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GENERAL INFORMATION

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The age of migrating Vistula sea trout and the variability of smolt recruitment to the sea before damming the river

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Abstract. The age structure of the two seasonal stocks of Vistula sea trout is described during the 1953-1968 period for both the river and sea periods of their life cycle. In both the winter (89%) and summer stocks (75%) it usually took sea trout two years to reach the smolt stage. However, the percentage of summer sea trout which reach the sea after spending one year in the river was significantly higher – on average 22%. Winter sea trout stayed in the sea for two (45%) or three (51%) trophic seasons until beginning their spawning migration. Summer sea trout usually started their spawning migration after three trophic seasons in the sea (60%). Fish younger than A.1^+ and older than A.3^+ were rare in both stocks. The percentage of fish which repeated spawning was about 1% for both winter and summer fish. The recruitment strength of winter sea trout smolt to the sea was more variable than in the case of summer sea trout in subsequent years. The recruitment variability coefficient for winter and summer sea trout was 88% and 67%, respectively.

Key words: original Vistula sea trout, summer stock, winter stock, age in river, age in sea, spawning marks, smolt recruitment variability

INTRODUCTION

Vistula sea trout once migrated over a thousand kilometers from the river mouth to their spawning grounds. While in its growing phase, it would migrate widely in the Baltic Sea, which is confirmed by the results of fish tagging over the last thirty years. These results were recognized by the international experts from the ICES* (Backiel and Bartel 1967, Bartel 1969, Christensen and Johansson 1975).

Distant feeding migrations in the Baltic Sea and spawning migrations to the Vistula River resulted in the creation of specific Vistula sea trout stocks with large-sized fish which had a differentiated time for ascending the river. Due to good growth in the sea and abundance, the Vistula sea trout was regarded as the finest in Europe and exceptional both as a natural specimen and from an economic point of view (Dixon 1931, Chrzan 1947, Żarnecki 1952, Pałka and Bieniarz 1983). The Vistula sea trout was characterized by an increase of spawning migration during two well-defined seasons, summer and late fall, forming two spawning runs, one in summer and one in winter. Specimens from the summer run were fully mature for the fall

*ICES – International Council for the Exploration of the Sea

spawning, while the winter sea trout would start their spawning migration with premature gonads and reproduction would occur in the fall of the subsequent year (Borzęcka 1998).

Environmental pollution, intensive commercial fishing and, especially, damming the Vistula River and its tributaries, which prevented fish from migrating to their spawning grounds, all seriously limited the sea trout of the Vistula River basin. To a great extent the dam near Włocławek, which was completed in October 1968 (Anon. 1994), rendered their spawning grounds in the upper Vistula system inaccessible. As a result, the Vistula sea trout stocks began to disappear (Wiśniewolski 1987). Annual stocking with hatchery-reared fish was carried out in order to save them. When the Vistula spawner resources decreased, the eggs of Pomeranian sea trout were transferred from the Koszalin-Słupsk area (Bartel 1993). Stocking the Vistula with *foreign* sea trout resulted in the mixing of the stocks and, finally, in a tendency towards the extinction of fish with *pure* Vistula characters.

The restitution program which is currently being realized in Poland and whose goal is, among others, the rebuilding of Vistula sea trout stocks (Sych 1998) requires knowledge of their previous, primary structures. In this work, which is based on data collected before the dam in Włocławek was built, the age distribution and repeatability of spawning and fluctuations of the recruitment to the sea in natural populations of Vistula sea trout from 1953-1968 are described.

MATERIALS AND METHODS

Sea trout scales were collected and measurements of fish length (*longitudo caudalis*) and mass were carried out near Tczew, 30-40 km from the Vistula River mouth, from 1953 to 1968. The fish were sampled from June to September and in November and December, according to their periods of appearance in the Vistula River (Borzęcka 1998). Sampling fish from the winter run was conducted from 1953 to 1968, while those from the summer run were sampled from 1960 to 1968.

Scales were taken from between the dorsal and the adipose fins from rows close to the lateral line (Tuszyńska 1983).

Only regular scales of each fish from the defined side were chosen under a projector and mounted on card soaked with vegetable glue. Then, according to the method described by Sych (1964), they were used for making scale impressions on plastic plates. The scale impressions were analyzed using a projector with an objective from 4x to 7x. All the data collected regarding the fish were saved and processed using a standard data base program.

In order to determine sea trout age, it was assumed that the fish are born (hatch) on 31 March. Therefore, specimens caught after 31 March had completed one year of life and had begun a new year (+). The age of fish caught in the lower Vistula in November and December was estimated by counting the number of annual rings which were visible in the scale picture (n, age n^+). In order to determine the age of fish caught in summer, the time when the annual ring is being formed, the marginal increment was also measured, i.e. the part of the scale between the last annual ring formed at sea and the scale edge. Measurements of marginal increments were presented in graphic form. Next, using two peaks of the marginal increment distribution curve, it was decided that small increments were from the current year, while large increments were from the previous year. Age was expressed as n^+ or $n{+}1^+$, respectively, where

n is the number of rings (Sych 1967). The estimation of the age of fish which repeated spawning and which had a so-called spawning mark on its scales (Backiel and Sych 1958) was carried out by using the number of annual rings and the scale increment before the spawning mark and before the edge.

Samples included scales of several dozen to several hundred specimens chosen randomly and were disproportional to the size of catches in a particular season and year (Table 1). Therefore, a second procedure was used for verification in which the fish age structure in the samples was recalculated into the numbers of fish in catches.

The age structure of sea trout stocks in combination with catch statistics also served as a basis for estimations of changes in sea trout smolt recruitment to the sea in subsequent calendar years.

The algorithms of information processing applied to combine the sampling data with the catch statistics are explained in the text.

RESULTS

Age structure of sea trout during the period of river life

Figure 1 presents percentages of the age distribution of winter and summer sea trout during their stay in the river. Only age groups 1.B+, 2.B+ and 3.B+ are presented. Specimens from age group 4.B+, which constituted only a fraction of a percent in the winter stock and were nonexistent in the summer stock, are not included in the Figure. In this short notation, the number reflects the years spent by the fish in the river as was read from its scale, B describes an arbitrary number of annual rings in the sea part of the scale, while + is the scale increment after the last annual ring.

Despite certain variability, which may be due to differences in generation abundance, the fish age structure seemed to be about the same from year to year, although it did vary between the stocks. Fish which descended to the sea after one year in the river ($1.B^+$) constituted on average 6% of the winter sea trout, but 23%, and in some years even over 30%, of the summer sea trout. The fish which reached the smolt stage after two years in the river ($2.B^+$) comprised a significant majority in both spawning runs, with an average of 88% of the winter stock and 74% of the summer stock. Fish ready to change environments from freshwater to sea water in the third year of river life ($3.B^+$) occurred much more often in the winter stock – from 1% to 19%, than in the summer stock – from 1% to 7%. The frequency of occurrence of this age group between 1953 and 1968 was, on average, 6% and 3% in winter and summer sea trout, respectively (Figure 1).

Using the χ^2 test, differences between the average distributions of the age of fish of both stocks were compared and the following results were obtained: $df = 2$, $\chi^2 = 122$, $P_{(\chi^2)} = 0.0000$. Since the χ^2 value was exceptionally high, the estimations were repeated using the Kołmogorow and Smirnow λ criterion, which is especially useful in determining differences between empirical distributions in which numbers are high (like the sums of samples in Table 1). The results were similar to those of the χ^2 test: $\lambda = 5.06$ and $P_{(\lambda)} = 0.0000$. This proves a statistically significant difference between age distributions of winter and summer Vistula sea trout in the smolt stage.

Table 1. Sizes of samples and catches of sea trout in the Lower Vistula from 1953 to 1968

Year	Winter sea trout samples	Sample size	Catch statistics	Summer sea trout samples	Sample size	Catch statistics
	Nov. and Dec.		Nov. and Dec.	June to Sept.		June to Sept.
	[specimens]	[%]	[specimens]	[specimens]	[%]	[specimens]
1953	347	8.4	4,091			
1954	102	2.5	3,962			
1955	339	16.4	2,066			
1956	255	1.0	1,589			
1957	186	5.8	3,166			
1958	205	20.8	983			
1959	206	1.4	1,250			
1960	200	4.3	4,603	125	8.4	1,486
1961	180	41.9	429	100	8.2	1,216
1962	200	9.5	2,098	100	11.0	903
1963	133	14.1	942	162	12.5	1,292
1964	201	8.7	2,302	203	7.0	2,873
1965	49	30.6	160	261	37.4	697
1966	175	3.9	547	39	7.7	501
1967	130	4.4	274	30	16.1	186
1968	306	23.2	1,314	202	9.5	2,105
Total	3,214			1,222		
Average	200.875	10.7	1,861	135.77	10.8	1,251

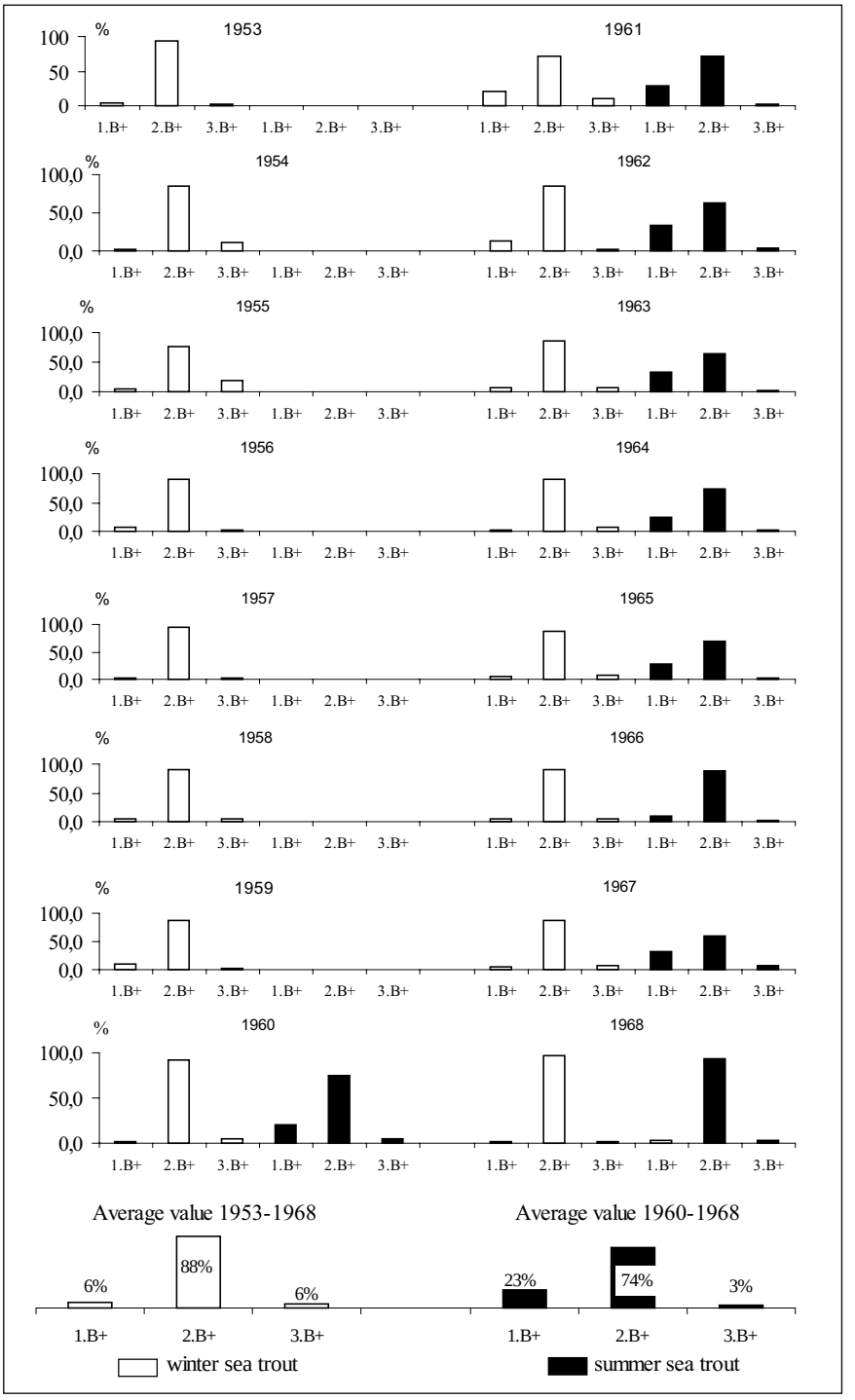

Fig. 1. Age distributions of winter and summer sea trout during the period of life in the river based on sampling data from 1953 to 1968

Age structure of sea trout during the period of sea life

Figure 2 presents the frequency of occurrence of specimens aged A.0^+, A.1^+, A.2^+.... in the samples from 1953 to 1968, where A describes the arbitrary age of the fish in the river before smolt migration to the sea.

The period of time which the fish spent in the sea was more differentiated than that in the river. Before beginning the spawning migration, the fish inhabited the sea for a period of between one to six trophic seasons. Although varied over the years, the most abundant age group was comprised of specimens which had undergone two or three growth phases in the sea; in the winter stock its frequency varied from 12.5% to 90% for sea trout aged A.1+ and from 9% to 84% for sea trout aged A.2+. In samples of summer sea trout, specimens which had been through two sea growth periods (A.1+) constituted, on average, 25%; their frequency in subsequent years varied from 0% in 1960 to 50% in 1968. Summer sea trout aged A.2+ dominated and they constituted from 47% to 83% in samples from subsequent years. Again, such high variations must have been the result of fluctuations in generation abundance.

The frequency of occurrence of specimens which had reached the age of A.3+ in the sea was, on average, 3.5% in the samples of winter sea trout. For summer sea trout this number was 13.2%. Fish aged A.4+ and A.5+ were very rare in both stocks. Fish aged A.0+, i.e. those returning to the river after less than one year in the sea, were very sporadic and occurred only in the winter stocks, constituting 0.2%, on average (Fig. 2).

The average distributions of fish age in the sea varied significantly between the winter and summer stocks. Using the two tests described above, the following results were obtained: df = 5, $\chi^2 = 175$, $P_{(\chi^2)} = 0.0000$; $\lambda = 7.86$ and $P_{(\lambda)} = 0.0000$.

