvae is similar to that of crustaceans. However, their contribution to the total zooplankton production and standing crop in the summer period, is not great being only a few per cent.

6. STRESZCZENIE

Badanie przeprowadzono w dwóch jeziorach charakteryzujących się obfitym występowaniem osobników dorosłych *D. polymorpha*: Tałtowisko (mezotroficzne, holomiktyczne) i Śniardwy (eutroficzne, pleomiktyczne). Występowanie larw stwierdzono prawie wyłącznie w epilimnionie (0—7 m).

Okres i długotrwałość występowania larw w badanych jeziorach i latach jest różny i wynosi od miesiąca do trzech — w okresie od czerwca do końca sierpnia (Fig. 1). Nie stwierdzono wyraźnej korelacji występowania larw ze zmianami temperatury powierzchniowych warstw jeziora (Fig. 1).

Dynamika liczebności larw miała charakter jedno- lub wieloszczetowy. Maksima liczebności dochodziły do 300—400 osobników/litr (Fig. 1), przeciętna liczebność wahała się około 70—90 osobników/litr.

Na podstawie wykonanych pomiarów larw (według schematu na Fig. 2) określono regresję pomiędzy długością (a) i wysokością (b), gdzie $b = 0.58 \, a^{1.08}$, oraz pomiędzy długością i szerokością (c), gdzie $c = 1.12 \, a^{0.74}$ (Fig. 3); a, b i c w mikronach.

Oceniono ciężar larw paroma metodami (Fig. 4). Przyjęto że ciężary larw oceniane na podstawie modeli plastelinowych są stosunkowo najbardziej wiarygodne. Oceniono zależność funkcjonalną pomiędzy ciężarem larwy (W) a jej długością (l) (Fig. 4 — krzywa nr 3):

$$W = 58.207 - 2.636 \cdot l + 0.037 \cdot l^2$$

gdzie W = ciężar 10^{-6} mg, l = długość w mikronach.

Dobowy przyrost ciężaru oceniono opierając się na założeniu, że długość życia larwy w planktonie trwa około 8 dni (Tab. I). Całkowita produkcja larw w okresie ich występowania w planktonie ma wartości różne w obu jeziorach i w obu latach badań, natomiast średnia biomasa w tym okresie jest podobna (Tab. II).

Wskaźniki tempa produkcji, tj. średni dobowy współczynnik P/B oraz przeciętny okres rotacji biomasy $\tilde{T}_B$, są zbliżone i wynoszą odpowiednio: 0,23—0,29, 3—4 dni (Tab. II). Względne tempo produkcji larw planktonowych jest podobne do analogicznego u skorupiaków. Jednak udział ich w całkowitej produkcji i biomasie zooplanktonu jest niewielki, nie przekraczający kilku procent.

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PREPARATION OF WATER SAMPLES FOR CARBOHYDRATE DETERMINATION

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ABSTRACT

The application of cadmium hydroxide to clarify water samples before the quantitative determination of dissolved carbohydrates was proposed. The recovery of added amounts of sugars as well as the removal of polysaccharides and coloured substances, both were complete. Samples analyzed by paper chromatography for sugars required further treatment with ion exchange resins or activated charcoal.

CONTENTS

1. INTRODUCTION

Natural shallow freshwater reservoirs are characterized by astatism of oxygen-organic matter regime due to the microbiol decay of plant remnants in water, particularly if situated under deciduous trees or if overgrown by plants (KLEKOWSKI 1966, REIMER 1954, SOLSKI 1962). Mass appearance of algae also produces frequently a subsequent increase in dissolved organic matter, followed by the development of microorganisms (OVERBECK, BABENZIEN 1964). An important part of this fresh organic material of plant origin dissolved in water consists presumably of carbohydrates, as it was observed in several cases (BURSA 1968, GAVRILESCU 1964, HAILOW 1968), as well as of tannins (DOWGIAŁŁO, FISCHER 1960).

In a series of experiments, where the plant material was exposed to decomposition in water tanks, the dissolved carbohydrates were supposed to be responsible for extremely high exygen demand and consequently these carbohydrates were analysed (DOWGIAŁŁO 1966). In the course of these experiments, a modified method of precipitation of cadmium hydroxide, directly in the solution to be tested, was used. The precipitation of an insoluble hydroxide results in removing most of substances interfering with sugar determination and, moreover, it allows to distinguish between low- and high-molecular compounds (SKOPINCEV 1957). Although the applied method differed slightly from the original one (FUJITA and IWATAKE 1931), it required further proof of its reliability for water analysis. The modification consists in using barium hydroxide instead of sodium hydroxide and in about ten times lower ratio of the reagent to the examined solution.

In the present paper a report is given on the value of cadmium hydroxide in the analysis of water soluble carbohydrates. In addition to the tests on recovery of added amounts of sugars, the removal from the solution of some organic compounds was examined, these compounds being considered as representatives of those occurring in polluted and unpolluted natural waters and interfering in sugar analysis.

2. MATERIAL AND METHODS

Water samples were taken either from a natural peat-pool or from experimental tanks with water and decaying plant remnants. The plant material used was: alder leaves (*Alnus glutinosa* Gaertn.) and reed plants (*Phragmites communis* Trin.). Cold and warm water extracts from plant material were also examined (Dowgiałło 1966). Standard solutions of xylose, glucose and rafinose were prepared in saturated aqueous benzoic acid and dilutions were made daily.

The solutions of $CdSO_4$ (ca 0.2 N) and of $Ba(OH)_2$ (ca 0.25 N) were used in equimolar ratio for clarifying. These solutions were added to a measured amount of sugar solution or a water sample (up to 80 ml) in a graduated cylinder, made up to 100 ml with distilled water, shaken occasionally within 15 minutes and filtered through hard filter paper. The clear filtrate was used for analysis. The maximum sedimentation speed was in accordance with the equivalent point (pH 6—7 of the filtrate). It was important to avoid the excess of $Ba(OH)_2$ because of the risk of $BaSO_4$ precipitation in anthrone reagent and erroneously high photometer readings. An excess of a drop of $CdSO_4$ or Na_2SO_4 solution, added after the settling of bulk portion of precipitate, warrants the removal of barium ions.

Total sugars were determined with anthrone, with 5 min. heating, after Blažka (1966). Hexoses were estimated using the same procedure with extention of heating time to 12 min. for the sake of selectivity. Pentoses and uronic acids were determined by means of the orcinol reagent (Brown 1946) and the aniline reagent (Tracey 1950), the latter being used for higher concentrations of xylose. The total reducing power of the solution towards cupric salt in the presence of methylene blue was established according to Lane and Eynon (1923 modified by Soczyński 1955). Hydrolysis of polisaccharides in aqueous extracts was carried out by acidifying with H_2SO_4 up to 1 N, boiling for 30 min., and neutralizing with barium carbonate at 80—90°C. The chemical oxygen demand was estimated by means of bichromate oxidation and water colour was expressed in platinum units (Standard Methods 1955). Gallic, salicylic and sulphosalicylic acids were determined colorimetrically as iron compounds (Snell, Snell 1953).

3. RESULTS

Tables I—III show the extent of losses of xylose, glucose and rafinose, respectively, on treatment of the aquaeous solutions with increasing amounts of cadmium hydroxide, where: c — initial concentration of sugar; dc and dc % — absolute and per cent value of the differences between the concentration after treatment and the initial one, per 1 ml $CdSO_4$/100 ml; $\overline{dc}$ % — mean difference for the whole range of sugar concentrations; $\overline{dc}$ % tot. — mean difference for the whole range of sugar concentrations for the total added

Table I. Adsorption of xylose on cadmium hydroxide (full data)*

C μg/ml	2 ml 0.1 M CdSO₄/100 ml		4 ml 0.1 M CdSO₄/100 ml	
	dc	$\overline{dc}\%$	dc	$\overline{\overline{dc}}\%$
10	+0.4	+4.0	+0.1	+1.0
20	−0.1	−0.5	+0.5	+2.5
40	+0.4	+1.0	—	—
60	+1.9	+3.2	—	—
80	+1.4	+1.7	−0.6	−0.7
100	−1.2	−1.2	−0.7	−0.7
200	−9.6	−4.8	+3.5	+1.7
Statistical evaluation				
$\overline{dc}\%$ / st		+0.5 / —		+0.8 / —
$\overline{dc}\%$ tot. / st		+1.0 / —		+3.4 / —

* Abbreviations in the text.

Table II. Adsorption of glucose on cadmium hydroxide (summarized data)*

ml of 0.1 M CdSO₄ per 100 ml / statistical evaluation	2	4	6	8
$\overline{dc}\%$ / st	−0.6 / —	−1.7 / —	−1.0 / —	−1.0 / —
$\overline{dc}\%$ tot. / st	−1.2 / —	−6.6 / —	−5.8 / —	−8.0 / —

* Abbreviations in the text.
c = 10, 20, 80, 100 and 200 μg/ml.

Table III. Adsorption of rafinose on cadmium hydroxide (summarized data)*

ml of 0.1 M CdSO₄ per 100 ml / statistical evaluation	2	4	6	8
$\overline{dc}\%$ / st	+1.3 / —	−2.1 / +	−2.0 / −	−3.0 / +
$\overline{dc}\%$ tot. / st	+2.7 / —	−8.3 / +	−11.9 / +	−24,5 / +

* Abbreviations in the text.
c = 10, 20, 40, 60, 80, 100, 200, 400, 600 and 800 μg/ml for 2 ml CdSO₄
c = 10, 20, 80, 100 and 200 μg/ml for 4, 6 and 8 ml CdSO₄.

6*

amount of $CdSO_4$ solution; st — statistical evaluation of the results at 95% confidence limit (Student's test): + — mean per cent difference significant, — mean per cent difference insignificant (BAILEY 1959).

The analysis of variance has been performed indicating that the results belong to the same sample over the whole range of concentrations of particular sugar. In addition to the results given in Table II, more concentrated glucose solutions (1—12 mg/ml) were treated with 4 ml $CdSO_4$ per 100 ml. The loss proved to be significant and averaged 7% for the total amount of $CdSO_4$ solution. Full data are exemplified in Table I. In Tables II and III only the summarized data, that is mean differences and their statistical evaluation are given. The data in Tables I—III indicate, that only the loss of rafinose is significant.

Table IV. Adsorption on cadmium hydroxide of organic compounds interfering in sugar determination in water

Material No.	Aqueous solution	Kind of analysis (units)	ml 0.1 M $CdSO_4$ per 100 ml	Initial value	Value after $Cd(OH)_2$ treatment	Removal in % of initial value
1	Water from experimental tank with fallen alder leaves (2 g//l), 3 months after filling (Carbohydrate content about 1 mg/l)	Chemical oxygen demand (mg O_2/l)	2 4 6	145 145 145	90 67 67	38 54 54
	The same water	water colour (mg Pt/l)	1 2 4 6	330 330 330 330	70 50 30 30	79 85 91 91
2	Water from peat pool (soluble humic acids)	water colour (mg Pt/l)	4 6	1 500 1 500	15 15	99 99
3	Exctract at room temperature of dry alder leaves (10 g/l), collected directly before fall. (tannin content about 0.3 g/l)	Reducing power towards cupric salt (mg glucose/l)	2 4 6 8	1 050 1 050 1 050 1 050	640 600 460 460	61 57 44 44
4	Gallic acid	gallic acid (mg/l)	2	200	0	100
	The same solution neutralized with $NaHCO_3$	gallic acid (mg/l)	2	200	1.5	98.5
5	Sulphosalicylic acid neutralized with NaOH	sulphosalic. acid (mg/l)	2 4	220 220	180 140	20 35
6	Salicylic acid neutralized with NaOH	salicylic acid (mg/l)	2 4	140 140	140 133	0 5

The effectiveness of remowal of some organic compounds from equeous solutions by means of cadmium hydroxide is presented in Tables IV and V.

Some of these compounds, e.g. phenol derivatives of plant origin (BLAŽKA 1966), not only increase the reducing power of the solution (like leaf extract — material 3, Tab. V), but also give too low results of anthrone test, as it has been proved in a separate test with gallic acid. The colour of water interferes by increasing the photometer readings.

Althought the discussed procedure of clarifying enables to remove from the solution almost quantitatively the coloured and high-molecular compounds as well as some low-molecular phenol derivatives, yet a large proportion of

Table V. Determination of sugars in solutions clarified with cadmium hydroxide

Material No.	Aqueous solution	Sugar determination	ml 0.1 M CdSO$_4$ per 100 ml	Sugar content in µg/ml		Sugar found in % of actual value
				actual	found	
1	Water from experimental tank with fallen alder leaves (2g/l), 3 months after filling (Colour 330 mg Pt/l)	Hexoses (as glucose)	0	1	2	—
	The same water with 40 or 50 µg glucose /ml added	Hexoses (as glucose)	0	41	42	102
			4	51	51	100
2	Water from peat pool (colour 1500 mg Pt/l)	Hexoses (as glucose)	0	0	9	—
			4	0	0	—
	The same water with 40 µg glucose/ml added	Hexoses (as glucose)	4	40	41	102
			6	40	40	100
3	Extract at room temperature of dry alder leaves (10/l) collected directly before fall.	Total sugars (as glucose)	0	840	920	112
			4	840	820	97
			6	840	810	95
	The same extract after hydrolysis	Total sugars (as glucose)	4	840	840	100
7	Extract at 100°C of dry reed plants (5 g/l)	Total sugars (as glucose)	0	305	317	104
			4	305	253	83
			8	305	210	69
			12	305	197	65
	The same extract after hydrolysis	Total sugars (as glucose)	4	305	305	100
8	Glucuronic acid	Glucuronic acid	4	10	10	100
9	Soluble potato starch (commercial)	Hexoses (as glucose)	4	10	0.7	traces

organic substances expressed in terms of chemical oxygen demand remains, in spite of the increase of the added amount of cadmium sulphate and barium hydroxide. Also sulphosalicylic acid hardly yields to clarifying treatment, and salicylic acid is practically not removed at all.