Fish which repeated spawning

Figure 3 illustrates the percentage of specimens from both winter and summer runs with spawning marks on their scales. In all the samples, fish which had repeated spawning migration constituted from 0% to 5.1% and from 0% to 3.2% among winter and summer sea trout, respectively. A total of 43 specimens of winter sea trout with spawning marks on their scales were found in samples collected between 1953 and 1968 (an average of 1.3%). In samples of summer sea trout which were collected between 1960 and 1968, a total of 13 specimens were found with spawning marks on their scales (an average of 1.1%, Figure 3).

By analyzing the position of spawning marks in the pictures of the scales, it was confirmed that over 70% of the specimens first spawned at the age of A.2^+ and rejoined the next spawning run at the age of A.3^+. About 25% of the fish first spawned at the age of A.3^+ and started the next spawning migration the following year at the age of A.4^+. Only a small group of winter sea trout which spawned at the age of A.3^+ undertook the spawning migration at the age of A.5^+, i.e. after a longer interval.

Verification of sample representativeness using catch statistics

It has been mentioned that the numbers of fish in the samples were not proportional to the numbers of fish caught (Table 1). Therefore, it was assumed, as in Jokiel and Backiel (1960), that the annual catch fluctuation reflects changes in the numbers of specimens in the stock and the age structure in the samples was recalculated according to the magnitude of catches.

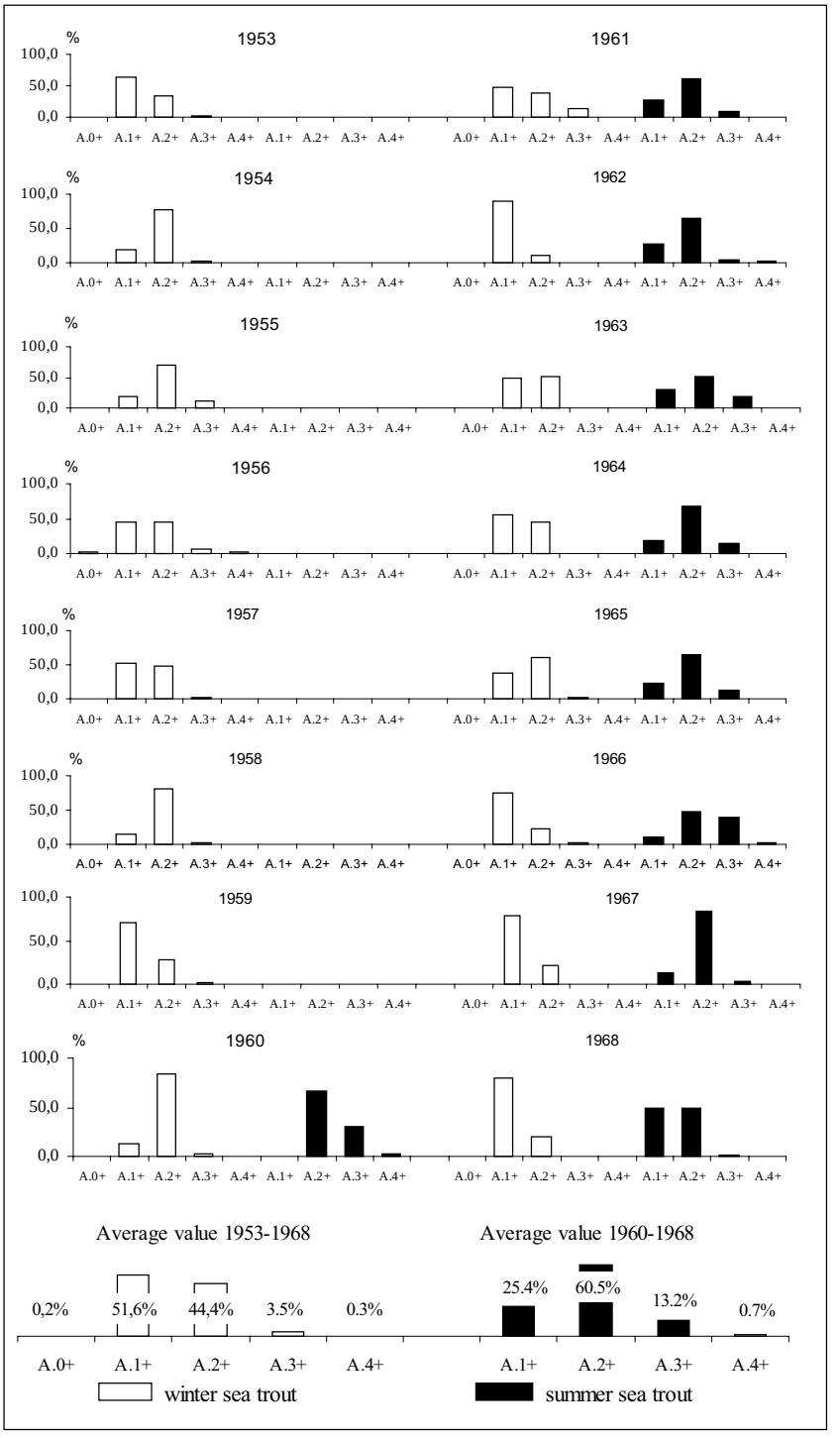

Fig. 2. Age distributions of winter and summer sea trout during the period of life in the sea based on sampling data from 1953 to 1968

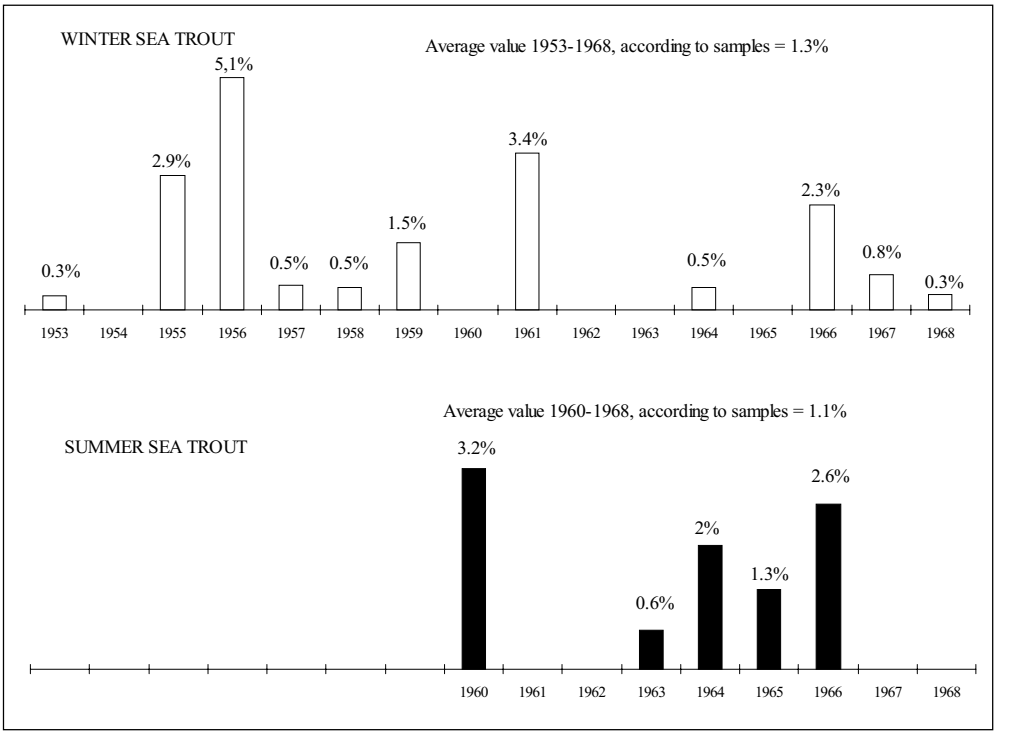

Fig. 3. Fish which repeated spawning in winter and summer sea trout samples from 1953 to 1968

Figures 4 and 5 present the catches of winter and summer sea trout divided into age groups in the river. The data from Figure 1 and Table 1 were used and the following formula was applied:

$$N_i \cdot u_{i\mathrm{A}} = N_{i\mathrm{A}} \quad [1]$$

where:

N_i – the number of winter or summer sea trout in catches in a particular year (i) using data from Table 1,

$u_{i\mathbf{A}}$ – the frequency of winter or summer sea trout aged 1.B+, 2.B+, 3.B+ in sample from year (i) using data from Figure 1,

$N_{i\mathrm{A}}$ – the number of sea trout aged 1.B+, 2.B+, 3.B+ in catches from year (i).

Frequencies ($u_{i\mathrm{A}}$) are percentages from Figure 1 divided by 100.

Figures 6 and 7 present the catches from Table 1 which were recalculated by using the age structure data of winter and summer sea trout inhabiting the sea. The calculations were made using the following formula:

$$N_i \cdot u_{i\mathrm{B}} = N_{i\mathrm{B}} \quad [2]$$

where:

N_i is as in formula [1],

$u_{i\mathrm{B}}$ – the frequency of winter or summer sea trout of age A.1+, A.2+, A.3+…in a sample from year (i) according to Figure 2,

$N_{i\mathrm{B}}$ – the number of Vistula sea trout specimens aged B+ from year (i).

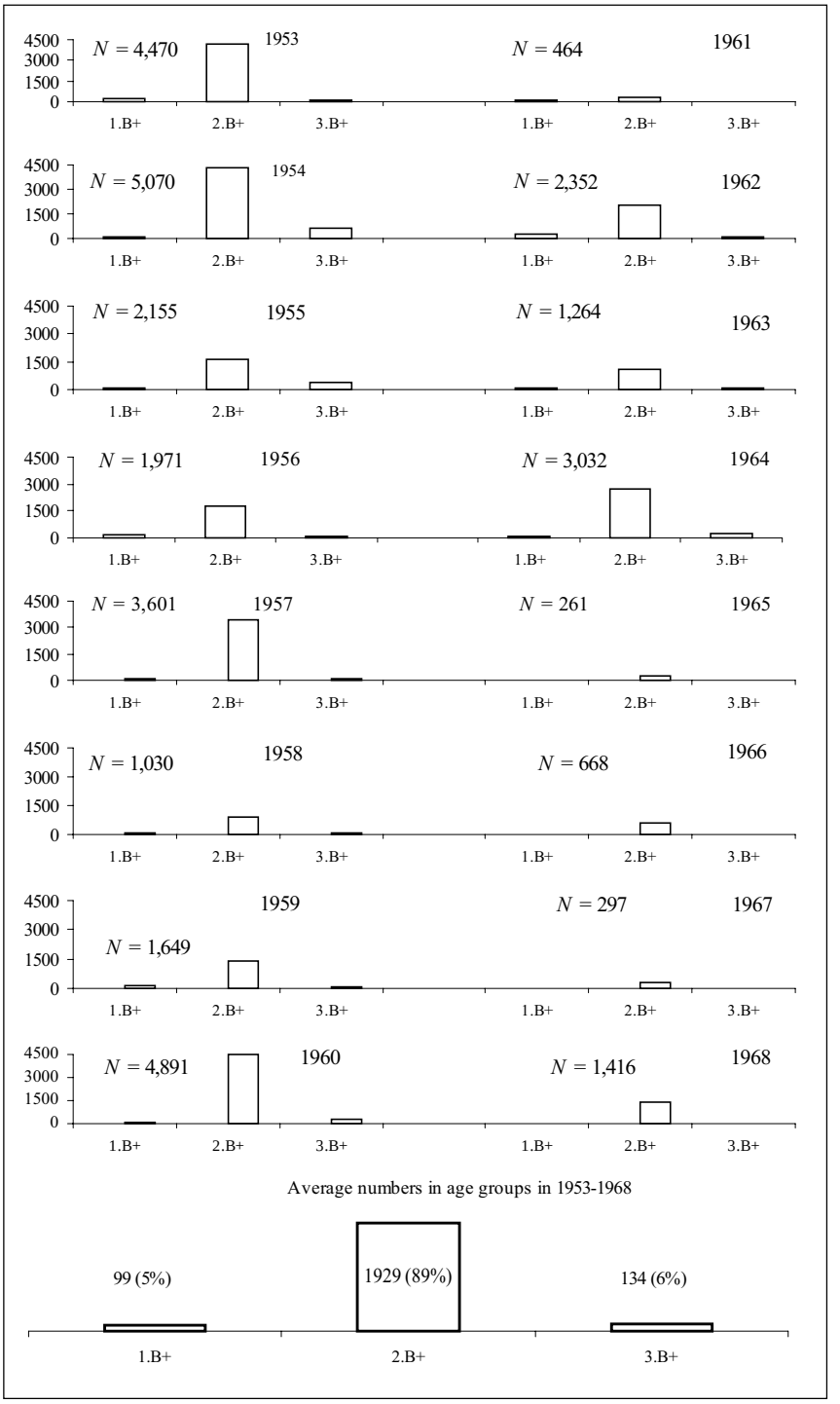

Fig. 4. Catches of winter sea trout from 1953 to 1968, divided into age groups 1.B+, 2.B+, 3.B+ (in numbers)

Similarly, Figure 8 presents the number of fish from the annual spawning run of winter and summer sea trout which repeated the spawning migration. The percentage of fish with spawning marks in samples was recalculated according to the catches, using the following formula:

$$N_i \cdot u_{i\mathrm{SM}} = N_{i\mathrm{SM}} \qquad [3]$$

where:

N_i is as in formula [1],

$u_{i\mathrm{SM}}$ – the frequency of winter or summer sea trout with spawning mark SM according to Figure 3,

$N_{i\mathrm{SM}}$ – the number of sea trout with spawning marks in catches from year (i).

The average distributions of winter and summer sea trout age in the river was compared for many years using data obtained from both samples (Figure 1) and catches (Figures 4 and 5). It was revealed that data obtained from samples which describe the age structure of sea trout in the river do not differ significantly from those which were obtained from catch statistics. This also holds true for the average of many years' data regarding the age structure of summer sea trout inhabiting the sea (Figures 2 and 7). The Kołmogorow-Smirnow test proved that the differences between distributions were coincidental: values of λ ranged from 0.2 to 0.5; $P(\lambda) > 0.05$, which means that the samples were satisfactorily representative. However, significant differences occurred between the results obtained from samples and catches with respect to the age structure of winter sea trout inhabiting the sea and which were obtained over a period of many years (Figures 2 and 6). The comparison of age distributions using the Kołmogorow-Smirnow test led to the following results: $\lambda_{\mathrm{emp.}} = 3.7$; $P_{(\lambda=3.7)} = 0.0000$. Therefore, it would be more appropriate to turn these data into catches, as is done in the bottom part of Figure 6.

Recruitment to the sea of summer and winter sea trout smolt

The magnitude of recruitment was expressed by the number of adult specimens originated from the smolt groups which migrate to the sea in subsequent years. Therefore, it was an indicative measure determined from the catches and fish age structure which illustrated the recruitment strength and its relative changes.

Figures 9 and 10 illustrate the abundance of fish caught during their spawning migration but which were classified with the smolt groups that had descended the Vistula in subsequent years between 1952 and 1965 or between 1959 and 1965 for the winter or summer stocks, respectively. The procedure of data choice and combination is presented in Figure 11; however, only fish of the most abundant age groups in the sea, i.e. $A.1^+$, $A.2^+$, $A.3^+$, were included. Therefore, the recruitment in 1952 was reflected by the abundance of age group $A.1^+$ in catches from 1953, $A.2^+$ in catches from 1954 and $A.3^+$ in catches from 1955. The abundance of fish aged $A.1^+$ from catches in 1954, $A.2^+$ from catches in 1955 and $A.3^+$ from catches in 1956 characterized the strength of smolt recruitment to the sea in 1953, etc. Indicators of annual recruitment of each sea trout stock (columns in Figures 9 and 10) were derived by summing the numbers of fish of particular sea age using data from Figures 6 and 7.

The comparison of Figures 9 and 10 shows that the indicator of smolt recruitment in the winter stock varied more than in the summer stock. The minimum recruitment of winter sea trout in 1964 in ratio to the maximum recruitment in 1952 was 1:30; the summer sea trout

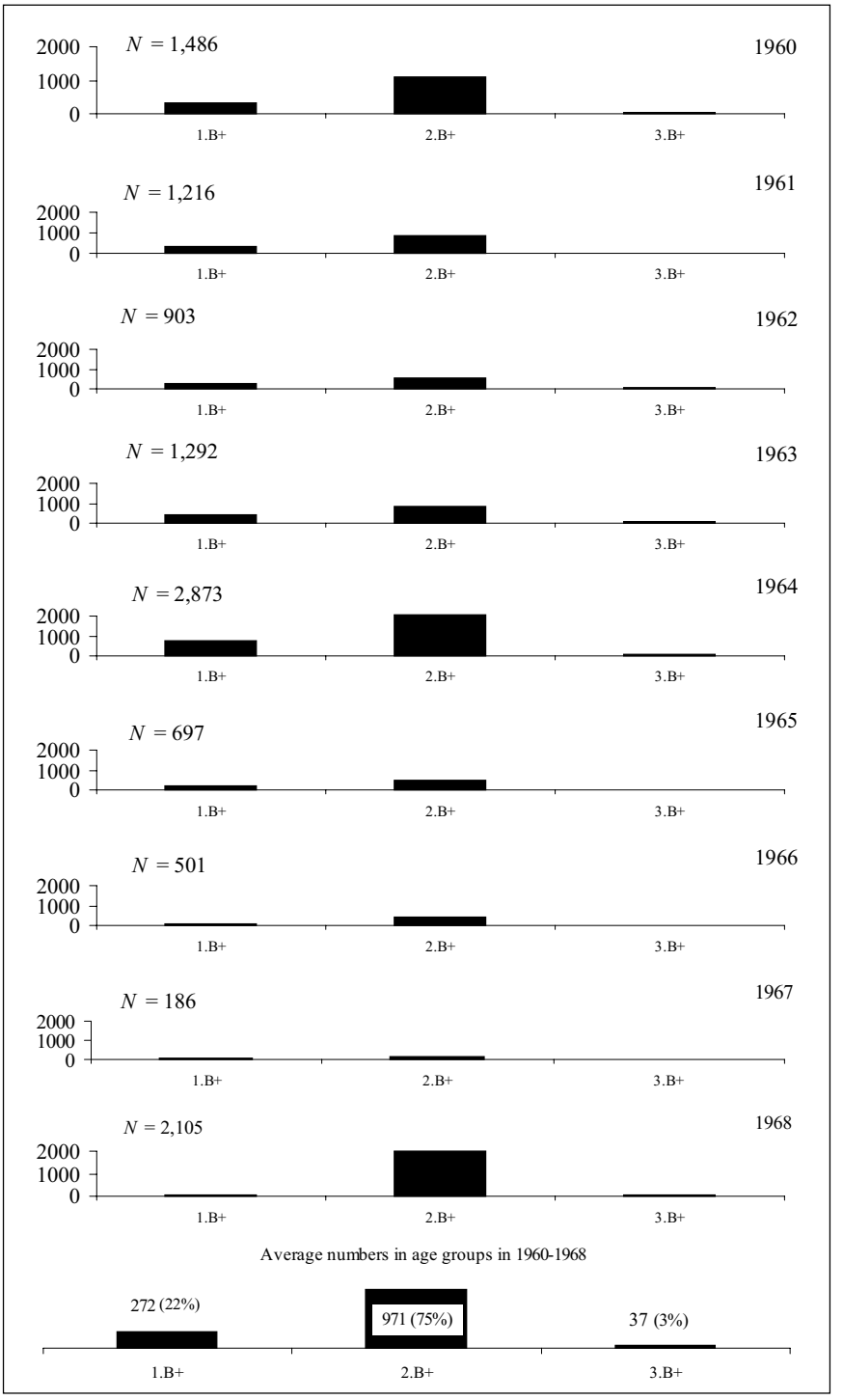

Fig. 5. Catches of summer sea trout from 1960 to 1968, divided into age groups 1.B+, 2.B+, 3.B+ (in numbers)

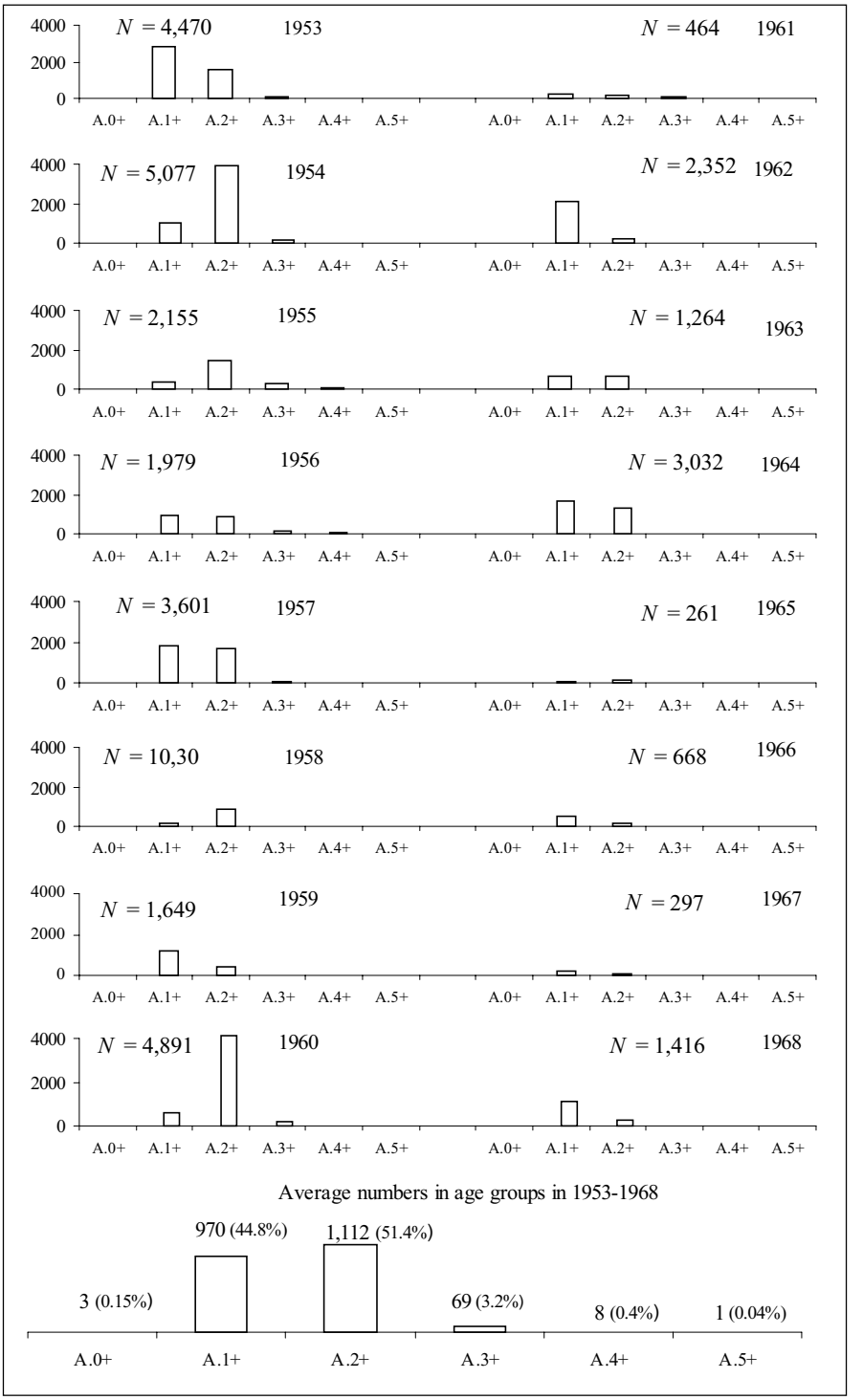

Fig. 6. Catches of winter sea trout from 1953 to 1968, divided into age groups A.1+ to A.5+ (in numbers)

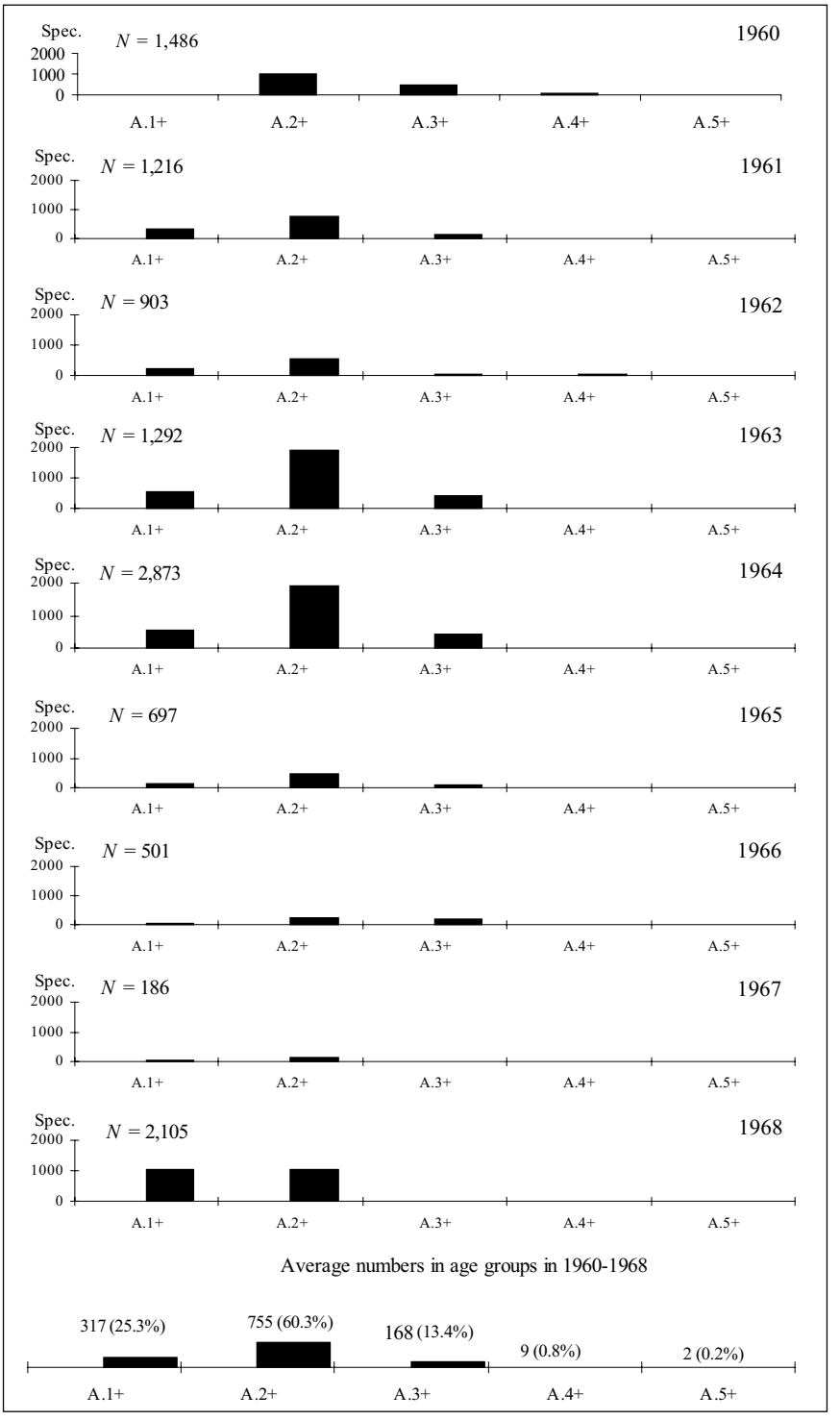

Fig. 7. Catches of summer sea trout from 1960 to 1968, divided into age groups A.1+ to A.5+ (in numbers)