Samples of water from experimental tanks and natural pools, concentrated after $Cd(OH)_2$ treatment to less than 1% of the initial volume under reduced pressure, showed again brown colour and a considerable salt concentration, thus disabling application of paper chromatography without further purification.

4. DISCUSSION

The process of clarifying by flocculation, e.g. with the use of aluminium or ferrum compounds, is widely used in water technology and it is generally assumed that coagulation of colloids prevails over adsorption (Skofincev 1957, Souček, Šindelař 1967). The latter phenomenon however cannot be excluded, for example when mineral compounds precipitate in water in a fine crystalline form (Alekin, Moričeva 1958).

The procedure of precipitation of cadmium hydroxide together with barium sulphate offers the advantages of both processes and moreover leaves no additional salts in the solution tested. Samples clarified by this method may be further analyzed for sugars, and, after concentration followed by desalting with ion exchangers, submitted to paper chromatography. Samples after sulphuric acid hydrolysis are treated in the same way tot establish the content of total soluble carbohydrates, the content of polysaccharides being calculated from the difference. The procedure of clarifying proved useful especially when the concentration of soluble carbohydrates in water exceeded the limit of 5 mg/l, below which the determination lacked in satisfactory accuracy. Solutions of lower carbohydrate content require concentration either by evaporation prior to clarifying, or by passing through a column with active carbon. The latter method, which permits to purify to a high degree samples for sugar analysis, is in preparation, a preliminary report being already published (Dowgiałło 1966, Golterman et al. 1965).

The proposed method of clarifying seems also to be applicable to sugar analysis in waste waters from paper or food industries. Although sulphosalicylic acid, as a low-molecular model substance for the sulphonated lignin derivatives, is not removed completely from the solution, this does not exclude the quantitative removal of lignosulphonic acids, since they are of higher molecular weight (Gańczarczyk 1959, Kratzl, Bleckmann, 1946, Pszonka, Sarnecki, 1958).

5. SUMMARY

The method of precipitation of cadmium hydroxide in equeous solutions of sugars was applied to remove accompanying substances which interfere with sugar analysis. The losses of the examined sugars and the degree, to which polysaccharides, some other high molecular compounds and phenol derivatives are removed, both were determined. It has been found, that the amount of cadmium hydroxide precipitated in the examined solution, about ten times lower than in the original method of deproteinizing (Fujita, Iwatake 1931), produces no statistically signi-

ficant losses of xylose, glucose and rafinose in the filtrate (Tab. I, II, III, V); at the same time it removes completely polysaccharides, humic compounds, free gallic acid and a high proportion of plant tannins (Tab. IV, V). The method is suitable for the preparation of sugar solutions for analysis, particularly, then their concentration exceeds 5 mg/l.

6. STRESZCZENIE

Zastosowano metodę strącania wodorotlenku kadmu w wodnych roztworach cukrów do usuwania substancji towarzyszących cukrom i przeszkadzających w ich analizie. Określono wysokość strat badanych cukrów oraz stopień usunięcia wielocukrów i innych związków wielocząsteczkowych oraz niektórych pochodnych fenoli. Stwierdzono, że wodorotlenek kadmu strącony w badanym roztworze w ilości ok. 10-krotnie niższej niż w oryginalnej metodzie odbiałczania (Fujita, Iwatake 1931) nie powoduje statystycznie istotnych strat ksylozy, glukozy i rafinozy w przesączu (Tab. I, II, III, V), natomiast usuwa całkowicie wielocukry, związki humusowe oraz znaczną część garbników roślinnych i wolny kwas galusowy (Tab. IV, V). Metoda nadaje się do przygotowania roztworów do analizy na cukry zwłaszcza, gdy stężenie ich przekracza 5 mg/l.

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THE FOOD AND FEEDING HABITS OF CHAETOGNATHA IN THE SEAS AROUND THE BRITISH ISLES

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ABSTRACT

Copepods were the main constituent of the food eaten by *Parasagitta elegans* Verrill and *Segitta setosa* Müller in the seas around the British Isles during the autumn 1964 and summer 1965. There are limits to the size of food these predatory Chaetognatha can take and these were determined; there is also a tendency for larger predators to take larger prey. Both species of Chaetognatha feed most intensively at night. There is a relationship between the frequency of food species in the gut contents of the predators and its frequency in the biotope. The distribution of both species of predators dependens to a very great degree on their trophic conditions.

CONTENTS

1. INTRODUCTION

Chaetognatha are permanent and one of the more numerous constituents of marine plankton. These predators play and important part not only as voracious predators play and important part not only as voracious predators of planktonic copepods but also as competitors with other planktonic predators. The list of food species recorded in the intestine of Chaetognatha is very extensive (Hyman, 1959, Alvarino, 1965), but the role of particular groups, or species has not been clarified until now. Although little is known about the feeding of Chaetognatha, a number of authors have suggested that the food influences the life cycle (Russell, 1932a, Alvarino, 1965), the occurrence and the density (Reeve, 1936) of the predator popula-

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tions. That abiotic factors may determine the distribution of Chaetognatha is well known. Associated with this, a number of species are widely recognised to be indicators of water masses (FRASER, 1952). Also some attempts have been made to use the size structure of Chaetognath populations as indicators of water movements (RAKUSA-SUSZCZEWSKI, 1967). The am of the present work is to amplity our knowledge about this important group in the marine plankton by analysing the trophic relationship of the two species, *Parasagitta elegans* Verrill (sensu TOKIOKA, 1965a, b) and *Sagitta setosa* Müller, which are abundant in the waters around the British Isles.

2. MATERIALS AND METHODS

During the first voyage, in September and October 1963, specimens were collected on the continental shell of the north western part of the North Sea, in the region of the Hebrides (the Stanton Bank), the Irish Sea, the Celtic Sea as well as the western part of the North Sea (Fig. 1, stations 142—186).
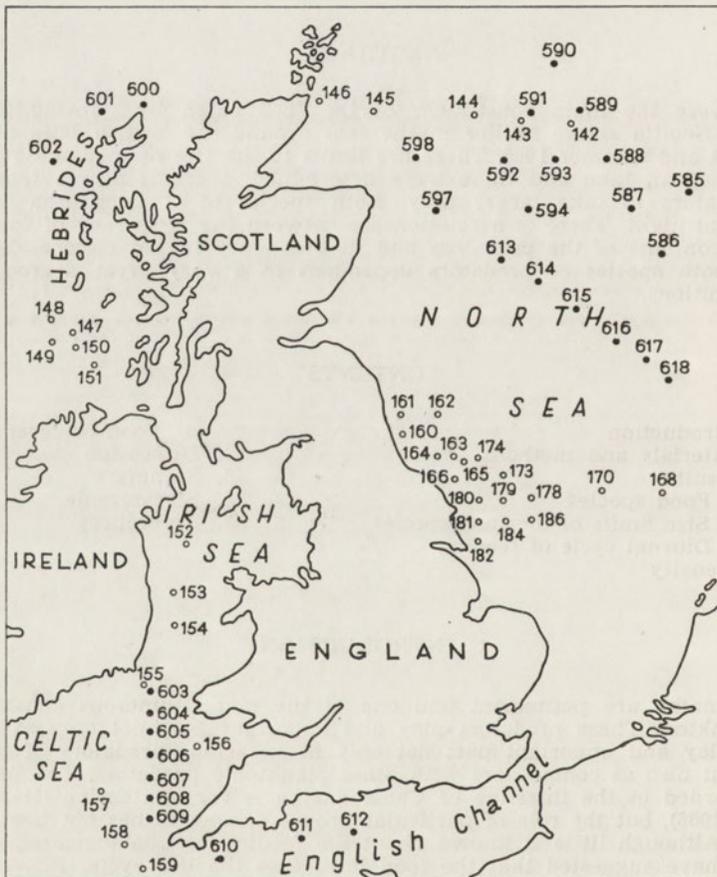

Fig. 1. Chart indicating the positions of the sampled stations. Ostations sampled in autumn 1963; ostations sampled in summer 1965. Details about positions of stations, depths, salinities and temperatures are given in Table I

Table I. Hydrographic data

No. of station	Date	Position	Depth in m	Salinity Surface Bottom	Temperature Surface Bottom
585	12.06.65	57° 40 N 04° 38,5 E	82	31.98 34.92	12.01 6.88
586	13.06.65	56° 59,5 N 04° 02 E	61	34.74 34.92	10.50 6.10
587	13.06.65	57° 30 N 03° 30 E	66	34.74 35.01	10.57 7.45
588	13.06.65	58° 00 N 53° 00 E	70	34.05 34.92	11.51 7.03
589	13.06.65	58° 30 N 02° 30 E	92	34.45 34.92	11.22 6.60
590	14.06.65	59° 00 N 02° 00 E	112	34.81 35.10	10.17 6.50
591	14.06.65	58° 30 N 01° 30 E	130	34.90 34.90	14.39 6.66
592	14.06.65	58° 00 N 01° 00 E	148	34.90 34.90	10.62 6.75
593a	14.06.65	58° 00 N 02° 00 E	87	34.81 34.90	10.62 6.75
b,c,d.	15.06.65	”	,,	” 34.90	” 10.50
594	15.06.65	57° 30 N 01° 30 E	92	34.90 34.90	10.50 6.30
597	20.06.65	57° 30 N 00° 20 W	102	34.76 34.90	10.57 7.33
598	20.06.65	58° 00 N 00° 40 W	109	34.76 34.90	10.88 7.00
600	22.06.65	58° 35 N 06° 18.8 W	74	34.72 34.72	11.32 10.15
601	22.06.65	58° 29 N 07° 00 W	70	34.72 34.90	11.60 9.10
602	22.06.65	58° 00 N 07° 54 W	70	34.99 34.99	11.55 9.43
603	28.06.65	52° 00 N 06° 00 W	92	34.81 35.05	13.22
604	28.06.65	51° 44 N 06° 00 W	120	34.72 34.99	13.00 9.04
605	28.06.65	51° 27 N 05° 59 W	106	34.83 35.05	13.00 8.70
606	28.06.65	51° 11 N 06° 00 W	90	34.83 35.01	13.85 8.50
607	28.06.65	50° 56 N 06° 00 W	94	34.83 35.10	13.62 8.75
608	28.06.65	50° 39 N 05° 59 W	90	34.83 35.19	.15.15 10.05
609	28.06.65	50° 23 N 06° 00 W	80	35.01 35.19	15.52 10.60
610	29.06.65	49° 55 N 04° 33.5 W	86	35.01 35.35	13.70 10.70
611	29.06.65	50° 08 N 03° 00 W	62	35.01 35.05	13.20 12.50
612	29.06.65	50° 17 N 02° 00 W	55	35.01 35.01	12.50 12.45
613	9.07.65	56° 59 N 00° 59 E	92	34.90 34.90	11.10 6.50
614	10.07.65	56° 42 N 01° 42 E	94	34.72 34.72	11.10 6.20
615	10.07.65	56° 24 N 02° 22 E	72	34.72 34.72	11.28 6.10
616	10.07.65	56° 07 N 03° 05 E	74	34.72 34.72	11.85 6.05
617	10.07.65	55° 48 N 03° 45 E	50	34.72 34.72	12.10 7.98
618	10.07.65	55° 31 N 04° 25 E	32	34.67 34.67	12.50 12.07

The plankton was collected from the deck of the ship m/t. Birkut with a standard Hensen net. Samples from stations 160—164 and 173—186 were obtained using a vertically hauled ring-trawl; this material has only partly been worked (RAKUSA-SUSZCZEWSKI, 1967). In the autumn 1963 the determination of the composition of Chaetognath food by analysis of the intestinal contents was carried out on 11498 individuals of *Parasitta elegans* and about 1000 *Sagitta setosa*. Hydrographical data from the sampled station as well as the numbers, age structure and size frequency distribution of both species of Chaetognatha have already been published (RAKUSA-SUSZCZEWSKI, 1967). In most cases, every individual in each sample was examined so that it is also possible to determine the feeding intensity of the population, that is, the percentage of individuals in the sample with food in their intestines.

In June and July 1965, plankton was collected in the northern part of the North Sea, the Hebrides region, the Celtic Sea, the English Channel and the middle part of the North Sea (Fig. 1, stations 585—618, Table 1). The Hensen ne was used, hauled from the bottom to the surface. Whenever atmospheric conditions permitted, three hauls were made at each station but only two were taken at station 601 and only one at station 602, 614 and 615. As before, the food composition of *Parasagitta elegans* and *Sagitta setosa* was determined by analysing the gut contents of very individual in the sample as well as determining its length (to an accuracy of 1 mm) and the developmental state of its gonads, identified according to RUSSELL (1932a, b). Particular attention was paid to the diurnal feeding cycle of *Parasagitta elegans*. At station 593, twelve hauld were taken throughout a period of twenty four hours, each haul taking about half an hour. This material was analysed quantitatively in four groups of three successive hauls. In all, 21,906 individuals of *Parasagitta elegans* and 2753 individuals of *Sagitta setosa* were examined.

In the 1965 material, the cladoceran and copepod species were treated quantitatively, with particular attention being paid to the size structure of *Calanus finmarchicus* Gunnerus, the five copepodite and the adult stages being differentiated Plankton from the three hauls at each station was concentrated to 0,5 litres and the number of Copepoda and Cladocera was determined in a 4 cm³ sub-sample of this. In such a three-haul sample taken with a Hensen net, the number of individuals in a 4 cm³ sub-sample, multiplied by 125, gives the number of individuals under 1 m² of the sea surface.

3. RESULTS

a. Food species

From the analysis of the gut contents of specimens collected around the British Isles (Tables II and III), the composition of the food of the two Chaetognath species is as follows:

Food species	*Parasagitta elegans*	*Sagitta setosa*
Copepoda	+	+
Metridia lucens Boeck	+	−
Centropages typicus Krøyer	+	+
Calanus finmarchicus Günn	+	+
Pseudocalanus elongatus Boeck	+	+
Paracalanus parvus Claus	+	−

Temora longicornis Muller	+	+
Centropages hamatus Lilljeborg	+	+
Isias clavipes Boeck	−	+
Acartia clausi Gisbrecht	+	+
Corycaeus anglicus Lilljeborg	+	+
Oithonia spp.	+	+
Microsetalla norvegica Boeck	+	+
Euterpina acutifrons Dana	+	−
Ova	+	+
Cladocera	+	+
Podon intermedius Lilljeborg	+	+
Podon leucarti Sars	+	+
Amphipoda	+	+
Themisto abyssorum Boeck	−	+
Cirripedia nauplii	+	−
Euphausiacea	+	−
Appendicularia	+	+
Pisces	+	+
Clupea harengus larva	+	−
Ova	+	+
Chaetognatha	+	+
Parasagitta/Sagitta	+	+

The group met most frequently in the food of these Chaetognaths were copepods, although in some samples the main food of *Sagitta setosa* was cladoceran (station 611). Eggs and fish larvae formed a minor constituent of the food compared with copepods. Attention is drawn to the absence of *Metridia lucens* from the food of *Sagitta setosa* and of *Isias clavipes* from the food of *Parasitta elegans*. A species recorded only in the food of *Sagitta setosa* was the amphipod *Themisto abyssorum*. Any other diferences in the species composition of the food of these two predators seems to be accidental.

In the region investigated, any changes in the copepod components of the food of the Chaetognaths were mainly quantitative. Thus, in the summer in the northern and central part of the North Sea, *Pseudocalanus elongatus* and *Calanus finmarchicus* were predominant in the food of *Parasagitty elegans*; in the Celtic Sea, the most frequent food species in the gut were *Pseudocalanus elongatus*, *Temora longicornis* and *Acartia clausi*. For *Sagitta setosa* in the English Channel, however, the food consisted mostly of *Temora longicornis* and the cladoceran *Podon intermedius*.

During the autumn, however, in the northern part of the North Sea, the most frequent species in the food of *Parasagitta elegans* was *Calanus finmarchicus* but was *Centropages typicus* and *Temora longicornis* in the midwestern region. *Centropages typicus* was also the main food species in the region of the Stanton Bank and in the Celtic Sea. In the Irish Sea, where the Chaetognath gut contents showed the greatest variety, the predominant species were *Temora longicornis* and *Pseudocalanus elongatus*.

In general, the number of species forming the food of the Chaetognaths is summer consisted of a greater number of species with two or three copepod species predominating whereas in autumn fewer species were present and the relationship between particular species was more miscellaneous.

b. Size limits of the food species

The identification of the copepodites and adult copepod stages in the Chaetognath gut contents made it possible to assess accurately the size of

Table II. The specific composition of the food and the numbers of *Parasagitta elegans* containing food organisms belonging to different species

Region stations		Copepoda														Others								
		Meridia lucens	Centropages typicus	Calanus finmarchicus	Pseudocalanus elongatus	Paracalanus parvus	Temora longicornis	Centropages hamatus	Acartia clausi	Corycaeus anglicus	Oithona spp.	Euterpina acutifrons	Microsetella norvegica	Ova	Indeterminable	Podon intermedius	Podon leucarti	Parasagitta sagitta	Appendicularia	Cirripedia nauplii	Clupea harengus larva	Ova-Pisces	Amphipoda	Euphausiacea
Northern North Sea 142—146, 585—598	a	1		30		9	3		4		7				22		1	2				1		
	s			179	175		2		1						341			7						
Central North Sea 613—617	s	8	1	146	124	8	6		8		15			1	283			10			1	1	1	1
Mid-western North Sea 160—186	a		322	55	10	4	374		44			1			122		8	15						
Hebrides 600, 601	s				27				1						10									
Stanton Bank 147—151	a		293	79	3		13	20	6		1				139									
Irish Sea 152—154	a		5	4	17	26	28		14						35									
						2																		
Celtic Sea 1955—159, 603—609	a	4	167	52	74		17	7	2	1	12	1	2	70	245	13	6	10	51	1	1	38		
	s		8	27	453		344	5	132	3			1	1	738			61						
English Channel 610—612	s			2	44		20		1					1	48	3	11					8		

a — autumn, s — summer.

Table III. The specific composition of the food and the numbers of *Sagitta setosa* containing food organisms belonging to different species

Food component	Region stations	Copepoda											Others					
		Centropages typicus	*Calanus finmarchicus*	*Pseudocalanus elongatus*	*Temora longicornis*	*Centropages hamatus*	*Isias clavipes*	*Acartia clausi*	*Oithona* spp.	*Microsetella norvegica*	Ova	Indeterminable	*Podon intermedius*	*Podon leucarti*	*Parasagitta sagitta*	*Themisto abyssorum*	Appendicularia	Ova-Pisces
a	Northern North Sea 142, 586–587	6	1									10		1				
s				1														
s	Central North Sea 613–617		11	8	3			3	2	1		43			9	2	1	
a	Mid-western North Sea 162–184	11		2	12		2											
a	Stanton Bank 150	1																
a	Irish Sea 152–154		1	1	11	2												
a	Celtic Sea 155, 157, 159, 603–609	11	1	2	2	1		2			6	32	1		1			
s					19										6		3	
s	English Channel 610–612			3	54	5		8	1			21	82		5			1

a — autumn, s — summer

prey organism which was taken by different sizes of the predator Chaetognaths. The size composition and age structure of the predator population is give in Figure 2 and Figure 3 presents the composition of the food of particular length classes of *Parasagitta elegans*. Usually, only one specimen of the prey organism was found in any individual predator but occasionally more were found, as in a *Parasagitta elegans*, 19 mm long, with eleven small *Pseudocalanus elongatus* in its gut. Figure 3 shows clearly that there is a relationship between the number of copepods eaten, and identifiable to species and stage and the
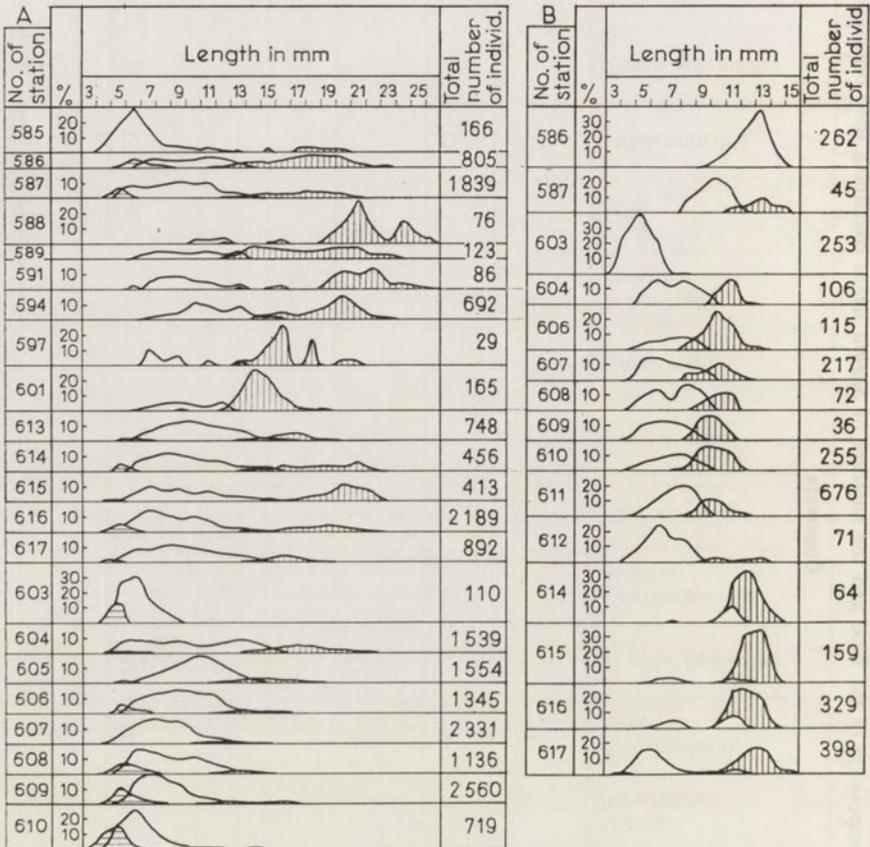
Fig. 2. The lenght frequency distribution and age structure of the populations of *Parasagitta elegans* (A) and *Sagitta setosa* (B) from different stations. The ordinate indicates the percentage occurence of different lenght classess in each sample and the total number of individuals under 1 m³ is given on the right

number of predators present. These results also demonstrate that there are limits to the size of food organism taken as well as a tendency for larger Chaetognaths to take larger prey. Figure 4 presents the food of *Sagitta setosa* and demonstrates the same two phenomena as in the previous species, despite the much fewer eaten Copepoda whose size could be established.

It proved difficult to delimit the size range of food organisms other than copepods although certain facts are worth recording. Appendicularia were found in the guts of *Parasagitta elegans* belonging to length classes 5—19 mm but were most frequent in classes 8—11 mm; Cladocera in classes 5—12 mm but most in classes 6—8 mm. Cannibalism occured in length classes 4—22 mm

Fig. 3. The food composition of *Parasagitta elegans* given as the ratio of the total number of devoured copepods to the total number of predators in each length class. This figure is based upon date summed for all the stations sampled in 1965. The length of copepods (measured together with abdomen) is given as a mean of the measurements taken from stations 587, 593, 594 only

without any peak frequency Cladocera were present in the gut of *Sagitta setosa* from 4 to 12 mm but mostly in the 8 mm class; cannibalism occured in the blasses 4—14 mm.

The above results reveal that the limits to prey size which can be taken and the tendency to take larger prey with increase in the size of the predator are both very real characteristics influencing the selection of food organisms by the populations of *Parasagitta elegans* and *Sagitta setosa* under natural conditions.
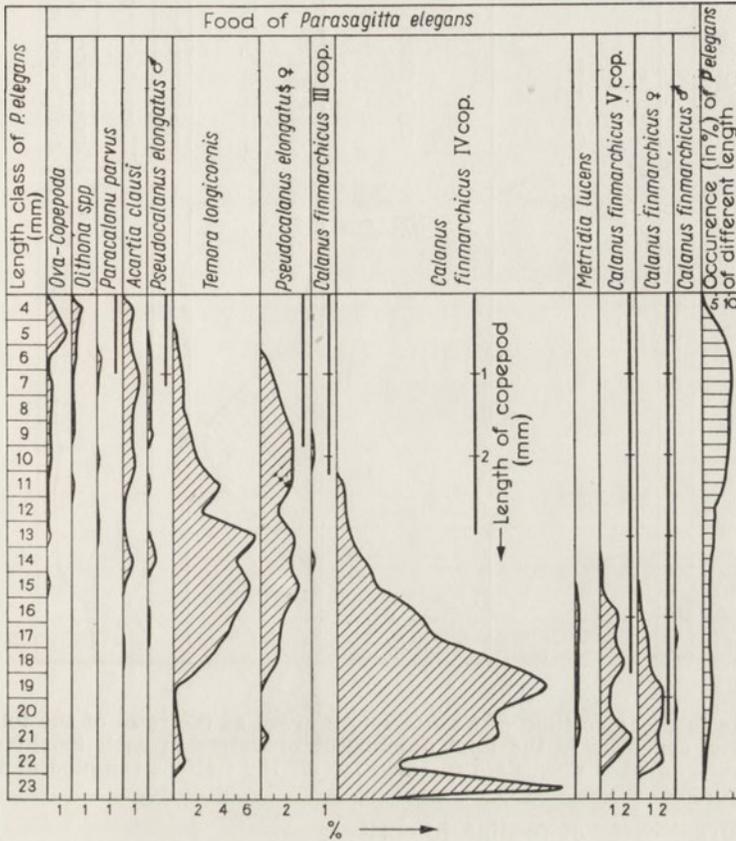
http://rcin.org.pl
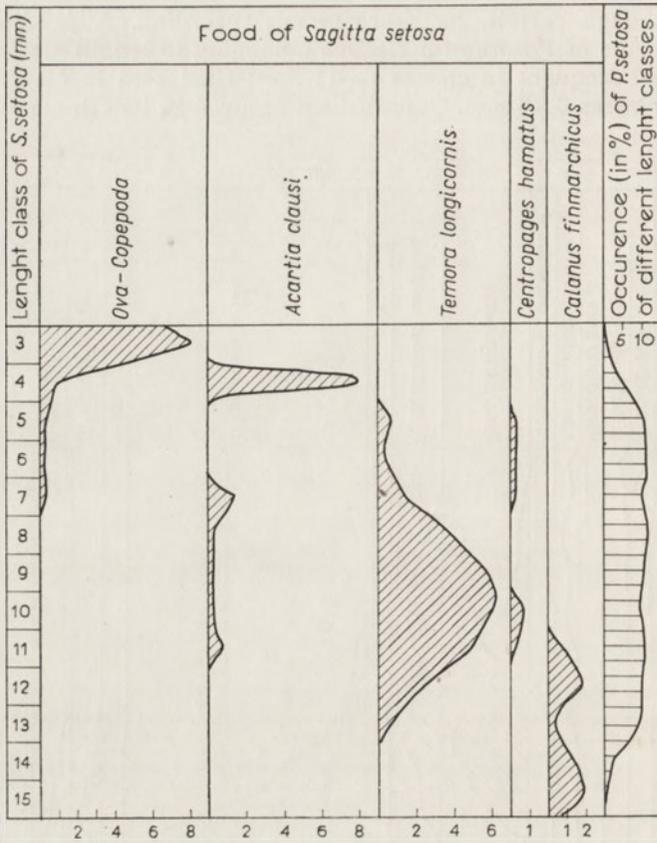
Fig. 4. The food composition of *Sagitta setosa* given as the ratio of the total number of devoured copepods to the total number of predators in each lenght class. This figure is based upon date summed for all the stations sampled in 1965