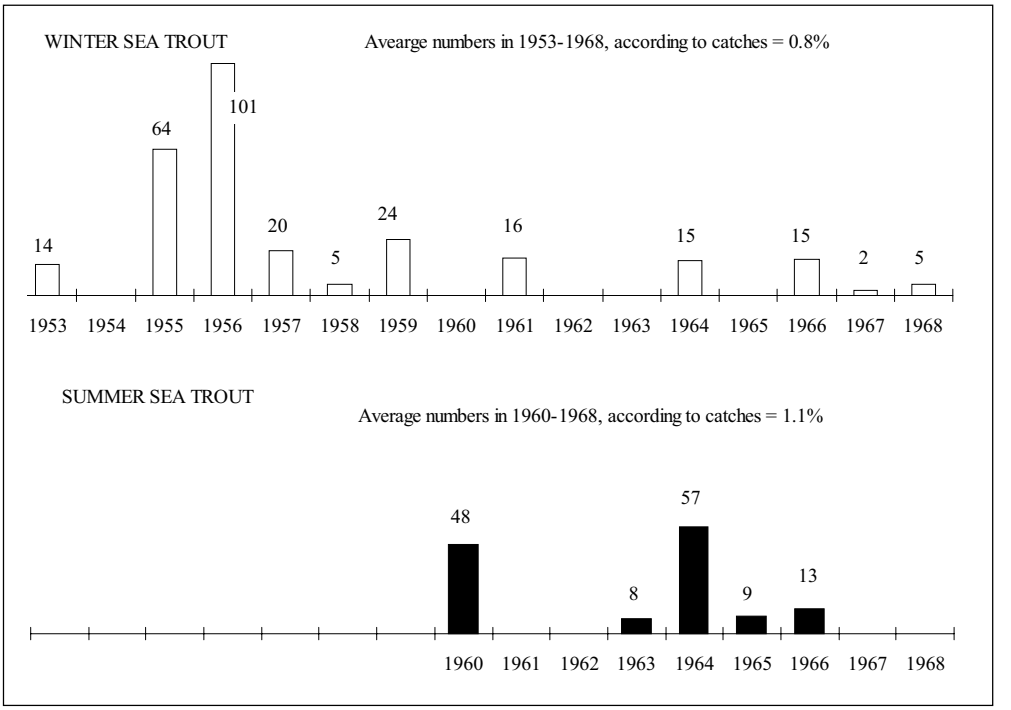

Fig. 8. Numbers of fish which repeated spawning in winter and summer sea trout catches from 1953 to 1968

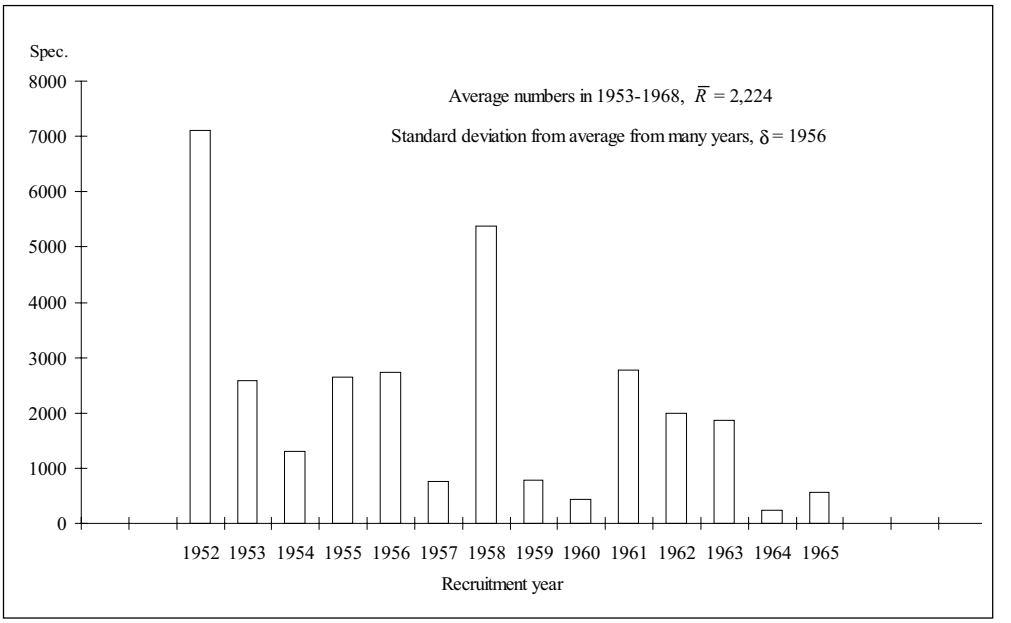

Fig. 9. Catches of winter sea trout aged A.1$^+$, A.2$^+$ and A.3$^+$ from subsequent years of smolt recruitment from 1952 to 1965

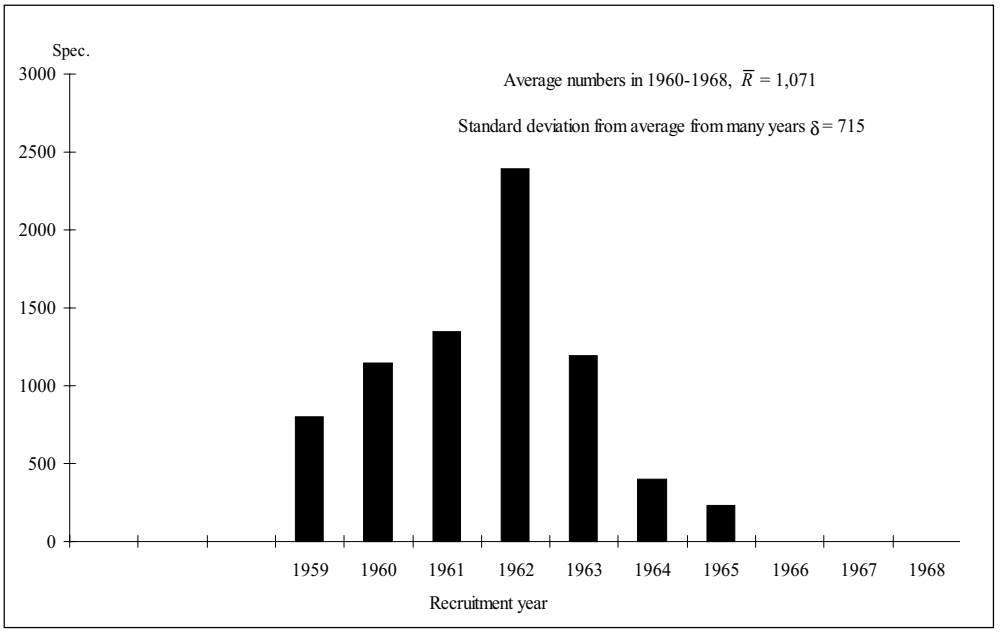

Fig. 10. Catches of summer sea trout aged A.1$^+$, A.2$^+$ and A.3$^+$ from subsequent years of smolt recruitment from 1959 to 1965

recruitment minimum from 1965 in ratio to the maximum from 1962 was 1:10. In addition, the percentage variability coefficient (V %) was determined from:

$$V\,\% = \frac{100 \cdot \delta}{\overline{R}}$$

where:

$\overline{R}$ – the average recruitment strength of smolt during the investigations,

δ – the standard deviation from the average over a period of many years (data from Figures 9 and 10). The percentage variability coefficient was equal to 88% for winter sea trout and 67% for summer sea trout.

Such a significant variability in smolt recruitment resulted from the appearance of numerous births, especially in the year $t - 2$ (t – recruitment year), since the majority of fish reached the smolt stage at the age of A = 2. The strong recruitment of winter sea trout smolts in 1952 (Figure 9) resulted from the highly abundant generation of fish which was born in 1950, i.e. the generation from the 1949 fall spawning. This highly abundant generation influenced the catches in subsequent years. For example, high catches of winter sea trout in 1953 and 1954 were the result of numerous smolt recruitment in 1952 and the subsequent return to the river of the most abundant fish generation of ages 2.1$^+$ in 1953 and 2.2$^+$ in 1954.

The indicator of summer sea trout smolt recruitment to the sea (Figure 10) increased gradually in subsequent years to reach its maximum in 1962, after which it continuously decreased. Here, the strong smolt recruitment in 1962 could have resulted from a high number of

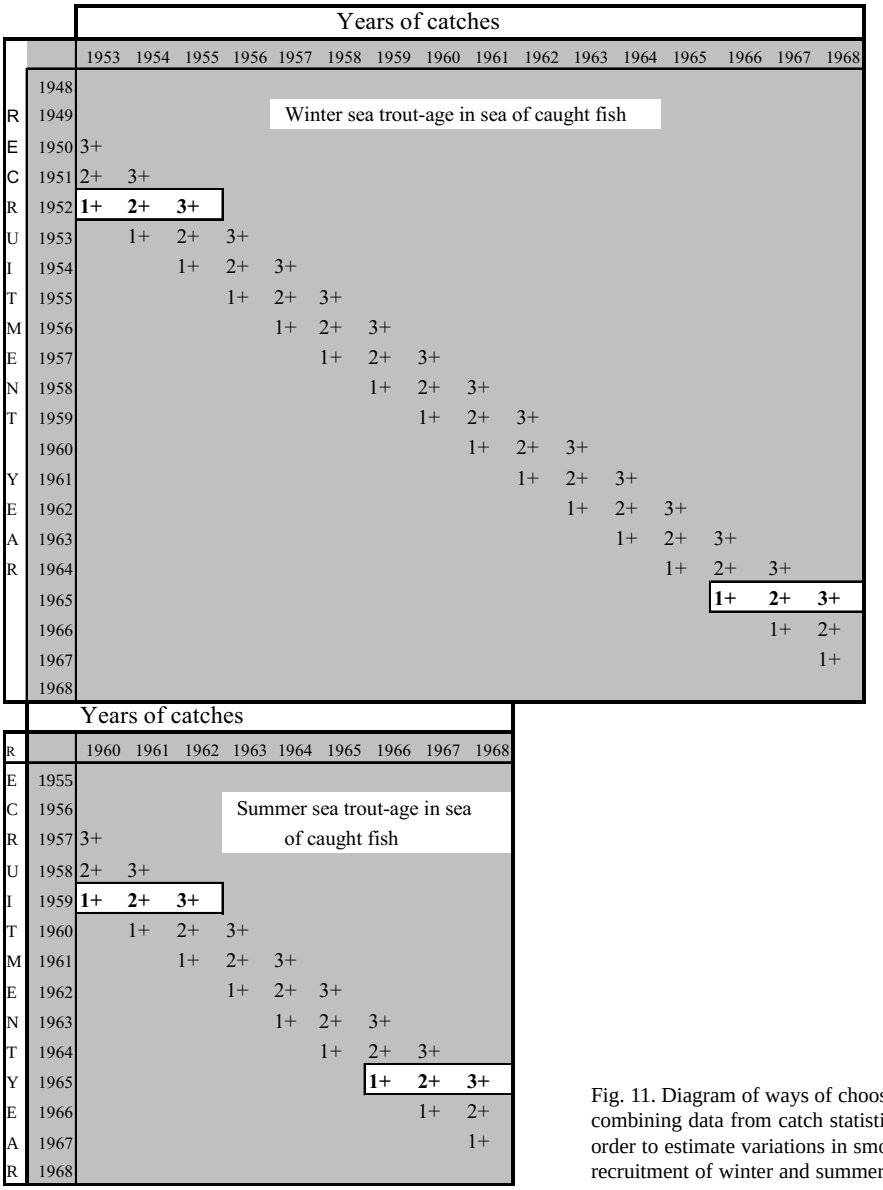

Fig. 11. Diagram of ways of choosing and combining data from catch statistics in order to estimate variations in smolt recruitment of winter and summer sea trout

births in 1960. It later influenced the catches in 1964 when the most numerous summer sea trout aged 2.2^{+} returned to the river for spawning. Four years later, this strong stock, which returned for spawning in 1964, produced another abundant generation which resulted in an abundant age group $A.1^{+}$ in the catches in the summer of 1968. After 1962, recruitment decreased (Figure 10), which is reflected by the small catches in 1967 and 1968.

The search for relationships between the abundance of births, recruitment and spawning stocks was possible due to the availability of data from many years. Figures 1, 2, 9 and 10 present the age structure and recruitment strength and Table 1 provides information regarding catches.

DISCUSSION

Age structure is one of the features which describes the population. In order to characterize a population of anadromous fish species, such as sea trout, it is important to know the age at which the fish leave the freshwater environment in the smolt stage and the number of trophic seasons it must spend in the sea to grow and mature before the spawning migration. According to the scale reading of adult Vistula sea trout, most of them spent two years in the river before they reached the sea (88% of specimens from the winter stock and 74% from the summer stock – Figure 1). This tendency was also observed in previous investigations (Dixon 1931 and Chrzan 1947). Only about 6% of the fish in the winter stock reached the smolt stage in less or more than two years. Specimens which had lived in the river for one year occurred more often in the summer sea trout. In some years they might have even constituted almost one third of the fish stock (Figure 1).

Fish of both seasonal stocks began their spawning migration most often after three, or less frequently, after two trophic seasons in the sea. However, the winter sea trout from the A.2+ and A.3+ age groups dominated alternatively from year to year; while, as a rule, summer sea trout aged $A.2^+$ dominated and constituted 60.3 % of the stock, on average (Fig. 7). Fish from both stocks which inhabited the sea for a period shorter than one year or longer than four years constituted a very small percentage; 0.2% of fish aged $A.0^+$ and slightly more than 0.4% of fish aged $A.4^+$ and $A.5^+$ were found among winter sea trout. No summer sea trout aged $A.0^+$ was found, while fish which had completed five or more trophic seasons constituted about 1% of the summer stock.

The summer sea trout had a tendency to achieve the smolt stage earlier and to start spawning migration after a longer stay in the sea. The origin of these differences may be found in the well-known biological regularities of salmon and sea trout, such as a normal relationship between body growth and development rate and the inverse relationship between the age at the smolt stage and the age of fish in the sea before maturity (Christensen and Larsson, 1979, Domagała 1986).

The mortality of fish after spawning was significant since, in both stocks, there was a similarly small percentage (about 1%) of fish which repeated spawning. Most often these fish began a second spawning migration the year following one trophic season spent in the sea, and only a few specimens of winter sea trout returned to the river for a second spawning after a longer interval.

It is a well-known fact that the abundance of a particular generation of salmonids is determined by the abundance of the parent stock. The character of generation fluctuations is shaped in a specific way under natural conditions and the amplitude of these fluctuations is connected with the complexity of the population structure, among other factors (Semko 1951, Monastyrskij 1952). Stocks with a complex structure are more stable. Perhaps this is one of the reasons why the winter sea trout, whose age structure did not change significantly in subsequent years, was more susceptible to environmental and anthropogenic pressure.

It was confirmed that the variability of Vistula sea trout smolt recruitment to the sea was significant over a period of many years and it also differed between the stocks. The coefficient of variation of smolt recruitment was 88% for winter sea trout and 67% for summer sea trout; the minimum to maximum ratio of this recruitment was three times higher for winter sea trout than it was for summer sea trout. These estimations were made using the relative coefficient in which the recruitment magnitude in a particular year was reflected as the size of the catches which followed. Similarly, Jokiel and Backiel (1960) thought that the sea trout catch rate in the Vistula River may have been a measure of migrating stock abundance.

These kinds of measures and indicators are based on the assumption that differences in the abundance of generations are created in an early period of the fish life cycle and that natural mortality (M_i) and fishing intensity (F_i) do not influence it significantly later (i-years after smolt recruitment). This assumption is proved in this paper. The minimum to maximum ratio of the recruitment indicator was 1:30. Neither population parameters nor exploitation parameters vary to such an extent. On the other hand, the analysis of age structure changes strongly indicated patterns which resulted from fluctuations in abundance of parent and offspring generations.

In this paper, terms such as *stock* and *population* refer to groups of specimens within one species which come together in terms of time and space in order to begin the reproductive migration. These terms are equivalent with the *spawning run* which, however, has a less structural than functional meaning connected with the movement of fish. This understanding of the concepts mentioned is not in discrepancy with definitions given by Trojan (1977).

In an earlier paper, the author presented the history of research on the differentiation of Vistula sea trout into winter and summer stocks (Borzęcka, 1988). The most important population features, such as the age structure, the number of specimens which repeat spawning and the strength of smolt recruitment to the sea, are described in this paper. Management and breeding procedures and, especially, protection and restitution projects which concern the original Vistula sea trout, must take into consideration the characteristics of the former stocks.

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Primary production in the southern Baltic Sea determined from photosynthetic light curves

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Abstract. This work presents photosynthetic light curves for phytoplankton of the southern Baltic Sea. The seasonal variability of phytoplankton assimilation numbers is described using the following formula: $AN_B = 3.54 - 1.83 \cdot \sin(\omega \cdot x + 0.79) + 0.32 \cdot \sin(2\omega \cdot x + 0.88)$. The application of parameters of the photosynthetic light curve, results of measurements of chlorophyll concentration, attenuation coefficient for scalar irradiance and the dose of PAR irradiation measured directly below the water surface to calculate primary production is presented. The results obtained are compared with the *in situ* measurements of the primary production. The correlation of results obtained from *in situ* measurements and based on calculations using the photosynthetic light curve is good. The mean assimilation numbers determined were used to calculate the average primary production in the Gdańsk Deep and the Bornholm Deep, which are, respectively, 133 and 102 g C $\cdot$ m^{-2} $\cdot$ year^{-1}.

Key words: primary production, assimilation number, photosynthetic light curve, southern Baltic

INTRODUCTION

Photosynthesis is one of the fundamental processes determining the oxygen and carbon balance on Earth (Li and Maestrini 1993). Investigations of primary production, and especially its measurement, are very tedious, difficult and time consuming (Platt and Sathyendranath 1993). Methods of primary production investigation, are often the subject of controversy among experts and the results obtained from various methods are not always comparable (Richardson 1991, Williams 1993, Nixdorf 1998). The most common methods for estimating primary production are based on measurements using *in situ* incubation (Steemann Nielsen 1952). However, such methods are very time consuming and they are also very costly in the case of marine investigations carried out from large ships, since these research vessels must stay in one place for long periods. Attempts to simplify methods of primary production measurement have been underway for many years. Special focus has been put on the replacement of time consuming and costly *in situ* incubation by employing an incubator which would allow for the incubation of phytoplankton to take place as the vessel is sailing (Steemann Nielsen 1958, Ryther (1956). This type of incubation, under simulated conditions, allows for the determination of the photosynthetic light curve which serves as the basis for precise calculations of the assimilation number and irradiation of saturation. The photosynthetic light curves which are determined in the incubator may be used in modeling biological production in the marine environment (Baretta *et al.* 1995, Tilzer *et al.* 1993, Lohrenz 1993).

The aim of this work is to enlarge the data base of photosynthetic light curves of Baltic phytoplankton (Renk and Ochocki 1998) and to utilize data to determine primary production. The results of *in situ* measurements of primary production are compared with the results obtained from calculations in which the photosynthetic light curves and certain environmental measurements, such as irradiance, light attenuation coefficient in the water and the chlorophyll *a* concentration were employed.

MATERIALS AND METHODS

The experiments were carried out at several stations on the southern Baltic, the co-ordinates of which are presented in Table 1.

Two types of measurements of primary production using the same radio-isotope method were used (Steemann Nielsen 1952):

1. measurement of primary production in an incubator in order to determine the photosynthetic light curves

2. *in situ* measurements of primary production in order to determine the real diurnal primary production

The incubation of phytoplankton from a depth of 2.5 m was carried out in an incubator in 50 cm^3 glass bottles for two hours. The *in situ* measurements of primary production were carried out in 100 cm^3 glass bottles for four hours, approximately around noon when possible, at the following depths: 0.5; 2.5; 5; 10; 15 and 20 m.

In order to illuminate the incubator, a set of fluorescent lamps (Philips 18W) was used. This setup provided a constant irradiance at 250 $kJ \cdot m^{-2} \cdot h^{-1}$. A system of filters and mirrors was used in order to obtain the correct irradiance. As a result, the following irradiance values were obtained (PAR): 435, 186, 124, 62, 37 and 2.5 $kJ \cdot m^{-2} \cdot h^{-1}$. A thermostat controlled the water temperature in the incubator to maintain the temperature from which the sample was collected.

In both types of incubation a carbon isotope ^{14}C was used in the form of an $NaHCO_3$ water solution, with an activity of 150 kBq per sample of incubated water (Steemann-Nielsen 1952, 1965a). The activity of phytoplankton samples after incubation was measured with liquid scintilation counter – Beckman 6000 IC (Aertebjerg-Nielsen and Bresta 1984).

The inorganic carbon in the water was determined by measuring the pH of water before and after acidification with 0.01n HCl at a ratio of 1:4 (BMEPC 1988).

Table 1. Location of measuring stations in the southern Baltic

		Position		
Station	Region	N	E	Depth [m]
P_1	Gdańsk Deep	54°50’	19° 20’	109
P_5	Bornholm Deep	55° 15’	15°19’	91
P_{140}	Gotland Deep	55° 33’	18° 24’	90
P_{16}	Ustka Region	54° 38’	16° 48’	20
ZN_2	Gulf of Gdańsk	54° 23’	18° 57.5’	15
SF	Słupsk Furrow	55° 20’	18° 00’	78
SK	Pomeranian Bay	53° 59’	14° 30’	11

The chlorophyll *a* concentrations were determined using the fluorometric extraction method using an 90% acetone solution and 24 hour pigment extraction in the dark at a temperature of approximately 4°C (Evans *et al*. 1987).

Mathematical formulae

Mathematical description of the dependence of the photosynthesis rate on irradiance

In order to determine the light characteristics of phytoplankton photosynthesis, the parameter – photosynthetic rate P_h is applied, which describes the ratio of primary production per hour PP_h to chlorophyll *a* concentration *Chl*:

$$P_h = \frac{PP_h}{Chl}$$

The photosynthesis rate P_h depends on many environmental factors, which usually change significantly during the investigations. The photosynthetic rate also depends on irradiance. A typical dependence of the photosynthetic rate on irradiance is presented in Figure 1. The highest photosynthetic rate occuring at the irradiance of saturation (Yentsch and Lee, 1966) is called assimilation number AN_{exp} (Parsons and Takahashi, 1973; Platt and Gallegos, 1980)*. Its experimental derivation is usually done with discrete values of irradiance. Therefore, this method does not allow for the precise determination of the assimilation number since the result of measurements of the maximum photosynthesis rate are not available. The values of irradiances as well as the assimilation numbers, accepted in this way are approximate values. More precise values of the irradiance of saturation and more precise assimilation numbers can be obtained by means of plotting the photosynthetic light curves, i.e. the dependence of the photosynthesis rate on irradiance, which is described by a particular mathematical formula.

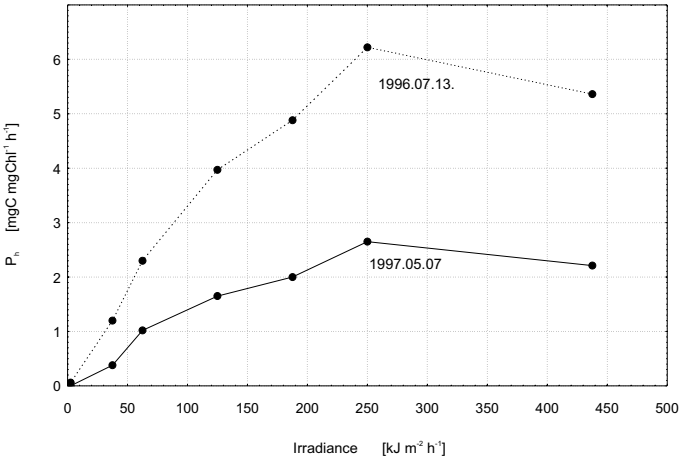

Fig. 1. Dependence of photosynthesis rate – P_h on irradiance – E in water collected from a depth of 2.5 m in the Gdańsk Deep

Many models which describe the dependence of the photosynthetic rate on irradiance can be found in the literature (Vollenweider, 1965; Platt *et al.,* 1977, Woźniak *et al*. 1989). The results of investigations of the dependence of the photosynthetic rate on irradiance in the Baltic

*Sometimes the assimilation number is defined as the daily primary production per unit of chlorophyll *a* [mg C · mg Chl^{-1} · day^{-1}] (Bannister and Laws, 1980, Woźniak, 1987, Woźniak *et al*., 1989).

Sea are best described by the equation proposed by Steele, (1962) for the North Sea (Renk, 1983, Renk and Ochocki, 1998), which is as follows:

$$P_h = AN \cdot \frac{E}{E_s} \cdot \exp(1 - \frac{E}{E_s}) \qquad [1]$$

where: P_h – photosynthetic rate expressed as the ratio of the primary production in one hour and the chlorophyll *a* concentration, $\left[\frac{mgC}{mgChl \cdot h}\right]$

E – irradiance [kJ . m^{-2} . h^{-1}] (photosynthetically available radiation – PAR)

AN and E_s – constants. AN $\left[\frac{mgC}{mgChl \cdot h}\right]$, E_s [kJ · m^{-2} · h^{-1}]

The physical sense of coefficients AN and E_s can be explained by the derivation of the function extreme [1] as follows: E_s denotes irradiance at which the photosynthesis rate is the highest (the so-called irradiance of saturation); it can be regarded as the optimum irradiance for photosynthesis, while AN is the maximum photosynthetic rate, i.e. the assimilation number. The AN value describes the real maximum of the function (function extreme) $P_h = f$ *(irradiance)* unlike the value of AN_{exp}, which describes the measured photosynthetic rate at the irradiance, which is regarded as optimum.

Primary production at a particular depth

To calculate the primary production on a given depth equation [1] has been employed. In this equation the scalar irradiance in the water column decreases with depth. In order to simplify the calculations it is assumed that the light attenuation coefficient in the water does not depend on depth. Thus, since the irradiance just below the water surface is $E(0)$, irradiance changes due to depth can be expressed as follows:

$$E(z) = E(0) \cdot \exp(-k \cdot z) \qquad [2]$$

where: $E(0)$ – irradiance just below the sea surface

k – diffuse attenuation coefficient for scalar irradiance.

Using formula [1] the photosynthetic rate at depth z can be expressed as follows:

$$P_h(z) = AN \cdot \frac{E(0) \cdot \exp(-k \cdot z)}{E_s} \cdot \exp\left[1 - \frac{E(0)}{E_s} \cdot \exp(-k \cdot z)\right] \qquad [3]$$

In formula [3] $E(0)$ is a function of time. For simplicity, it is assumed that changes of irradiance during the standard day can be described by the function introduced by Vollenweider (1965):

$$E(t) = \frac{E_m}{2}(1 + \cos\frac{2 \cdot \pi \cdot t}{\lambda}) \qquad [4]$$

where: t – time measured since noon, i.e.: $-\frac{\lambda}{2} \le t \le \frac{\lambda}{2}$,

E_m – maximum irradiance at noon,

λ – length of day, in hours.