c. Diurnal cycle of feeding intensity

The intensity of feeding, that is, the percentage of individuals in a sample with food in their guts, was investigated during 1963 for *Parasagitta elegans* and during 1965 for both species. A comparison of this feeding intensity with the hour of collection of the sample gives a picture of the diurnal cycle of feeding intensity for these predators and is presented in Figure 5A, B, C.

In *Parasagitta elegans*, the feeding intensity increased during the night hours. This result was also found at station 593 (Figs 6A, B, C and D) where the feeding intensity of successive samples was 37.1%, 70.1%, 57.3% and 46.9% and the most intensive feeding took place between 0^{00} and 1^{20}. The feeding intensity depends not only on time but also on the nature of the food; this is shown in Figure 7 where the proportion of *Parasagitta elegans* feeding on *Calanus finmarchicus* showed very little change in successive samples taken at different hours. On the other hand, the numbers consuming *Pseudocalanus elongatus* increased considerably during the period from $0.^{00}$—$1.^{20}$ and $4.^{00}$—
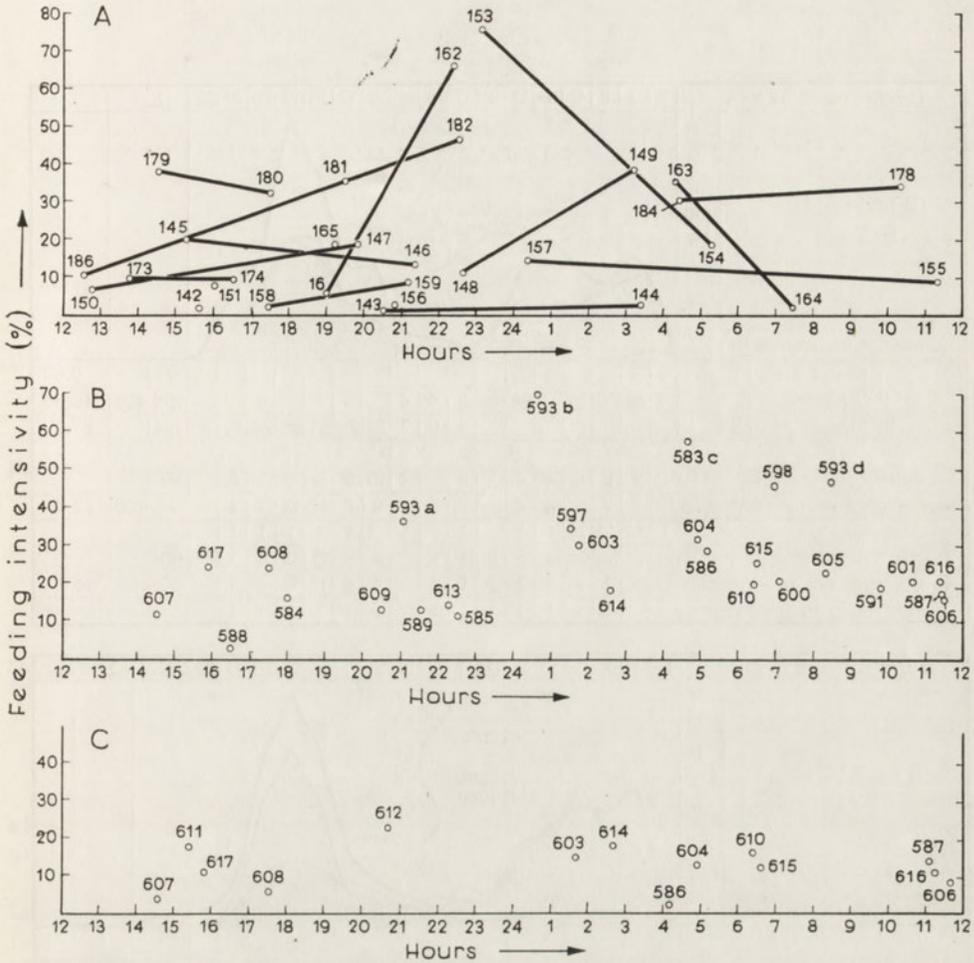
Fig. 5. The diurnal (twenty-four hour) feeding cycle. The numbers above each point indicates the station number. The lines join stations with similar predator length and age compositions. Feeding intensity is the percentage of individuals in the sample containing food organisms in their alimentary canals. A — *Parasagitta elegans* autumn 1963; B — *P. elegans* summer 1965; C — *Sagitta setosa* summer 1965

5.^{20} and the population showed an increased feeding intensity during the hours of the night.

Sagitta setosa fed much less intensively than *Parasagitta elegans* and its summer diurnal feeding cycle was less marked (Fig. 5C). An interesting phenomenon was observed at station 611 where one of the periods of more intensive feeding was recorded but between the hours of 15^{00} and 16^{00} the prey consisted of the cladoceran, *Podon intermedius*.

Thus, both in *Parasagitta elegans* and *Sagitta setosa*, the intensity of feeding increased during the hours of the night, although the actual hour of maximum intensity was not always the same.

7*

STATION 593 a

Length class in mm	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Σ		%
Number of individuals in																				
I Stage 1	4	3																7		0.69
II Stage 2	14	29	20	25	34	24	6	5	4	4								165	406	40.36
III Stage 3							4	6	7	26	25	51	66	28	19	2		234		57.27
FOOD																				
No. *P. elongatus* eaten	10	9	8	6	4	4		2		3	10	5	13	13	7	3		97		
No. *P. elegans* with ate *P. elongatus*	10	8	7	5	4	4		2		3	9	5	12	12	7	3		91	/406	22.4
Ratio of prey to predator	1	1.1	1.1	1.2	1	1		1		1	1.1	1	1	1	1	1				
No. *C. finmarchicus* eaten			1IIIc	3IIIc	3IIIc	2	2	1	3		4	6	11	13	8	3		60		
No. *P. elegans* with ate *P. elongatus*			1	3	3	2	2	1	3		4	6	11	13	8	3		60/406		14.7
Ratio of prey to predator			1	1	1	1	1	1	1		1	1	1	1	1	1				

Inset diagram labels: *Calanus* 2.4 mm / 2.1 / 1.8 / *Pseudo-calanus* 1.5 / 1.2 / 0.9 / 50%

STATION 593 b

Length class in mm	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Σ		%
Number of individuals																						
in I Stage 1																						
II Stage 2	9	49	41	44	35	30	9	16	3	2										238	524	45.3
III Stage 3								6	11	16	26	59	83	60	15	5	3	2		286		54.6
FOOD																						
No. *P. elongatus* eaten	8	29	34	52	36	28	8	10	11	7	13	11	44	64	45	13				413		
No. *P. elegans* which ate *P. elongatus*	8	24	28	32	24	16	4	5	6	3	7	10	21	39	24	6				257/524		49.0
Ratio of prey to predator	1	1.2	1.2	1.6	1.5	1.7	2	2	1.8	2.3	1.7	1.1	2	1.6	1.8	2.1						
No. *C. finmarchicus* eaten			1III	2III	4	1	3	5	7	9	12	22	24	18	6			2		116		
No. *P. elegans* which ate *P. elongatus*			1	2	4	1	3	5	7	9	10	21	23	17	6			2		111/524		21.1
Ratio of prey to predator			1	1	1	1	1	1	1	1	1.2	1	1	1	1			1				

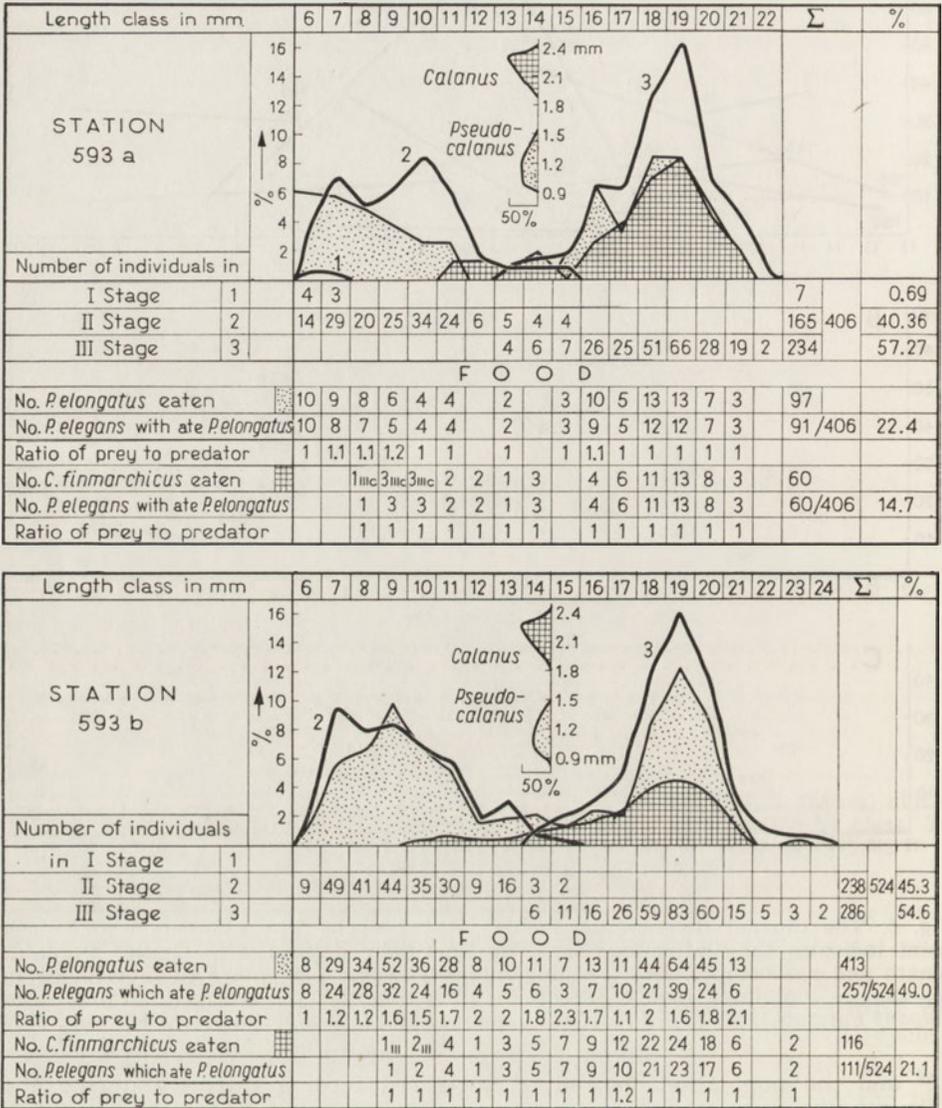Inset diagram labels: *Calanus* 2.4 / 2.1 / 1.8 / *Pseudo-calanus* 1.5 / 1.2 / 0.9 mm / 50%

Fig. 6. The composition of food for different sizes and stages of *Parasagitta elegans*. The curves labelled by the arabic numbers 1,2,3, refer to the percentage occurrence of stages 1,2,3, of *Parasagitta elegans*

Inset diagram: The length frequency distribution of *Calanus finmarchicus* and *Pseudocalanus elongatus*
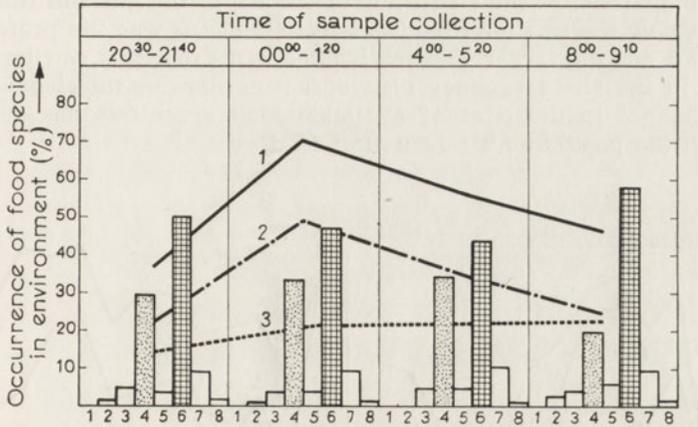
Fig. 7. The food of *Parasagitta elegans* during different periods of the twenty-four hour cycle at station 593

Indices (curves):

$$1 \quad \frac{\text{number of individuals with full guts}}{\text{number of all individuals of } P. \text{ elegans}} \cdot 100$$

$$2 \quad \frac{\text{number of } P. \text{ elegans with } P. \text{ elongatus in gut}}{\text{number of all individuals}} \cdot 100$$

$$3 \quad \frac{\text{number of } P. \text{ elegans with } C. \text{ finmachicus in gut}}{\text{number of all individuals}} \cdot 100$$

Food animals: 1. *Acartia clausi*; 2. *Paracalanus parvus*; 3. *Metridia lucens*; 4. *Pseudocalanus elongatus*; 5. *Calanus finmarchicus* III cop.; 6. *Calanus finmarchicus* IV cop.; 7. *Calanus finmarchicus* V cop.; 8. *Calanus finmarchicus* ♀+♂

d. Food preferences

Differences in the abundance of species in the environment and in the alimentary canal of the Chaetognaths from station to station provides aboundant material to assess their food preferences (Fig. 8).