In order to calculate the maximum irradiance below the sea surface at noon $E_m(0)$, a daily dose of solar radiation η_d transmitted through sea surface PAR was used (taken into consideration the transmitance across the sea surface – Dera 1995). Integrating formula [4] over a whole day (from $-\frac{\lambda}{2}$ to $\frac{\lambda}{2}$), the daily dose of solar radiation is obtained as follows:

$$\eta_d = \int_{-\frac{\lambda}{2}}^{\frac{\lambda}{2}} \left(\frac{E_m(0)}{2} (1 + \cos \tfrac{2\cdot\pi\cdot t}{\lambda} \right) dt \qquad [5]$$

Integration leads to: $\eta_d = \frac{E_m(0)\cdot\lambda}{2}$ thus

$$E_m(0) = \frac{2\cdot\eta_d}{\lambda} \qquad [6]$$

Combining formulae [6] and [4] results in:

$$E(t) = \frac{\eta_d}{\lambda}(1 + \cos\frac{2\cdot\pi\cdot t}{\lambda}) \qquad [7]$$

Irradiance at depth „ z” as a function of time is expressed as follows:

$$E(z,t) = \frac{\eta_d}{\lambda}\cdot\exp(-k\cdot z)\cdot(1+\cos\frac{2\cdot\pi\cdot t}{\lambda}) \qquad [8]$$

In order to obtain the photosynthetic rate at time t and at depth z formulae [3] and [7] must be combined:

$$P_h(z,t) = AN\cdot\frac{\eta_d\cdot\exp(-k\cdot z)\cdot(1+\cos\frac{2\cdot\pi\cdot t}{\lambda})}{\lambda\cdot E_s}\cdot\exp\left[1-\frac{\eta_d\cdot\exp(-k\cdot z)\cdot(1+\cos\frac{2\cdot\pi\cdot t}{\lambda})}{\lambda\cdot E_s}\right] \qquad [9]$$

The primary production at depth z is obtained by multiplying formula [9] by chlorophyll *a* concentration.

$$PP_h(z,t) = AN\cdot Chl\cdot\frac{\eta_d\cdot\exp(-k\cdot z)\cdot\left(1+\cos\frac{2\cdot\pi\cdot t}{\lambda}\right)}{\lambda\cdot E_s}\cdot\exp\left[1-\frac{\eta_d\cdot\exp(-k\cdot z)\cdot\left(1+\cos\frac{2\cdot\pi\cdot t}{\lambda}\right)}{\lambda\cdot E_s}\right] \qquad [10]$$

Primary production under the area of one square meter

Primary production (in time unit) in the water column which stretches from the sea surface to depth H can be obtained by the integration of formula [10] over depth z from 0 to the limit of the euphotic layer H:

$$Prod_h = \int_0^H AN \cdot Chl \cdot \frac{\eta_d \cdot \exp(-k \cdot z) \cdot \left(1 + \cos\frac{2 \cdot \pi \cdot t}{\lambda}\right)}{\lambda \cdot E_s} \cdot \exp\left[1 - \frac{\eta_d \cdot \exp(-k \cdot z) \cdot \left(1 + \cos\frac{2 \cdot \pi \cdot t}{\lambda}\right)}{\lambda \cdot E_s}\right] dz \qquad [11]$$

The daily primary production $Prod_d$ in the water column can be obtained by integrating formula [11] over time from sunrise to sunset, i.e. from $-\frac{\lambda}{2}$ to $\frac{\lambda}{2}$.

$$Prod_d = \int_{\frac{-\lambda}{2}}^{\frac{\lambda}{2}} \int_0^H AN \cdot Chl \cdot \frac{\eta_d \cdot \exp(-k \cdot z) \cdot \left(1 + \cos\frac{2 \cdot \pi \cdot t}{\lambda}\right)}{\lambda \cdot E_s} \cdot \exp\left[1 - \frac{\eta_d \cdot \exp(-k \cdot z) \cdot \left(1 + \cos\frac{2 \cdot \pi \cdot t}{\lambda}\right)}{\lambda \cdot E_s}\right] dz \cdot dt \qquad [12]$$

RESULTS

Photosynthetic light curves

The photosynthetic light curve for the Gdańsk Deep derived from formula [1] by means of the least squares method is presented in Figure 2. The coefficients in formula [1] for the open waters of the southern Baltic are presented in Table 2. It was revealed that photosynthetic light curves and thus coefficients AN and E_s in formula [1] vary in particular seasons (Fig. 3). The seasonal variability of the assimilation number is presented in Figure 4. The curve which describes changes of the assimilation number for the Gdańsk Deep, which was derived by means of the least squares method, can be presented by the following formula:

$$AN_{GD} = 3.63 - 2.30 \cdot \sin(2 \cdot \pi \cdot y + 0.70) + 0.69 \cdot \sin(4 \cdot \pi \cdot y - 0.45) \qquad [13]$$

where: y = time in years, (i.e. year + subsequent day divided by 365).

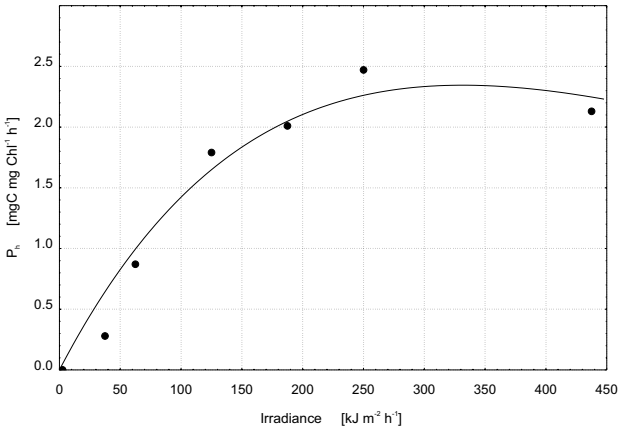

Fig. 2. Photosynthetic light curve derived from formula [1]; Gdańsk Deep, 23 April 1997

Table 2. Coefficients in formula [1] which describe the dependence of photosynthesis rate on irradiance

		AN	$AN_{\exp}$	E_s
Date	Station	$\left[\frac{mgC}{mgChl \cdot h}\right]$	$\left[\frac{mgC}{mgChl \cdot h}\right]$	$\left[\frac{kJ}{m^2 \cdot h}\right]$
25. 01. 98	SF	2.02	2.01	242.84
25. 01. 98	P_5	1.99	1.86	235.17
02. 02. 98	P_1	1.80	1.77	273.20
05. 02. 98	P_{140}	1.80	1.72	228.32
11. 11. 98	P_1	3.22	3.54	272.10
12. 11. 98	P_{140}	2.38	2.33	307.61
13. 11. 98	P_5	1.94	1.94	336.82
18. 03. 99	P_1	2.22	2.16	334.63
20. 03. 99	P_5	2.23	2.13	253.30
15. 04. 99	ZN_2	2.05	2.03	355.73
16. 04. 99	P_1	2.41	2.45	373.78
17. 04. 99	P_{140}	2.19	2.08	365.78
18. 04. 99	P_5	1.59	1.53	332.39
19. 04. 99	SK	2.13	2.04	290.43
20. 04. 99	P_{16}	2.93	2.75	343.21
11. 06. 99	P_5	5.35	4.48	517.67
12. 06. 99	P_{140}	2.36	2.55	295.07
13. 06. 99	P_1	3.18	3.64	277.17
18. 08. 99	P_1	7.60	5.73	718.61
18. 08. 99	ZN_2	7.90	5.40	886.29
19. 08. 99	P_{140}	6.83	4.70	860.86
20. 08. 99	P_5	9.47	7.47	662.87
20. 08. 99	P_{16}	8.75	7.81	520.31
5. 10. 99	ZN_2	3.13	3.12	304.04
8. 10. 99	P_5	5.95	5.77	390.42
18. 10. 99	P_{140}	3.48	3.42	326.90
20. 10. 99	P_1	5.03	4.93	406.57
3. 11. 99	P_1	2.60	2.57	263.21
4. 11. 99	ZN_2	4.08	3.99	332.67
11. 11. 99	P_1	6.58	7.52	270.19
12. 11. 99	P_{140}	3.73	3.81	258.39
13. 11. 99	P_5	3.28	3.12	251.67
13. 12. 99	ZN_2	2.70	2.53	282.28
14. 12. 99	P_1	4.61	4.53	230.21
15. 12. 99	P_{140}	4.00	3.86	256.10
16. 12. 99	P_5	3.44	3.54	265.98
16. 12. 99	P_{16}	2.18	2.14	221.22

The mean monthly assimilation numbers are presented in Table 3. The highest assimilation numbers were recorded in summer and early autumn, while the lowest numbers were noted in winter.

It was revealed that the average variations of coefficients AN and E_s for open Baltic waters, especially in the Bornholm Deep, the Gdańsk Deep and the southern part of the Gotland Deep (stations P_1, P_5 i P_{140}) do not exceed 20%. However, bay waters and coastal areas are characterized by spatially more differentiated assimilation numbers. Mean assimilation numbers were determined for open waters during each expedition. Seasonal changes of averaged

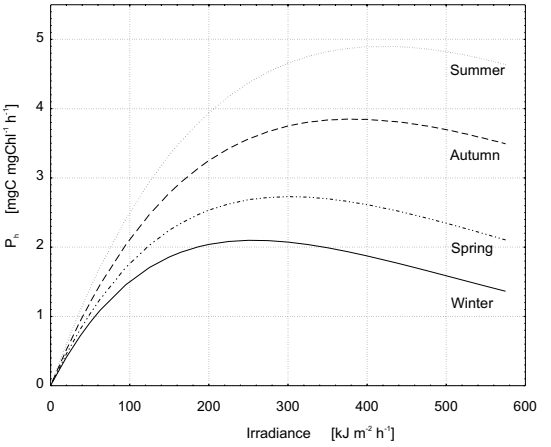

Fig. 3. Photosynthetic light curves in different seasons of the year

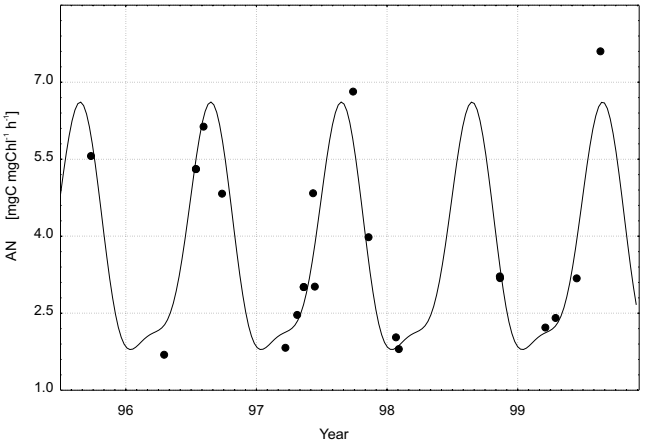

Fig. 4. Seasonal changes of the mean assimilation number in the Gdańsk Deep

Table 3. Mean parameters of the light curves of photosynthesis in particular months

	Assimilation number		Saturation irradiance		
Month	AN $\left[\frac{mgC}{mgChl \cdot h}\right]$	SD_{AN} $\left[\frac{mgC}{mgChl \cdot h}\right]$	E_s $\left[\frac{kJ}{m^2 \cdot h}\right]$	SD_E $\left[\frac{kJ}{m^2 \cdot h}\right]$	Number of observations
January	2.01	0.03	239.01	5.42	2
February	1.80	0.01	250.76	31.73	2
March	2.26	0.37	279.95	63.25	7
April	2.42	0.46	348.51	104.36	13
May	2.48	0.46	335.81	63.38	3
June	4.08	1.25	436.80	139.95	8
July	5.82	0.71	474.84	212.27	3
August	6.37	2.37	603.80	188.03	9
September	4.62	1.11	432.93	135.20	9
October	4.40	1.32	356.98	49.28	4
November	3.35	1.26	307.83	52.06	12
December	3.39	0.97	251.16	25.24	5

Table 4. Mean assimilation numbers in particular seasons

Season	AN $\left[\frac{mgC}{mgChl \cdot h}\right]$	SD $\left[\frac{mgC}{mgChl \cdot h}\right]$
winter (January, February, March)	2.10	0.43
spring (April, May, June)	2.73	0.95
summer (July, August, September)	5.79	1.91
autumn (October, November, December)	3.85	0.41
Average	3.61	1.87

SD - standard deviation

assimilation numbers for open waters of the southern Baltic are described by the trigonometric polynomial, as follows:

$$AN_B = 3.54 - 1.83 \cdot \sin(\omega \cdot x + 0.79) + 0.32 \cdot \sin(2 \cdot \omega \cdot x + 0.88) \quad [14]$$

where: x = subsequent day, $\omega = \frac{2 \cdot \pi}{365}$.

The formula above allows for the determination of the mean assimilation number on an arbitrary day and, next, for its application to estimations of primary production. Mean assimilation numbers in particular seasons in the southern Baltic are presented in Table 4.

Daily primary production

Using the photosynthetic light curve and other necessary data such as irradiation dose PAR which penetrates the sea surface, the diffuse attenuation coefficient of scalar irradiance, chlorophyll *a* concentration and by applying formula [10], primary production at arbitrary depths can be calculated. Several examples of vertical distributions of photosynthetic rate determined *in situ* and derived from formula [9] are presented in Figure 5**.** Relevant data is presented in Table 5. The curves in Figure 5 confirm a relatively good correlation between the primary production calculated by formula 10 and that experimentally obtained at various depths. In order to confirm this, the dependence of primary production for one cubic meter derived from formula [10] and obtained *in situ* is presented in Figure 6. The correlation coefficient is 0.98.