During the summer in the region of the North Sea investgated the prey taken by *Parasagitta elegans* was mainly *Pseudocalanus elongatus* and *Calanus finmarchicus*, with the former species predominating, whereas in the environment *Calanus finmarchicus* was the more abundant species (Fig. 9). Thus there was a positive preference for Pseudocalanus and a selection against Calanus since, as is shown in figure 9, its percentage frequency in the gut is much less than in the environment.

For the Celtic Sea, Figure 8C and D compares the percentage frequency of species in the environment at various stations with the percentage frequency of these in the gut contents. At stations 604 and 605, where the population of Parasagitta consisted of larger animals than in the other stations, the prefered food organism was the large copepod *Temora longicornis* because its percentage frequency in the gut was greater than in the environment. The next most frequent food species was *Pseudocalanus elongatus* however, its frequency in the gut was less than in the plankton, suggesting a selection against this species as food. *Acartia clausi*, a small copepod, occurred least frequently in the gut but, because it was scarce in the plankton, showed a higher frequency in the gut compared with the environment and so was another preferred species. Starting from station, 606, the situation changed. The individuals in the Parasagitta population were much smaller.

A similar comparison of the frequency of species in the gut and the plankton reveals that now the smaller *Pseudocalanus elongatus* was the preferred food organism and not the larger *Temora longicornis*. From this can be seen that differences in the size frequency distribution of *Parasagitta elegans* and the resulting changes in the sizes of available food organisms has a very real influence on the population's selection of food.
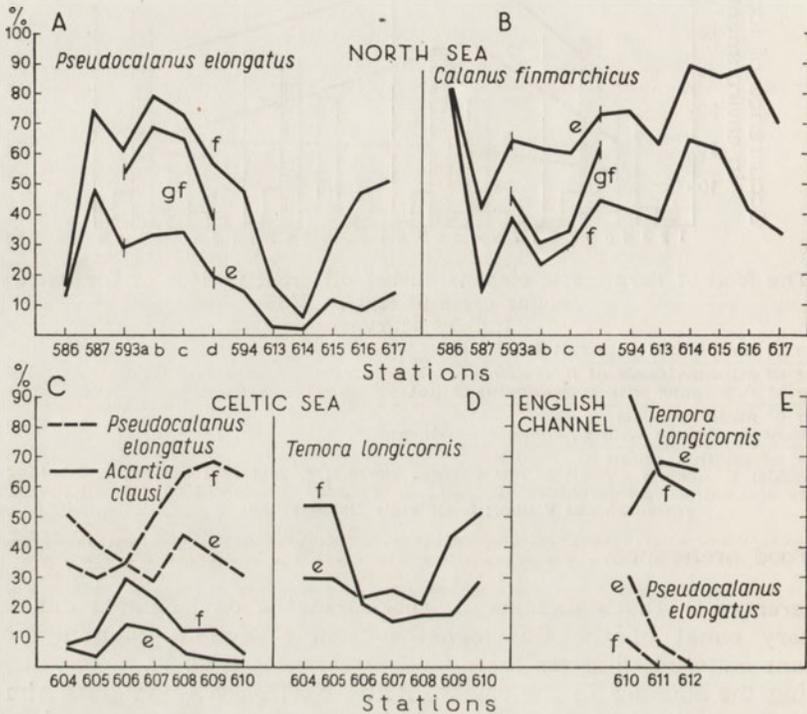

Fig. 8. A comparison of changes in the abundance (frequency of occurrence) of particular food species of Copepoda in the environment and in the food of populations of *Parasagitta elegans* (A, B, C, D) and *Sagitta setosa* (E) from selected stations. e — changes in the abundance (frequency of occurrence) of a copepod food species in the environment, given as percentage of all copepod species present at each station; f — changes in the abundance (frequency of occurrence) of a copepod food species in the food of the predator populations, given as percentage of copepod species present at each station; gf — changes in the abundance (frequency of occurrence) of copepod species in the food of *Parasagitta elegans* longer than 11 mm, given as percentage of all food species.

The somewhat variable food composition of *Parasagitta* and *Sagitta* in the Celtic appears to be the result of differences in the size distribution of both predator populations. *Parasagitta elegans* had a greater range of sizes than *Sagitta setosa* but with more abundant smaller sizes, whereas, *S. setosa* with a smaller range of sizes consisted of larger animals (Fig. 1). As a result, *Pseudocalanus elongatus* was the most frequent species in the gut of *P. elegans* with *Calanus finmarchicus* also appearing. However, *Calanus finmarchicus* was not found in the gut of *S. setosa* in which the most abundant species was *Temora longicornis*, a copepod larger than *P. elongatus*.

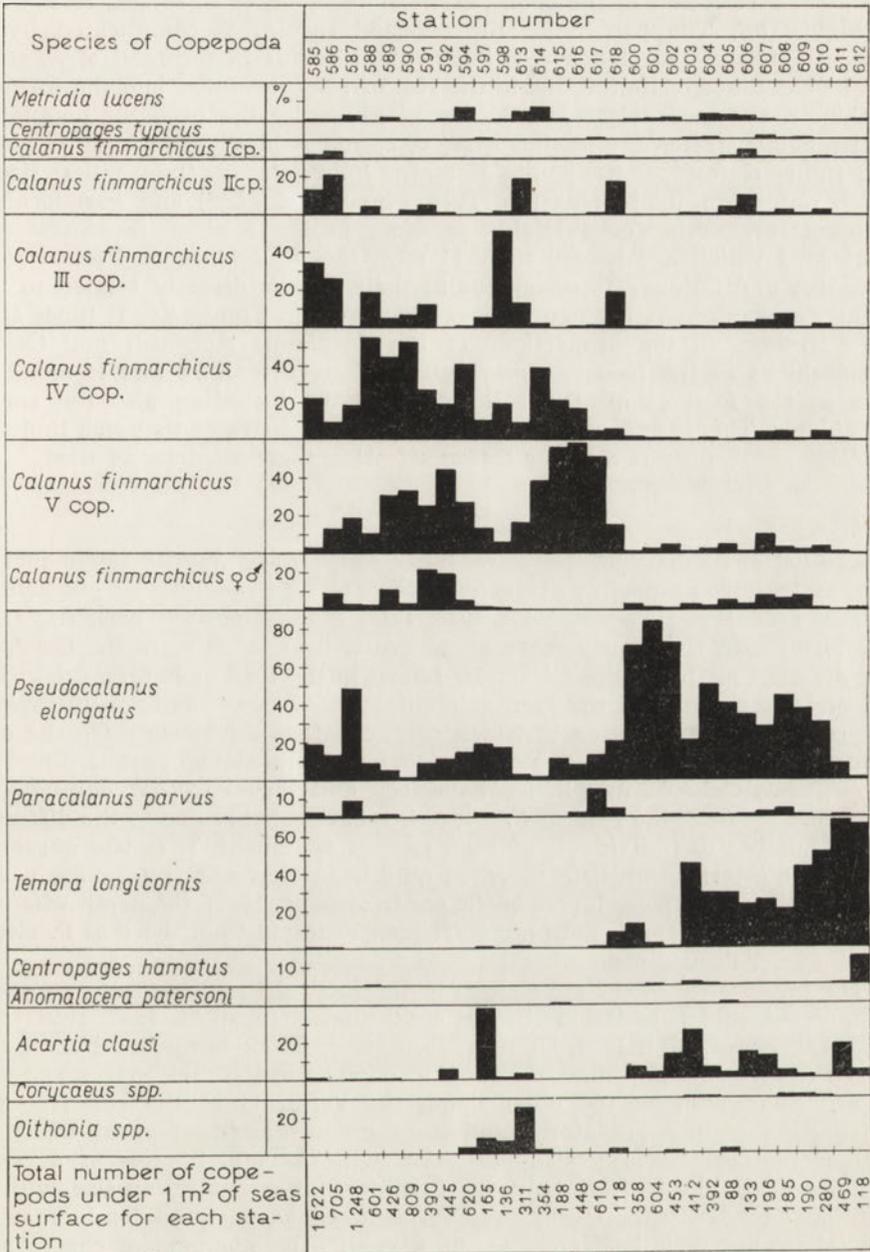In the English Channel, diffrences in the abundance of species in the

Station number

Species of Copepoda		585 586 587 588 589 590 591 592 594 597 598 613 614 615 616 617 618 600 601 602 603 604 605 606 607 608 609 610 611 612
Metridia lucens	%	
Centropages typicus		
Calanus finmarchicus I cp.		
Calanus finmarchicus II cp.	20	
Calanus finmarchicus III cop.	40 / 20	
Calanus finmarchicus IV cop.	40 / 20	
Calanus finmarchicus V cop.	40 / 20	
Calanus finmarchicus ♀♂	20	
Pseudocalanus elongatus	80 / 60 / 40 / 20	
Paracalanus parvus	10	
Temora longicornis	60 / 40 / 20	
Centropages hamatus	10	
Anomalocera patersoni		
Acartia clausi	20	
Corycaeus spp.		
Oithonia spp.	20	
Total number of copepods under 1 m² of seas surface for each station		1622 705 1248 601 426 809 390 445 620 165 136 311 354 188 448 610 358 604 453 412 392 88 133 196 185 190 280 469 118

Fig. 9. Frequency of occurrence of various species of copepods (and of copepodite stages of *Calanus finmarchicus*) in the sampled stations, given as percentage of all the copepod individuals present

plankton is reflected in the composition of the food of *S. setosa*, as is shown in Figure 8E. The preference for copepod species is complicated by the predominance of the cladoceran, *Podon intermedius* in the food of *S. setosa.*

The existance of limitations to the size of prey devoured and the influence of this on the food selected from the plankton by the predator populations is also demonstrated for station 593a, b, c, and d in Figure 6A, B, C and D. This figure shows that the length 11 mm is for *P. elegans* the smallest size for which *Calanus finmarchicus* (the IVth copepodite stage) and *Pseudocalanus elongatus* are edible or available as food. In the food of those classes of *P. elegans* which are longer than 11 mm, the abundance of *Pseudocalanus elongatus* and *Calanus finmarchicus* in their guts is directly related to their abundance in the environment. But, as is shown in Figure 8A, B (lines G, F), the diffrences in the proportions of *Pseudocalanus elongatus* and *Calanus finmarchicus* in the food of these animals longer than 11 mm is much less than in the food of all the collected animals, including also the smaller individuals. This is and important point and demonstrates that size limitation in chaetognath prey is a major factor affecting their selection of food.

4. DISCUSSION

The list of food species for *Parasagitta elegans* and *Sagitta setosa* includes most systematic groups, as determined to date from analysis of gut contents of both predators (Lebour, 1922, 1923, Lea, 1955, Mironov, 1960, Alvarino, 1965). The most frequently represented group by species were the Copepoda. The presence of the copepod *Metridia lucens* in the food of *Parasagitta elegans* and of *Isias clavipes* in the food of *Sagitta setosa* corresponds to the specific differences of the plankton to which each chaetognath belongs. On the other hand the presence in the food of *P. elegans* of *Pracalanus parvus, Euterpina acustrifrons,* ciripede naupli. Euphausiacea and larval *Clupea harengus* but their absence from the food of *S. setosa* is most probably due to the difference in the number of individuals of each species examined. *Themisto abyssorum* and *Podon intermedius*, both recorded only in the gut of *S. setosa*, are usually found in the sub-surface layers of the sea (Raymont, 1963), the depth where the other prey of this species are more frequently found than those of *P. elegans* which prefer deeper waters.

The importance of certain species in the food of the predators corresponds to their seasonal fluctuations in the environment (Glover, 1957, Harvey, et al., 1935), Bode et al. 1965, Glover, Robinson, 1965): however, this may not be a true picture. The range of sizes in copepod species, their stages and sexes on one hand and, on the other hand, the variation in the size frequency distribution of the predator populations creates a situation in which the phenomenon of the prey size limitation will operate. Species of a certain size are available as food only for predators of a particular size with the additional tendency for larger prey to be taken as the predator increases in size (Mironov, 1960, Reeve, 1966). As a result, the numbers of chaetognaths feeding on a determined size of food organisms tends to show a symmetrical size frequency distribution as is shown in Figures 3 and 4.

Reeve (1964) demonstrated an intense night feeding in *Sagitta hispida*. Planktonio Cheaetognatha originate from benthic forms (Tokioka, 1965a) among which the genus Spadella does not show any intense feeding at night (Parry, 1944). During the present work, in a large number of guts of *P. elegans*

and *S. elegans*, the copepod remains were found with their cephalothorax — pointing towards the anal opening. Very often, after digestion, the copepod chitinous skeleton was telescoped into the cephalothorax and was easily grasped and drawn out as a "faecal pellet". As BAINBRIDGE (1952) has shown, the movement and position of Chaetognatha in the water is mainly horizontal and their mouth opening is ventral to their body and this horizontal position. Copepod migration upwards to the surface is performed with the cephalothorax anterior (HARDY, BAINBRIDGE, 1954). The capture of food and the observed increase in the chaetognathis population feeding intensity corresponds to the period of planktonic migration to the surface layers. This is an advantageous moment for predators both because of the position of the prey as well as the increased likelihood of meeting they prey during their migration upwards. Therefore, the nocturnal migration of planktonic may influence the feeding intensity of these chaetognaths. According to WIMPENNY (1936) higher feeding intensities were observed in the populations of *P. elegans* in the North Sea during the period just before the breeding seasons.

The results presented earlier show that the specific composition of the food taken from the environment by the predators is closely related to the abundance and specific composition of the Copepoda in the plankton with all their local fluctuations at different stations. This correspondence between abundance in the gut and in the plankton applies only to those copepod species "available" as food to the predator sizes present.

The predominance of one species or even one stage of Copepoda is often observed in marine plankton, so that whether or not these stages are of an edible size may prove decisive for the survival and for the coexistence of these two species of predators. The sizes of Chaetognatha present may be very varied. An analysis of the developmental stages of *P. elegans* shows they attain a greater size and wider range of sizes than *S. setosa*. According to BAINBRIDGE (1963), *P. elegans* is most numerous in the northern and north-western parts of the North Sea. The young stages usually occur near the surface layers and may be transported more quickly southwards by surface currents, as RUSSEL (1936) and WIMPENNY (1936) already observed much earlier. With advancing flow of water from the north in the northern North Sea, the number of small "shelf" and neritic species of copepods decreases and the nature of the plankton changes. The older copepodite stages of Calanus and the larger oceanic species become predominant and these cannot be taken as food by the younger smaller individuals of *P. elegans*. Thus, there may be a decrease in the population density and a change in its composition to mainly older, larger sizes. On the other hand, in the southern regions, the food conditions are very good for the younger, smaller stages of *P. elegans* as well as for *S. setosa*, because of the small copepod species characteristic of these waters and of a size edible by both species of predators. It is therefore possible to suggest that the presence and coexistence of these two species of Chaetognatha is determined to as great and extent by their trophic conditions as by the salinity or temperature of their environment (FRASER, 1952, SOUTHWARD, 1962).

5. SUMMARY

1. An analysis of the food composition and certain other aspects of feeding in the Chaetognatha (*Parasitta elegans Verril and Sagitta setosa* Müller) suggest that their occurrence and coexistence depends on their trophic conditions.

2. Samples were collected in September and October 1963 in the North Sea, near the Hebrides (Stanton Bank), in the Irish Sea, Celtio Sea and in the central and western part of the North Sea. In June and July 1965, plankton samples were taken again in the northern North Sea, in the Hebrides, Celtic Sea, English Channel and Central North Sea. A Hensen type net was houled vertically from the bottom to the surface, usually three times at each station. The contents of the intestines of 33 404 individuals of *P. elegans* and 3753 individuals of *S. setosa* were examined and the length of each individual measured to 1 mm.

3. The gut analysis revealed that the food of both species consisted mainly of Copepoda. The copepod species occurring in the food of both species were those characteristic of the plankton association to which each chaetognathan species occurred.

4. The share of any particular species in the food of these predators reflects both seasonal and local differences on that species in the plankton. During the summer in the northern and central part of the North Sea, *Pseudocalanus elongatus* and *Calanus finmarchicus* were the main food species of *P. elegans*: in the Celtic Sea, the most frequent food species were *P. elongatus Temora longicornis* and *Acartia clausii*. In the English Channel the food of *S. setosa* consisted mostly of the fladoceran *Podon intermedius* but the copepod *Temora longicornis* was also numerous. In autumn in the northern part of the North Sea, *Calanus finmarchicus* was predominant in the food of *P. elegans* whereas the main food species were *Centropages typicus* and *Temora longicornis* in the central-western part. At Stanton Bank and in the Celtic Sea, the food consisted mainly of *Centropages typicus*. In the Irish Sea the dominating species in the food were *T. longicornis* and *P. elongatus.*

5. Only certain species or stages of Copepoda are available as food for particular sizes of predators and there is a tendency for the size of prey to increase with size of predator. Thus, the size frequency of the predators feeding on food organisms of a certain size shows a symmetrical distribution.

6. An examination of the population feeding intensity, that is, the percentage of individuals in the sample with food in their guts, shows that both species feed most intensively during the night hours. However, the actual hour of maximum feeding is not always the same. In summer, the feeding intensity is greater in *P. elegans* than in *S. setosa.*

7. Usually, the guts of both predator species contained only a single copepod individual.

8. Which food organism can be selected from the plankton is limited to a very considerable extent by the chaetognath's inability to take all the sizes present in the plankton.

6. STRESZCZENIE

Analiza składu pokarmu i niektórych zagadnień w odżywianiu się Chaetognatha (*Parasagitta elegans* Verrill i *Sagitta setosa* Müller) daje obraz troficznych zależności ich występowania i współwystępowania. Materiały zebrano we wrześniu i październiku 1963 na M. Północnym, w rejonie Hebrydów (Stanton Bank) na M. Irlandzkim, Celtyckim i w środkowo-zachodniej części M. Północnego. Ponownie w czerwcu i w lipcu 1965 roku materiały planktonowe zebrano w północnej części M. Północnego, w rejonie Hebrydów, M. Celtyckiego, Kanału Angielskiego i środkowej części M. Północnego. Używano sieci typu Hensena wykonując pionowe zaciągi od dna do powierzchni 3 razy. Na podstawie analizy zawartości jelita 33 404 osobników *Parasagitta elegans* i 3753 osobników *sagitta setosa* ustalono, że głównym pokarmem obu drapieżców są Copepoda. Skład Copepoda w pokarmie *Parasagitta elegans* i *Sagitta setosa* odpowiada charakterystycznym różnicom w zespołach gatunków, z którymi występują badane Chaetognatha. Latem w północnej i centralnej części M. Północnego w pokarmie *Parasagitta elegans* dominuje *Pseudocalanus elongatus* i *Calanus finmarchicus*. W rejonie M. Celtyckiego najliczniejszymi gatunkami w pokarmie są *Pseudocalanus elongatus* i *Calanus finmarchicus*. W rejonie M. Celtyckiego najliczniejszymi gatunkami w pokarmie są *Pseudocalanus elongatus, Temora longicornis* i *Acartia clausi*. W rejonie Kanału Angielskiego w pokarmie *Sagitta setosa* dominuje Cladocera *Podon intermedius* i licznym jest Copepod *Temora longicornis*. Jesienią w północnej części M. Północnego w pokarmie *Para-*

sagitta elegans dominuje *Calanus finmarchicus,* w części środkowo-zachodniej — *Centropages typicus* i *Temora longicornis.* W rejonie Stanton Bank i na M, Celtyckim pokarm stanowi głównie *Centropages typicus.* Na M. Irlandzkim dominującymi gatunkami w pokarmie są *Temora longicornis* i *Pseudocalanus elongatus.* Udział poszczególnych gatunków w pokarmie drapieżców wykazuje sezonowe i lokalne różnice odpowiadające zmianom liczebności tych gatunków w środowisku. Określone gatunki i stadia Copepoda są dostępne jako pokarm Chaetognatha jedynie dla określonej wielkości drapieżców. W odżywianiu się Chaetognatha stwierdzono tendencję do pobierania pokarmu większego wraz ze wzrostem wymiarów drapieżców. W rezultacie liczebność drapieżców odżywiających się określonej wielkości pokarmem w całej populacji stanowi grupę osobników o wymiarach rozkładających się w przybliżeniu symetrycznie. Analizując stopień najedzenia, czyli procent osobników w próbach, w których znaleziono pokarm w jelicie stwierdzono, że intensywność odżywiania się obu gatunków drapieżców wzrasta w godzinach nocnych. Nie jest to jednak związane z określoną stałą godziną doby. Latem intensywność odżywiania się większa jest u *Parasagitta elegans* niż u *Sagitta setosa.* Udział gatunków Copepoda w pokarmie *Parasagitta elegans* i *Sagitta setosa* odpowiada jedynie względnym ilościom tych gatunków w środowisku. Dostępność morfologiczna jest jednym z istotnych czynników ograniczających wybiórczość pokarmu, która jest silnie zaznaczona.

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RESPONSE OF LAKE FAUNA TO LIGHT

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ABSTRACT

With the use of a light trap of the autor's own construction, the phototaxis of aquatic animals in different zones of a lake has been investigated. A considerable variation of the light response was found among aquatic species. The highest attraction to light was displayed by the following species: *Bythotrephes longimanus*, *Polyphemus pediculus*, *Leptodora kindtii*, *Eurycercus lamellatus*, *Bosmina coregoni*, *Scapholeberis mucronata*, *Heterocope appendiculata*, *Megacyclops gigas* and *Pollasea* quadrispinosa. The lowest phototaxis was observed in almost all the species of the Cyclopoida suborder and in the majority of littoral Cladocera, in *Daphnia cristata longiremis*, *Daphnia cucullata*, and *Eurytemora lacustris*. In Daphnia, the males showed a higher response to light than the females. The adults of *Daphnia cucullata* were more attracted to light than the young. *Asplanchna* spp. and the Chaoborus larvae showed no response to light.

CONTENTS

1. Introduction
2. Methods
3. Results
4. Discussion

5. Summary
6. Streszczenie
7. References

1. INTRODUCTION

The response to light, observed in many species, has been already broadly used in practice. A great deal of marine species of fish have been caught basing on this reaction (BORISOV 1955, NIKONOROV 1963). Light has been similarly used by the Japanese fishermen for catching squids and by the Philipine fishermen to collet shrimps for commercial purposes (NIKONOROV 1963). Pest insects which are active at dusk or during the night have been also caught by means of light traps (MAZOHIN-PORŠNJAKOV 1956). The reaction to light in freshwater invertebrates has been studied hitherto almost exclusively in laboratory conditions, the experiments being mainly done with Cladocera and especially with Daphnia (SCHULTZ 1928, CLARKE 1932, SKADOVSKIJ 1939). Only a few such experiments have been carried out in natural conditions. GESSNER (1928/1929) has performed some experiments of this type by catching aquatic animals into an illuminated plankton net or trap. The reaction to light was found to change with the light colour. OYE and LUYTEN (1934) examined the reaction to light in Cladocera by catching them beneath the

water surface of a pond which had been illuminated for 10 to 15 min. before the catching began. However, the results which they obtained were inconsistent. BAYLOR and SMITH (1953) used a light trap of a rather complicated structure and operation for collecting Cladocera.

This paper delas with the phototactic reaction induced by artificial light in animals occurring in different zones of a lake. It also includes the laboratory results obtained by Barbara Szlauer, M. Sc. for the fauna of a small pond.

2. METHODS

The main part of the study has been carried out in a mesotrophic lake Ińsko (337 ha in area, max. depth of 41 m) of the north-western part of Poland (Szczecin district) in September 1967. The remaing observations were carried out in November 1967 on the material collected from permanent small ponds of the Szczecin parks.