Primary production in the water column measured over a period of four hours is compared with calculated primary production (four hours proposed by BMEPC 1988). Primary production in time Δt in the water column from the surface to the limit of the euphotic layer is obtained from formula [11] integrated over time Δt*:*

$$Prod_{\Delta t} = \int_{t1}^{t2} \int_{0}^{H} AN \cdot Chl \cdot \frac{\eta_d \cdot \exp(-k \cdot z) \cdot \left(1 + \cos\frac{2 \cdot \pi \cdot t}{\lambda}\right)}{\lambda \cdot E_s} \cdot \exp\left[1 - \frac{\eta_d \cdot \exp(-k \cdot z) \cdot \left(1 + \cos\frac{2 \cdot \pi \cdot t}{\lambda}\right)}{\lambda \cdot E_s}\right] dz \cdot dt \quad [15]$$

For calculations the results of the above equation of the average values of chlorophyll *a* concentrations in the euphotic layer were used. The comparison of results of primary production measurements over a four hour period with the calculated values is presented in Table 5. The ratio of the calculated production to the measured production ranges from 0.80 to 1.22,

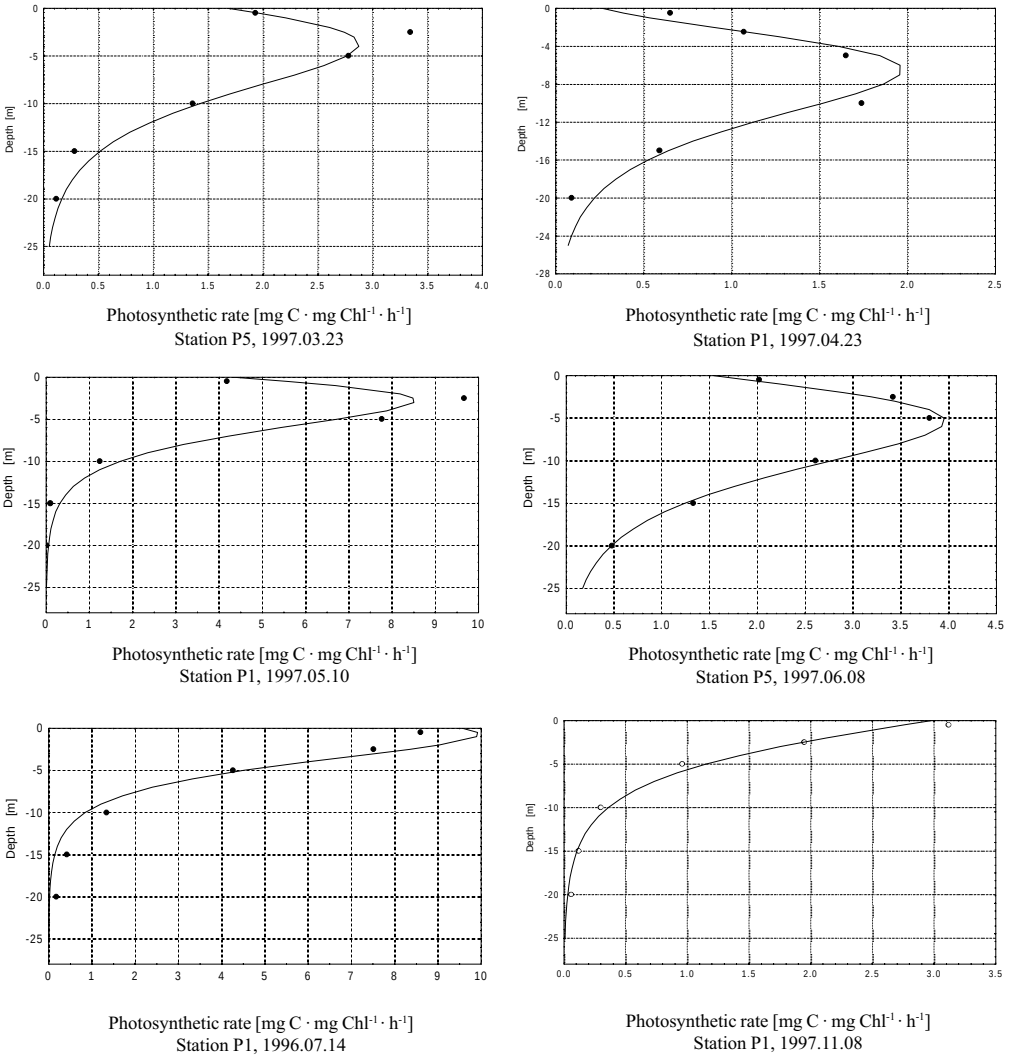

Fig. 5. Vertical distribution of photosynthetic rate around noon [mg C · mg Chl^{-1} · h^{-1}]. Points denote results of *in situ* measurements. Solid line denotes results from calculations based on formula [9], data for calculations are in Table 5

with the average value being 0.96. Figure 7 illustrates the dependence of primary production in the water column calculated for a four hour period on the value measured *in situ* at the same time. Both the linear relation in Figure 7 and the results in Table 5 indicate that there is a good correlation of calculations and results obtained from measurements. The above calculations confirm that the chosen method of primary production calculations based on the results of measurements in incubators may replace *in situ* measurements. In the last column of Table 5 the results of calculations of daily primary production, which is described by formula [12], are given.

Table 5. Primary production measured *in situ* and calculated from formulae [15] and [12] and parameters necessary for calculations

Station	Day	AN $\left[\frac{mgC}{mgChl \cdot h}\right]$	E_S $\left[\frac{kJ}{m^2 \cdot h}\right]$	η_d [PAR] $\left[\frac{kJ}{m^2 \cdot d}\right]$	$\eta_{\Delta t}$ [PAR] $\left[\frac{kJ}{m^2 \cdot \Delta t}\right]$	k [m^{-1}]	Chl $\left[\frac{mg}{m^3}\right]$	$Prod_{\Delta t\ measur}$ $\left[\frac{mgC}{m^2 \cdot \Delta t}\right]$	$Prod_{\Delta t\ calc}$ $\left[\frac{mgC}{m^2 \cdot \Delta t}\right]$ [15]	$\frac{Prod_{\Delta t\ measur}}{Prod_{\Delta t\ calc}}$	$Prod_{d\ calc}$ $\left[\frac{mgC}{m^2 \cdot d}\right]$ [12]
P_1	29.02.96	1.88	265	1,614	1,157	0.31	0.75	32.7	32.7	1.00	51.2
P_{140}	01.03.96	1.88	265	3,808	2,467	0.30	0.60	30.1	36.8	0.82	67.1
P_1	16.04.96	1.69	218	10,234	4,668	0.23	9.87	773.4	780.4	0.99	2116.9
P_{140}	17.04.96	1.59	260	9,090	3,793	0.29	9.28	544.7	536.8	1.01	1414.8
P_5	18.04.96	1.96	295	10,032	4,466	0.21	4.34	433.8	426.3	1.02	1117.4
P_1	14.07.96.	5.29	444	6,471	1,396	0.37	2.43	218.9	204.3	1.07	777.2
P_1	04.08.96	6.12	451	11,070	5,047	0.30	1.93	411.3	401.6	1.02	1061.8
P_{140}	05.08.96	3.18	349	10,842	4,814	0.20	2.70	449.7	447.7	1.00	1229.5
P_5	06.08.96	4.66	481	11,387	5,012	0.21	1.57	362.1	348.7	1.04	919.6
P_1	25.09.96	4.82	401	4,277	2,376	0.56	5.80	335.7	418.5	0.80	821.1
P_{140}	26.09.96	4.25	262	4,809	2,376	0.30	2.59	368.4	362.1	1.02	759.9
P_5	27.09.96	4.38	277	4,792	2,697	0.22	1.72	351.0	348.2	1.01	690.7
P_5	23.03.97	2.88	289	6,031	1,964	0.27	2.23	165.6	171.9	0.96	525.2
P_1	23.04.97	2.46	383	9,953	3,282	0.25	1.99	131.3	149.3	0.88	514.4
P_5	26.04.97	3.08	337	14,504	7,382	0.28	4.03	457.7	466.5	0.98	1293.1
P_{140}	27.04.97	2.85	262	19,081	8,294	0.24	2.95	439.4	378.4	1.16	1135.4
P_1	11.05.97	3.00	432	11,026	4,736	0.35	2.84	260.7	247.3	1.05	669.0
P_{140}	07.06.97	4.19	477	12,328	4,633	0.26	102	177.1	162.7	1.09	474.8
P_5	08.06.97	3.96	431	11,306	4,317	0.26	0.64	118.3	97.1	1.22	283.3
P_1	11.06.97	3.02	345	11,496	4,578	0.24	1.22	162.6	160.4	1.01	480.2
P_1	08.11.97	3.98	349	824	503	0.20	0.98	57.8	57.9	1.00	94.5
P_{140}	09.11.97	3.40	385	2,100	1,497	0.27	1.39	116.2	116.9	0.99	173.6
P_5	10.11.97	4.08	410	1,606	1,133	0.27	1.79	134.4	143.7	0.94	213.5
P_1	11.11.98	3.22	272	780	270	0.52	2.09	22.1	29.5	0.75	55.5
P_{140}	12.11.98	2.38	308	1,522	1,060	0.36	1.65	65.9	68.0	0.97	95.1
P_5	13.11.98	1.94	337	1,739	1,255	0.31	1.70	69.7	69.6	1.00	97.3

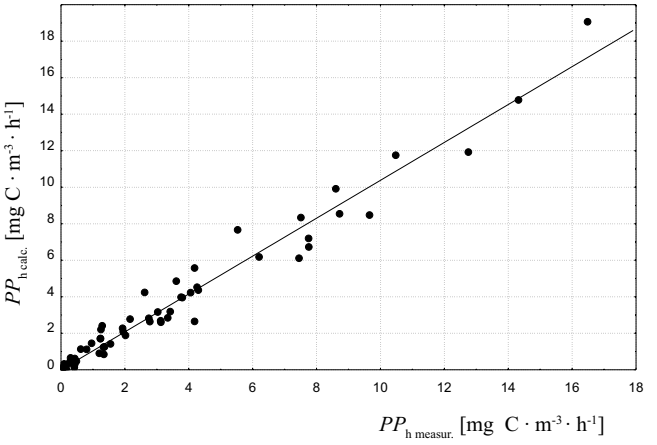

Fig. 6. Primary production [mg C · m^{-3} · h^{-1}] measured *in situ* versus primary production calculated from formula [10]. The curve was derived from the following formula: $P_{calc.} = 1.038 \cdot P_{measur.}$

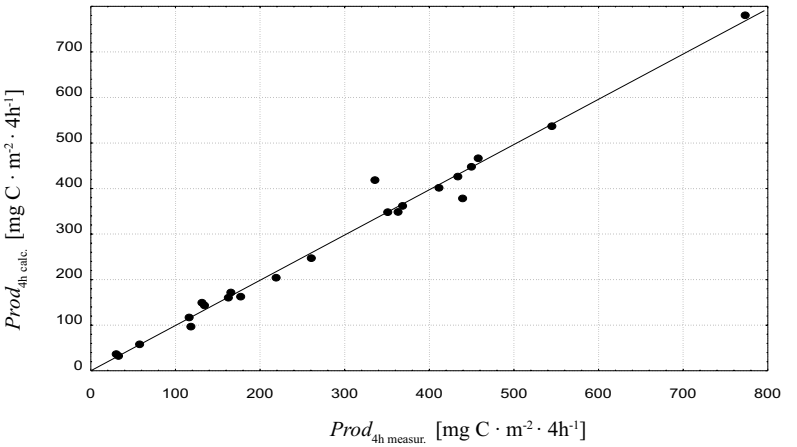

Fig. 7. Primary production measured *in situ* over a period of four hours versus primary production calculated from formula [15] integrated over the same incubation time (data for calculations in Table 5). The curve was derived from the following formula: $Prod_{4h\ calc.} = 0.993 \cdot Prod_{4h\ measur.}$

DISCUSSION

In the open waters of the Baltic Sea mean assimilation numbers in particular months vary from 1.80 to 6.37 mg C · mg Chl^{-1} · h^{-1}. This variability can result from the variability of environmental conditions and changes in phytoplankton species composition. In the paper Renk *et al*. 1999 the influence of temperature on the parameters of light curves was indicated. Seasonal changes of assimilation numbers in the Baltic Sea are also reported by Woźniak *et al*. (1989). In this work, (Woźniak *et al.* 1989) the assimilation number refers to the whole day and not just to one hour; therefore, the observed seasonal changes of assimilation numbers were also concerned with changes in day length. Also, differences of assimilation numbers in the Gulf of Gdańsk and the Pomeranian Bay were observed (Renk *et al*. 1999). These differences may be related to temperature changes, significant differences of nutrient concentration in these areas, phytoplankton species composition and the reaction of particular phytoplankton populations to changes in environmental conditions.

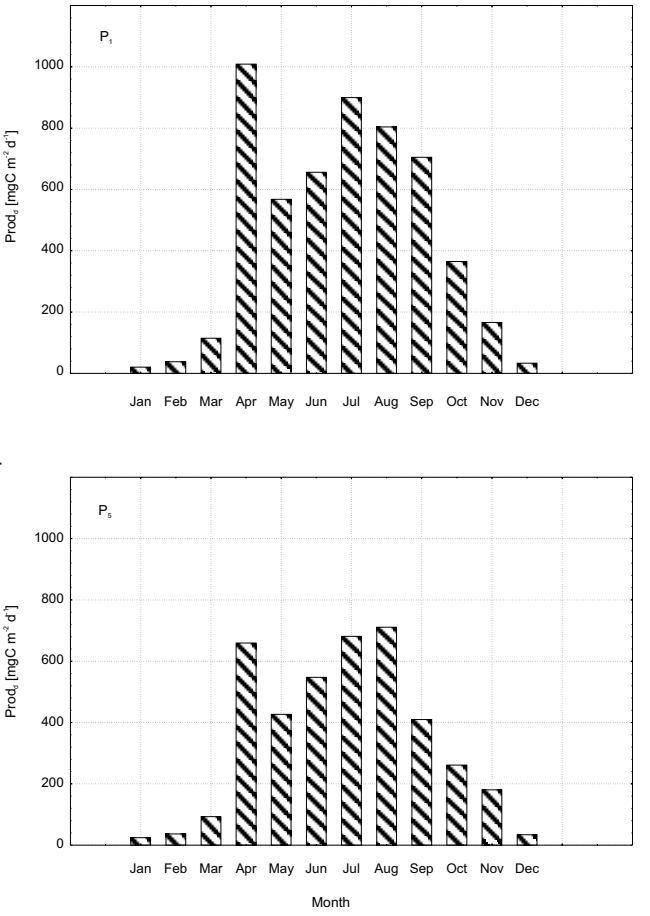

Fig. 8. Average primary production in particular months in the Gdańsk Deep (P_1) and the Bornholm Deep (P_5) [mg C · m^{-2} · d^{-1}]

Primary production calculated using assimilation numbers and formula [10] varies slightly from primary production measured *in situ.* The differences may result from the following simplifications which have been assumed:

- the light attenuation coefficient is independent of depth,
- the uniform photosynthetic light curve in the whole euphotic layer; in reality phytoplankton species composition and its physiological reactions to irradiance may vary with depth,
- the uniform average chlorophyll *a* concentration in the whole euphotic layer. Long-term observations (Renk 1983, 1997) reveal that this condition does not involve significant error except in spring when a thermocline is created within the euphotic layer. During thermocline creation at a depth range from 2-8 meters, significant chlorophyll gradients occur along with a significant decrease of primary production (Renk 1983).