For the field experiments, a light trap was constructed by the author (Fig. 1). Its main part consisted of a tin bucket, 10 l in volume with a ballast attached to its rim so that the trap could sink with its bottom up. In the top of the bucket filled with air, there was a battery of 4.5 V which fed a waterproof 3.5 V flashlight bulb submerged in the water filling the lower part of the apparatus (Fig. 1B). The light from the bulb pased through 16 holes cut symmetrically in the lower part of the apparatus. Eight holes were larger measuring, 5 cm², the other eight-smaller, of 1 cm² each. The animals attracted by the light entered the trap through these holes. They gathered around the bulb and were later caught into a stilon, 0.2 mm mesh net while removing the trap from water. HUNGERFORD, SPANGLER, and WALHER (1955) used a similar trap based on the same principle for catching insects and other animals. Relatively large inlets in the present trap (5 cm²) were supposed to permit larger animals to enter the trap. Additional trials which showed that the traps with larger oppenings produced rather fore abundant yields than
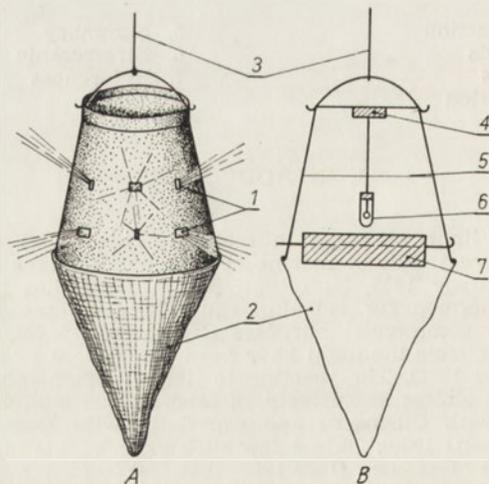

Fig. 1. Light trap. A — general view of illuminated apparatus; B — section;
1 — holes, 2 — net, 3 — attachment, 4 — battery, 5 — level, of water, 6 — bulb in casing, 7 — ballast

those with smaller ones were decisive where the size of the inlets is concerned. The light, bright at the beginning of the exposure, was found to fade out due to the running out of the battery. To prevent this, the traps were exposed only for 3 hours. They were set up in the lake at dusk (19:00) and removed at 22:00. Four identical traps were exposed within a small area at a time, three of them being illuminated. The fourth trap was dark and served as a control. Catches, with a plankton net of the same mesh as that used for collection of the trap contents, were carried out in the evening, just before placing the traps in water, in the vicinity of the place where the traps were submerged. They supplied information on the percentage composition of the fauna living in this area.

On 29th Septemper, 4 traps were placed at a far distance from the lake shore in a place 25 m deep. They were suspended at 2.5, 10, and 15 m from the water surface. The control trap was placed at a depth of 5 m. It was not possible to increase the number of control traps on account of technical difficulties, thus the results of the catches without light can be only considered as orientative ones. The bulbs in the traps were screened in order to prevent the light from passing down into the water. The net catches were done with a cone-shaped net, 40 cm in diameter at the entrance, by dragging it from the bottom up to the water surface, collecting thus all the animals present in the water column. This permitted the comparison of the net cath with those made with the light traps to be made as the latter by being suspended at different levels, sampled almost the whole column.

On September 5th, the traps were placed on the bottom of the littoral zone, at a depth of 25 m. The bottom there was covered with gravel mixed with mud, and the pebbels were overgrown by green algae. These observations were carried out in the same place of the lake as those made in the pelagial zone on September 29.

On September 5th, the traps were placed on the bottom of the littoral zone at a depth of 3 m. The bottom in this place was covered with a sparse vegetation of submerged plants, amoung which *Myriophyllum* spp. was most aboundant.

On September 6th, the catches were made in an area overgrown with reeds, *Phragmites communis,* trap I being placed at a depth of 0.7 m, and traps II and III — at depths of 1.0 and 1.5 m, respectively.

For each series of catches, the results from 3 light traps which functioned simultaneously were pooled together.

Conclusions concerning the response of aquatic animals to light were based on the comparison between the light trap catches and the net catches. The ratio between the percentage occurrence of a species in the light trap catches, A, to that in the net catches, B, was accepted as a measure of the intensivity of light response in this species. This index will be further termed as A : B ratio. It is identical with the index introduced by Šarygin (1939) for describing food selection in fish. In Tables I, II, III and V species were arranged according to the value of this ratio. Such taxonomic groups as Ostracoda, Hydracarina, and Ephemeroptera, in which the species were not identified, were excluded from this sequence irrespective of the value of the ratio and are listed at the end of the table.

In order to check the functioning of the light traps under conditions more suitale for observation, the experiments were carried out on the small pond

fauna in the laboratory. For these experiments, a miniature trap with 14 lateral holes was sevised, its volume being 10 times smaller than that of the field traps (1 l). During each experiment, two such traps were placed in an aquarium witch held a known number of animals. One trap emitted light, the other one was dark — used as control. After 30 min., the traps with animals imprisoned inside them were removed from the aquarium. The experiment was run at a room temperature in two evenings, November 4th, 6th 1967. There were four replications of this experiment; the response to the light was also measured by the A : B ratio.

During the field observations, the traps emitting light created a spectacular view. The light spread out the from of horizontal and slant wafts, reaching far from its source due to a high transparency of the water. During the investigations, the visibility of a white disk amounted to 7 m. Crustaceans and aquatic insects moved along the wafts and entered the traps through he holes. Inside, they gathered around the bulb. Usually, the animals were not observed to leaved to leave the traps.

3. RESULTS

On September 29th, the typically planktonic crustaceans were almost exclusively caught in the pelagial zone (Tab. I). A group of animals with an extremely high A : B ratio was distiguished among them. Accepting this ratio as a measure of the intensity of the response to light, this group was defined as animals most intensely attracted to light. This group included: *Bythotrephes longimanus*, *Megacyclops gigas*, *Leptodora kindtti*, and males of *Daphnia longispina* and *Daphnia cucullata*. High differences in the response to light were observed among the species of Cladocera. The predatory species, *B. longimanus* and *L. kindtii*, revealed a clearly higher response to light than the filtrators. In the genus of *Daphnia*, the highes response was that of *D. longispina*, smaller in *D. cucullata*, and the smallest in *D. cristata longiremis*. The genus of Bosmina, represented by *B. coregoni crassicornis* and *B. longirostris*, showed a high response to light. The species of Cyclopida, on the contrary, were the least attracted to light. *Megacyclops gigas*, a species occurring directly over the lake bottom, was the only exception in this group and responsed strongly to light. A low response was also observed in copepods of the Calanoida suborder with the exception for *Heterocope appendiculata* which was rather highly attracted to light. *Eurytemora lacustris*, on the other hand, was very little attracted to light. *Eudiaptomus gracilis* held an intermediate position in this respect. It is interesting to notice that in *Daphnia cucullata* and even more in *Daphnia longispina*, the males showed higher response to light than did the females. A similar phenomenon was found to occur in *Cyclops scutifer*. The results included in Table I point also to the higher response of the adults of *Daphnia cucullata* than of its young. The table shows also differences in the number of Crustacea caught in the light traps at different depths. In general, the highest numbers of crustaceans were caught at the surface, the lowest ones — near the bottom. However, not all of the species showed such a tendency. Some of them were caught more numerously in traps exposed at higher depths, e.g., *Megacyclops gigas*, *Cyclops scutifer*, *Daphnia longispina*, *Daphnia cristata longiremis*, and *Bosmina longirostris*.

Table I. Number of individuals caught into the light traps and to the net in pelagic zone of the lake (29.09. 1967)

Species	Traps with light					Trap without light depth 5m	Vert. net catch		Coefic. A:B
	Depth in m			Total I+II+III	%			%	
	I 2.5	II 10	III 15	C	A		D	B	
Bythotrephes longimanus Leydig ♀	400	750	0	1150	5.1	0	8	0.015	340.0
Megacyclops gigas Claus ♀,♂	0	100	25	125	0.6	0	8	0.015	40.0
Leptodora kindtii Focke ♀,♂	700	200	0	900	4.0	5	72	0.1	40.0
Daphnia longispina O.F.M. ♂	0	4100	350	4450	19.8	75	425	0.8	24.7
Bosmina coregoni crassicornis Lill. ♀	4150	75	30	4255	19.0	20	1850	3.5	5.4
Daphnia longispina O.F.M. ♀	100	625	65	790	3.5	10	425	0.8	4.4
Heterocope appendiculata G.O. Sars ♀,♂	325	0	0	325	1.4	10	192	0.4	3.5
Bosmina longirostris O.F.M. ♀	50	275	230	555	2.5	15	500	0.9	2.8
Daphnia cucullata G.O. Sars ♀	100	1125	25	1250	5.6	0	1200	2.3	2.4
Eudiaptomus gracilis G.O. Sars ♀	800	0	0	800	3.6	0	1100	2.1	1.7
Daphnia cucullata G.O. Sars ♀	3225	175	80	3480	15.5	55	8200	15.4	1.0
Eudiaptomus gracilis G.O. Sars ♂	275	0	0	275	1.2	0	700	1.3	0.9
Cyclops scutifer G.O. Sars ♂	0	0	175	175	0.8	5	500	0.9	0.9
Daphnia cucullata G.O. Sars juv. ♀	2250	125	140	2815	12.6	185	16850	31.7	0.4
Daphnia cirstata longiremis Sars ♀	0	75	50	125	0.5	0	1450	2.7	0.2
Mesocyclops leuckarti Claus ♀,♂	275	0	25	300	1.3	25	3500	6.6	0.2
Cyclops scutifer G.O. Sars ♀	0	25	30	55	0.2	20	700	1.3	0.2
Eurytemora lacustris Poppe ♀,♂	175	200	120	495	2.2	15	8950	16.9	0.1
Thermocyclops oithonoides G.O. Sars ♀,♂	25	25	25	75	0.3	25	3650	6.9	0.04
Asplanchna sp. ♀	25	0	15	40	0.2		2750	5.2	0.04
Total	13175	7875	1385	22435	100.0	465	53030	100.0	

A low catch was obtained with the control, dark trap (Tab. I) *Daphnia cucullata*, a dominant species in the plankton community, was preveiling in it. It is interesting to note that in spite of their sporadical occurence in the habitat, relatively high numbers of males of *Daphnia longispina* were caught in this trap. The control trap yielded also many individuals of *Asplancha* spp., much more than the average light trap.

The catches which were carried out with the light traps near the bottom comprised mostly individuals of *Pallasea quadrispinosa*, 2—16 mm in lenght, including males, females, and young (Tab. IV). In addition, a few individuals of *Megacyclops gigas* and some not specified Turbellaria were caught in the light traps. Since they were not found in the net catch dragged along the bottom, it can be inferred that these animals ahowed a very high, positive response to the light.

In the littoral zone, *Heterocope appendiculata* was abundantly caught in the light traps, althought it was very rare in the natural habitat as evidenced by its absence in the net sampling (Tab. II). Since it was not possible to calculate the A:B ratio in this species the symbol n was introduced to denote an extremely high response to light. Among Crustacea which occurred in the Myriophyllum meadow, the highest tendency to move towards the light was also observed in *Eurycercus lamellatus* and *Megacyclops viridis* apart from the above mentioned species. A high tendency was likewise found in Ostracoda and Hydracorina. Among Cladocera of this zone, only *Eurycercus lamellatus* showed an intense reaction to light. The remaining species, i.e. *Ceriodaphnia quadrangula*, *Acroperus harpae*, *Sida crystallina*, and *Chydorus spaericus*, showed a much lower reaction. In Cyclopoida, the least sensitive to light were: *Mesocyclops leuckarti*, *Macrocyclops albidus*, and *Eucyclops macruroides*; *Megacyclops viridis* was an exception in this group but its scant material made this finding a rather tentative one. Catches made with separate traps were rather similar. *Ceriodaphnia quadrangula*, a species which was most abundant in the net samplings, prevailed also in the control trap.

In the shallow part of the littoral zone, among reeds, the highest response to light was that of Cladocera, and especially of *Polyphemus pediculus* (Tab. III). A high reaction to light was also found in *Bosmina coregoni longispina*, which dominated in the light traps but was rarely encountered in nets. *Scapholeberis mucronata* — a neuston species, and *Eurycercus lamellatus* should be also classified as the species with a clearly positive response to light. *Heterocope appendiculata*, which also occurred in this zone, showed a similar, intense reaction to light. The remaining species of Cladocera, namely *Sida crystallina*, *Acroperus harpae*, *Peracantha truncata* and especially *Ceriodaphnia quadrangula*, were characterized by a low response to lingth. *Eucyclops macrurus* and *Mesocyclops leuckarti* should be also included to the group of species showing the lowest reaction. The low reaction to light was also found in Ostracoda of this zone (Tab. IV). Apart from crustaceans, Coleoptera larvae and adults of Trichoptera were found inside the light traps exposed in this zone. The latter must have entered the traps in the pupal stage. Since specimens belonging to these two taxonomic groups occured only sporadically in the environment, they can be considered as strongly attracted to light. The individual catches in this zone showed considerable differences, both qualitative and quantitative ones. The highest numbers of Crustacea were caught in trap 1, which was located at the nearest distance from the shore,

Table II. Number of individuals caught to the light traps and to the net in littoral zone overgrown by Myriophyllum (5.09.1967)

Species	Traps with light					Trap without light	Net catch		Coefficient A:B
	I	II	III	Total I+II+III	% A		B	% B	n
Heterocope appendiculata G.O. Sars ♀,♂	700	200	550	1450	15.4	0	0	0.0	n
Eurycercus lamellatus O.F.M. ♀	540	550	520	1610	17.2	0	400	1.9	9.0
Megacyclops viridis Jurine ♀,♂	60	0	70	130	1.4	0	60	0.3	4.7
Ceriodaphnia quadrangula O.F.M. ♀	850	990	2070	3910	41.6	290	9800	46.2	0.9
Acroperus harpae Baird ♀	170	80	70	320	3.4	20	1450	6.8	0.5
Sida crystallina O.F.M. ♀	200	120	50	370	3.9	10	2100	9.9	0.4
Chydorus sphaericus O.F.M. ♀	200	40	0	240	2.5	10	1500	7.0	0.3
Eucyclops macruroides Lilljeborg ♀,♂	40	30	30	100	1.1	20	1050	4.9	0.2
Mesocyclops leuckarti Claus ♀,♂	190	80	60	330	3.5	50	3350	15.8	0.2
Macrocyclops albidus Jurine ♀,♂	30	10	0	40	0.4	0	1140	5.4	0.1
Ostracoda	110	140	210	460	4.9	90	50	0.2	24.5
Hydracarina	150	150	140	440	4.7	20	350	1.6	2.9
Total	3240	2390	3770	9400	100.0	510	21250	100.0	

Table III. Number of individuals caught to the light traps and to the net in littoral zone overgrown by Phragmites (6.09.1967)

Species	Traps with light					Trap without light	Net catch		Coefficient A:B
	I	II	III	Total I+II+III	% A		B	% B	n
Polyphemus pediculus O.F.M. ♀	0	266	3	269	0.7	0	0	0.0	n
Heterocope appendiculata G.O. Sars ♀,♂	1775	7	6	1788	4.7	1	25	0.3	15.7
Bosmina coregoni longispina Leydig ♀	22815	2009	180	25004	66.1	8	425	4.9	13.5
Scapholeberis mucronata O.F.M. ♀	275	119	12	406	1.1	0	25	0.3	3.7
Eurycercus lamellatus O.F.M. ♀	500	189	150	839	2.2	2	100	1.1	2.0
Sida crystallina O.F.M. ♀	6700	749	129	7578	20.1	9	1075	12.3	1.6
Eucyclops macrurus G.O. Sars ♀,♂	300	14	0	314	0.8	0	125	1.5	0.5
Peracanta truncata O.F.M. ♀	125	0	6	131	0.3	13	175	2.0	0.1
Acroperus harpae Baird ♀	200	42	78	320	0.8	4	500	5.7	0.1
Mesocyclops leuckarti Claus ♀,♂	75	0	48	123	0.3	4	275	3.2	0.1
Ceriodaphnia quadrangula O.F.M. ♀	450	14	66	530	1.4	20	5350	61.5	0.02
Ostracoda	350	49	33	432	1.1	6	600	6.9	0.2
Hydracarina	100	7	39	146	0.4	0	25	0.3	1.3
Total	33665	3465	750	37880	100.0	67	8700	100.0	

amongst sparsely growing reeds, on the bottom covered with Isötes. *Heterocope appendiculata*, a mid-lake species, was next to the most abundant species in this catch. A considerable differentation in the horizontal distribution of the fauna occurring within the reead belt can be inferred from the high differences between the catches of separate traps. The dark, control trap exposed in this zone comprised only a few specimens of Crustacea.

Table IV. Number of individuals caught into the light traps and to the net in profundal zone of the lake (7.09. 1967)

Species	Traps with light				Trap without light	Net catch
	I	II	III	Total I+II+III		
Pallasea quadrispinosa Sars	188	121	45	354	4	0
Megacyclops gigas Claus	26	2	3	31	5	0
Turbellaria	11	1	0	12	0	0

The results obtained in the laboratory by means of light traps are summarized in Table V. The animal tested in this experiment have been collected from permanent small ponds. The data are the sums of 4 replications. They suggest that all the species examined shawed a rather low A:B ratio, this being an indication of a weak reaction to light in these animals as compared with that of the lake fauna. Among the pond fauna, a cladoceran *Chydorus sphaericus* was most attracted to linght. On the contrary, *Eucyclops serrulatus* and *Diacyclops bicuspidatus* were very slightly attracted to light.

Table V. Results of catches carried out with light trap in an aquarium. Arthropoda derived from a small pond (4—6.11.1967)

Species	In aquarium		Catch into trap			Coefic. A:B
		% B	with light		without light	
				% A		
Chydorus sphaericus O.F.M. ♀, ♂	17 980	48.5	6550	73.3	187	1.5
Simocephalus exspinosus Koch ♀,♂	1 060	2.8	140	1.6	9	0.6
Eucyclops serrulatus Fischer ♀,♂	230	0.6	14	0.1	2	0.2
Diacyclops bicuspidatus Claus ♀,♂	2 660	7.2	125	1.4	39	0.2
Ostracoda	8 420	22.7	609	6.8	107	0.3
Ephemeroptera (larvae)	6 720	18.2	1502	16.8	77	0.9
Total	37 070	100.0	8940	100.0	421	

Using a similar method, the reaction to light was also tested experimentally in *Chaoborus* spp. but the species showed no response to this factor.

4. DISCUSSION

The A:B ratio, calculated for separate species, are a measure of the degree of reaction to light in these species, i.e. the response to light, or positive phototaxis. Such a conclusion was reached by comparing the results of catches

made with the light trap with those obtained with the dark trap, when they were both exposed simultaneously in the same area. The yields of the light traps were, as a rule, higher than those of the dark traps (Tab. V). It follows that the catching of animals into light traps results from an attraction to light. A rotifer, *Asplanchna* spp., was the only exception out of all the species examined since it has been caught in higher numbers in dark traps than by means of the light ones (Tab. I). With the mothod applied, basing on the accepted premises, only this species can be considered as one which showed a negative phototaxis. The above reasoning emphasizes also the importance of the use of dark, control traps for such studies. With these two kinds of traps it was possible to determine the type of reaction of the animals to light, whereas the A:B ratio allowed to measure the intensity of this reaction. This intensity was found to be highly differentiated with the species examined. Some of them, being extremely rare in the habitat, were caught numerously in the light traps, revealing therefore a high positive response to light. This group comparises all the species listed in Tables I, II, and III which had the A: B ratio higher than 2, and the species listed in Table IV. The second group with a low response to light includes those species listed in Tables I, II, III and IV which had the A:B ratio lower than 2. The division into these two groups is, of course, an arbitrary one, but it was necessary to accept it on account of the necessity of classification of the species according to their different degree of attraction to light, in spite of the lack of natural criterion of such a classification. The differentiated reaction of the plankton species to visible stimuli was reported by GESSNER (1928/1929) who, using for his studies a plankton net with a bulb inside, has found a higher response to light in *Daphnia longispina* and *Leptodora kindtii* than in *Diaptomus vulgaris*.

The group of animals highly sensitive to light distinguished in this paper consists of various species, differing both biologically and taxonomically. It includes Cladocera, Copepoda, one species of Amphipoda (*Pallasea quadrispinosa*), and also some insect larvae. Cladocera of this group include all predatory species as well as many filtrating species. They are typical of different habitats: typically planktonic, littoral, neuston, and profundal forms. A similar taxonomic and biological differentiation was found in the group of species with the low light response. The situation found in crustaceans is similar to that described in fish. The fish species with showed a positive reaction to light also differed biologically (BORISOV 1955).

It was not possible to find any common feature which fould account for the light response in certain species. Neither it was possible to find it for the other group, that is for the species with a low response to light. One should except that the biological factors responsible for a strong reaction to light would differ with species. Attraction to light found in all the predatory Cladocera which prey on plankton crustaceans (MCRDUHAJ-BOLTOVSKAJA 1956) allows to connect this reaction with the type of feeding. It should be mentioned here that the case of fish the plankton feeders are distinguished from the other fish by highest response to light (NIKORONOV 1963). A strong reaction to the light found in all the profundal species (*Pallasea quadrispinosa*, *Megacyclops gigas*, Turbelaria) permits to conclude that this is a common trait for the whole fauna which occurs in the dark lake zone. This tendency is perhaps, of the same type as that observed in the insects active at dusk and night, and attracted to lamplight. On can also except this attraction to

depend on thermophilous characteristics of these crustaceans. Almost all of them are summer forms (Cladocera and *Heterocope appendiculata* of Copepoda). It is also difficult to point out any biological characteristic which would explain a lower reaction to light in the second group of species.

The problem of light reaction in related species is rather interesting. In Bosmina, the species occurring in the mid-lake zone as well as *Bosmina coregoni longispina* occurring in the littoral zone, showed similarly strong reaction to light. In Cyclopoida, the pelagic, littoral, and small-pond species, all were characterized by an equally low reaction to light. Only *Megacyclops gigas*, a deep water species, was an exception. A thoroughly different situation was observed in Daphnia. *Daphnia longispina* showed a higher reaction to light than *Daphnia cucullata* and a much higher one than *Daphnia cristata longiremis*.

Others results suggest that a certain intensity of reaction cannot be considered as a trait common for all stages or forms in one species. The different intensity of reaction in young and mature individuals of *Daphnia cucullata* suggests that this reaction is age-dependent. Its intensity is also different in the two sexes. The males of *Daphnia longispina* and *Daphnia cucullata* were more attracted to light than were the females of these species. These differences can be considered as another evidence of differentiated behaviour in males and females od Daphnia. This problem was the subject of an earlier publication (Szlauer 1964).

Large differences were found between the catches done at different water layers and at different places within the reed vegetation (Tab. I and III). The first type of differences can be explained by a known phenomenon of vertical stratification of zooplankton; the horizontal differentiation in the distribution of zooplankton can probably account for the second type of differences found between the catches carried out within the reed vegetation.

The animals which were abundant in the habitat, as proved by the mass occurrence in the net samples, were usually caught in the dark traps. This speaks in favour of the random entering into these traps. However, the mass presence of the *Daphnia longispina* males in the dark traps (Tab. I) was probably conditioned by a tendency in these animals to attach themselves to some kind of substratum.

The results of this paper are based on the data obtained in series of 3 replications since each experiment consisted of an exposure of there identical light traps at the same time. The significance of differences pointed out in the paper was verified by the Hills' statistics (1961), which permits to ascertain the reliability of conclusions. It should be emphasized, however, that this reliability was different in particular cases. Some species as, for example, *Heterocope appendiculata* and *Mesocyclops leuckarti*, were examined in three different habitats, and the results were consistent. Other results seem to be reliable on account of a high frequency of certain species in the traps. Those results which were based on a small number of individuals caught in one trap only (e.g. *Polyphemus pediculus*) are relatively less reliable.

It cannot be overemphasized that the results obtained apply only to the particular conditions under which the observations were performed, since the light reaction depends on a number of factors, as evidenced by other experimental studies (Schulz 1928, Skadovskij 1939, and others).

The above described experiments make it possible to evaluate the method

in question. The trap can be considered as a very useful device for studies of the light reaction in aquatic animals especially of in natural aquatic environments. It works well due to the simplicity of its construction and infallibility of operation even at higher depths. It can be also successfully applied for catches of rare species, highly attracted to light, and also for gathering large numbers of animals inhabiting submerged plants, otherwise unaccessible.

5. SUMMARY

1. A light trap of the author's make was constructed. It is suitable for examining the response of animals to light, for recording their space distributions as well as for collection of animals from he overgrown habitats of submerged plants.

2. A high differentiation was found in the reaction to light among the species examined.

3. A group of species with a high positive response to light was distinguished. It was diversified, both taxonomically and biologically. All predatory Cladocera (*Bythotrephes longimanus, Polyphemus pediculus, Leptodora kindtii*), cladocerans of the *Bosmina genus*, some profundal species (*Pallasea quadrispinosa, Megacyclops gigas*) as well as *Daphnia longispina, Eurycercus lamellatus, Scapholeberis mucronata*, and *Heterocope appendiculata* belong to this group.

4. The lowest response to light was found in all the species of Cyclopoida, in most of the littoral forms of Cladocera, and also in *Daphnia cristata longiremis, Daphnia cucullata*, and *Eurytemora lacustris*.

5. Males of *Daphnia cucullata*, and even more those of *Daphnia longispina*, showed a higher reaction to light than the females of these species.

6. Matured individuals of *Daphnia cucullata* revealed a higher response to light than their young.

7. *Asplanchna* spp. and the larvae of *Chaoborus* spp. were not attracted to light.

6. STRESZCZENIE

1. Skonstruowano samołówkę świetlną, która nadaje się do określania stopnia dążności drobnych zwierząt wodnych do światła, rejestruje ich przestrzenne rozmieszczenie, a także pozwala wyławiać zwierzęta z gąszczu roślin podwodnych.

2. Stwierdzono bardzo duże zróżnicowanie dążności do światła u badanych gatunków.

3. Wyróżniona grupa gatunków o dużej dążności do światła cechowała się ogromnym zróżnicowaniem pod względem systematycznym i biologicznym. Znalazły się tu wszystkie bez wyjątku drapieżne Cladocera (*Bythotrephes longimanus, Polyphemus pediculus, Leptodora kindtii*), Cladocera z rodzaju Bosmina, gatunki profundalowe (*Pallasea quadrispinosa, Megacyclops gigas*), a ponadto *Daphnia longispina, Eurycercus lamellatus, Scapholeberis mucronata i Heterocope appendiculata*.

4. Najniższą dążność do światła wykazywały prawie wszystkie gatunki z podrzędu Cyclopoida, większość litoralowych wioślarek, a ponadto *Daphnia cristata longiremis, Daphnia cucullata i Eurytemora lacustris*.

5. Samce *Daphnia cucullata*, a zwłaszcza samce *Daphnia longispina* odznaczały się większą dążnością do światła od samic.

6. Dorosłe osobniki *Daphnia cucullata* wykazywały większą dążność do światła od młodocianych.

7. *Asplanchna* sp. i larwa *Chaoborus* sp. w ogóle nie podążały do światła.

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