The formulae presented (especially formula 12) may be used to calculate average primary production for each day of the year. Figure 8 presentes the results of calculations of average primary production for particular months at stations P_1 and P_5 . The following parameters were used in the calculations:

- photosynthetic light curves from Renk and Ochocki 1998,

Table. 6. Annual primary production in various regions of the Baltic Sea

Region	Period	Primary production [g C · m^2 · $year^{-1}$]	Author
Kattegat	1954-1960	97,5	Steemann Nielsen 1965b
Kattegat	1964-1969	90.4	Gargas *et al*. 1978
Kattegat	1988-1990	290	Richardson and Christoffersen 1991
Belt Sea	1953-1957	86	Steemann Nielsen 1965b
Belt Sea	1975-1977	116,5	Gargas *et al*. 1978
Sund	1972	70-77	Edler 1978
Sund	1973	73-183	Edler 1978
Kiel Bay	1971-1973	158	Bodungen et al.1975
Bornholm Basin			
Arkona Deep	1971-1974	85	Renk 1983
Arkona Deep	1967-1978	94,3	Schulz and Kaiser 1976
Mecklenburg Bight	1969-1978	130	Kaiser et al. 1981
Bornholm Deep	1967-1972	59-138	Schulz and Kaiser 1973, 1974, 1975
Bornholm Deep	1971-1975	95	Renk 1983
Bornholm Deep	1987-1991	123	Renk 1997
Gulf of Gdańsk			
Gulf of Gdańsk	1971-1974	140	Renk 1997
Gulf of Gdańsk	1987	304	Renk 1997
Puck Bay	1965-1991	198	Renk 1997
Gdańsk Deep	1971-1974	107	Renk 1997
Gdańsk Deep	1981-1985	129	Renk 1997
Gdańsk Deep	1987-1991	172	Renk 1997
Gotland Sea			
Gotland Deep	1970	38	Schulz and Kaiser 1973
Gotland Deep	1973	91	Ackefors and Lindahl 1975,
Gotland Deep	1974	116	Lindahl 1977
Gotland Deep (Southern part.)	1987-1991	141	Renk 1991, 1997
Aland Sea	1974-1976	66-94	Lindahl 1977
Gulf of Bothnia	1973-1974	18-70	Lindahl 1977
Gulf of Finland	1967-1971	30-65	Niemi 1975, Bagge and Niemi 1971
Gulf of Finland		78	Forsskahl *et al*. 1982
Helsinki Region	1968	150-200	Bagge and Lehmusluoto 1971

• the average daily doses of irradiation PAR described by the following formula (Renk 1989, 1997):

$$\eta_d = 8.67 + 8.29 \cos(\omega \cdot x - 3.03) + 0.69 \cos(2\omega \cdot x - 5.80)$$

• the transmission of PAR radiation through the sea surface which was taken into account (Baker and Frouin 1987, Dera 1995),

• the average light attenuation coefficient for scalar irradiance, $k = 0.3\ m^{-1}$,

• the average concentrations of chlorophyll *a* from data collected between 1970 and 1995 (Renk 1997).

Figure 8 has served as a data source for calculations of average annual primary production in the Gdańsk Deep and the Bornholm Deep, which is 133.22 and 101.64 g C · m^{-2} · $year^{-1}$, respectively. Since long-term average values are used, it follows that this production is also average, while in particular years there may be a significant difference. However, the calculated data fit in the range of values which were published earlier (Renk *et al.* 1992, Renk 1997, Kaczmarek *et al*. 1997), and which are, to some extent, presented in Table 6. It must be emphasized that primary production over the last three decades has shown a tendency to increase (Renk 1991, Schulz *et al.* 1997, Steemann Nielsen 1965b, Schulz 1986, Aertebjerg Nielsen *et al*. 1981).

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List of symbols

PP_h	Primary production per unit time in a unit volume of water	$[mgC \cdot m^{-3} \cdot h^{-1}]$
Chl	Chlorophyll *a* concentration	$[\ mgChl\ \cdot m^{-3}\ ]$
P_h	Photosynthetic rate determined as the ratio $\frac{PP_h}{Chl}$	$[mgC \cdot mgChl^{-1} \cdot h^{-1}]$
AN	Assimilation number evaluated from the photosynthetic light curve	$[mgC \cdot mgChl^{-1} \cdot h^{-1}]$
$AN_{\exp}$	Assimilation number determinated as the observed maximal ratio $\frac{PP_h}{Chl}$	$[mgC \cdot mgChl^{-1} \cdot h^{-1}]$
AN_B	Mean assimilation number for the southern Baltic Sea	$[mgC \cdot mgChl^{-1} \cdot h^{-1}]$
AN_{GD}	Mean assimilation number for the Gdansk Deep	$[mgC \cdot mgChl^{-1} \cdot h^{-1}]$
$Prod_h$	Primary production in water column per hour	$[mgC \cdot m^{-2} \cdot h^{-1}]$
$Prod_{\Delta t}$	Primary production in water column during Δt	$[mgC \cdot m^{-2} \cdot \Delta t^{-1}]$
$Prod_d$	Daily primary production in water column	$[mgC \cdot m^{-2} \cdot d^{-1}]$
E	Irradiance PAR	$[kJ \cdot m^{-2} \cdot h^{-1}]$
$E(0)$	Irradiance at a depth 0 m (just below the sea surface)	$[kJ \cdot m^{-2} \cdot h^{-1}]$
$E(z)$	Irradiance at a depth of „z”	$[kJ \cdot m^{-2} \cdot h^{-1}]$
E_s	Irradiance PAR at which the saturation of photosynthesis is achieved	$[kJ \cdot m^{-2} \cdot h^{-1}]$
η_d	Daily irradiation (daily dose of irradiance) PAR just below the sea surface	$[kJ \cdot m^{-2}]$
$\eta_{\Delta t}$	Dose of irradiance PAR during Δt hours just below the sea surface	$[kJ \cdot m^{-2}]$
k	diffuse attenuation coefficient for scalar irradiance PAR	[m^{-1}]
λ	Length of the day	[h]
H	Thickness of the euphotic layer	[m]
y	Time expressed in years	
x	Time expressed in subsequent days of the year	
	$\omega = \frac{2 \cdot \pi}{365}$, π = 3.14	

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The ichthyofauna of the King George Island (Antarctica) shelf waters and its value to commercial fishing

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Abstract. King George Island is one of islands in the Scotia Ridge in the Atlantic sector of Antarctica. This work presents the results of fishing and ichthyological investigations carried out from 1978 to 1988 on the shelf which extends from the island to the northwest. They indicated that the ichthyofauna composition there was very similar to that of Admiralty Bay, which is located on the south coast of King George Island. The mean density of exploitable fish species is comparable to that of other Antarctic regions, which qualifies this fishing ground for exploitation.

Key words: Antarctica, King George Island, ichthyofauna, density, fishery resources

INTRODUCTION

The western part of the Atlantic sector of Antarctica consists of islands and their shelves which together form the Scotia Ridge. These shelves reach depths of 500 m and great concentrations of fish occur here. Therefore, these areas are of great interest to commercial fishery. The area of these fishing grounds is smaller than that of grounds in other parts of the world. The most important fishing area in the Scotia Ridge is the South Georgia shelf. However, the South Shetland archipelago shelf may also play an important role as a fishing ground. King George Island is the largest island in the archipelago.

The southern coast of King George Island is composed of large bays and Admiralty Bay is the largest of them (Fig. 1). Its ichthyofauna is well described thanks to investigations which have been carried out at the Henryk Arctowski Polish Antarctic Station since its inception on 26 February 1977 (S. Rakusa-Suszczewski 1989). The ichthyological investigations have mainly focused on the morphology and systematics of fish, their biology, physiology and parasitology. An extensive bibliography of these types of works was compiled by J. Kulesz and A. Kompowski (1997), and J. Kulesz (1998).

On the northwestern side of King George Island, the shelf creates a convenient region for fishing and this fishing ground has become a point of interest for Polish deep-sea fisheries. The R/V PROFESOR SIEDLECKI carried out preliminary investigations in this area between January and March 1979. On two occasions relatively high concentrations of fish were found and,

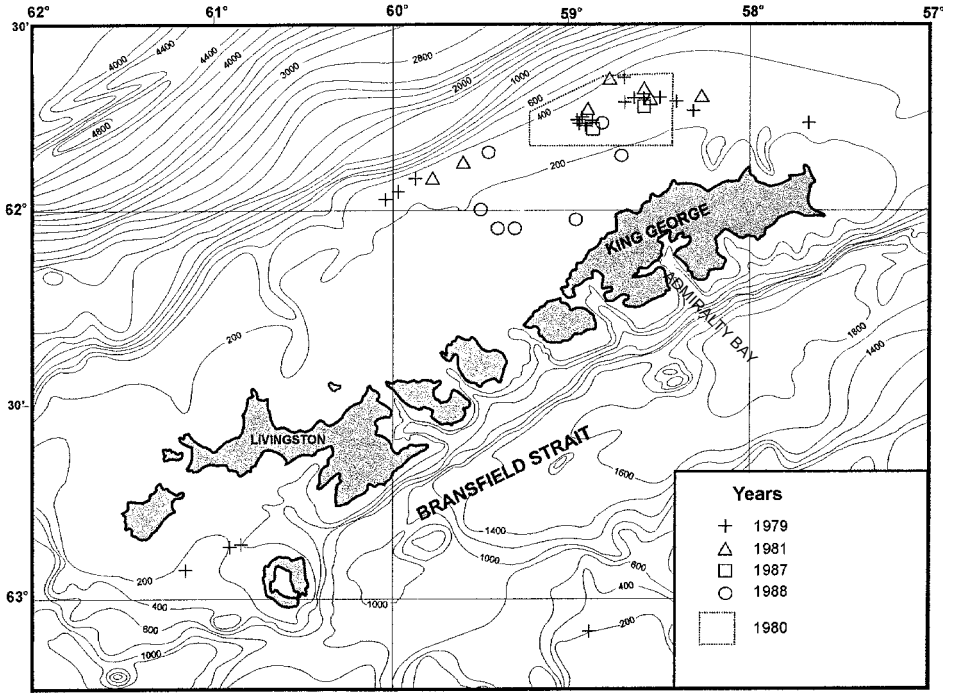

Fig. 1. Location of sample collection

subsequently, caught (Sosiński 1979). The next fishing survey, which was carried out by the M/T LIBRA in February 1980, confirmed the possibility of fishing in these fishing grounds. Then in March 1981 and February 1987 and 1988 the R/V PROFESOR SIEDLECKI carried out control investigations of fish resources in the basin.

The aim of the present paper is to describe the ichthyological and fishing samples which were collected during these five cruises and to compare the results which were obtained. These concern the composition of the ichthyofauna on the northwestern shelf of King George Island, the percentage and density of exploitable fish species as well as their biological characteristics.

MATERIALS AND METHODS

Ichthyological and fishing observations were carried out during cruises of the R/V PROFESOR SIEDLECKI in 1978-1979, 1980-1981, 1986-1987 and 1987-1988 and during the cruise of the commercial vessel M/T LIBRA in 1979-1980. The input data for this work were taken from the reports of these cruises (unpublished data, Sea Fisheries Institute, Gdynia) and from the work by K. Skóra and J. Sosiński [1983].

The control catches were carried out on the northwestern shelf of King George Island (Fig. 1) using a WD 32/36 bottom trawl at a speed of 3 to 4 knots.

Until 1981, taxonomic classification of fish was determined at sea according to the Norman (1938) and Regan (1913) keys. Beginning in 1986, fish were classified using the FAO/CCAMLR Key (Fischer and Hureau, 1985). In the present work, systematic classification has been unified according to the FAO/CCAMLR.

Total fish length (*longitudo totalis*) was measured and rounded down to the nearest centimeter and the fish were sorted into one centimeter length classes. The fish were weighed to the nearest gram.

Reproductive maturity was determined using either the Maier scale (until 1985) or the Everson scale (from 1986).

In the present work, the data was unified according to the Everson scale (1977). Stomach fullness was determined on a scale from 0 to 4.

The fish density per area unit was determined using the swept area method with a catchability coefficient of $q = 1$.

RESULTS

Ichthyofauna composition

The taxa which were identified characterize the benthic ichthyofauna which inhabits the northwestern shelf of King George Island. During cruises of R/V PROFESOR SIEDLECKI between 1979 and 1988, a total of 39 taxa belonging to 9 families were observed; the species of 37 of them was determined (Table 1). The majority of them are endemic to the Southern Ocean. Only 6 wide-spread species were confirmed: *Notolepis coatsi* from the Paralepididae family, *Gymnoscopelus (Gymnoscopelus) nicholsi* and *Electrona antarctica* from the Myctphidae family, *Micromesistius australis* from the Gadidae family, *Notothenia (Lepidonotothen) squamifrons* from the Nototheniidae family and *Lycodichthys antarticus* from the Zoarcidae family.

The most common was the Nototheniidae family with 15 species and the Channichthyidae family with 9 species.

The distribution and species composition of exploitable fish concentrations

Exploitable fish are those whose species occur on a massive scale and whose technological qualities make it possible to use them either for human consumption or as animal feed.

In the investigated area, only 9 species of the 39 which were identified possessed these qualities, including the following from the Channichthyidae family:

Champsocephalus gunnari Lönnberg, 1905
Pseudochaenichthys georgianus Norman, 1937
Chaenocephalus aceratus Lönnberg, 1906
Chionodraco rastrospinosus De Witt and Hureau, 1979
Chaenodraco wilsoni Regan, 1914
and the following from the Nototheniidae family:
Notothenia rossii marmorata (Fisher, 1885)
Notothenia (Notothenia) neglecta Nybelin, 1951
Notothenia (Gobionotothen) gibberifrons Lönnberg, 1905
Dissostichus mawsoni Norman, 1937.

Table 1. Fish taxa found during R/V PROFESOR SIEDLECKI bottom trawl surveys on King George shelf area

Taxa	Dates			
	01-03.79	03.1981	02.1987	02.1988
Fam. RAJIDAE				
Bathyraja eatoni (Günther, 1876)			+	
*Bathyraja maccaini** Springer, 1971		+		+
Bathyraja spp.	+	+	+	
Fam. PARALEPIDIDAE				
Notolepis coatsi Dollo, 1908		+		
Fam. MYCTOPHIDAE				
Gymnoscopelus (Gymnoscopelus) nicholsi (Gilbert, 1911)	+	+		
Electrona antarctica (Günther, 1878)			+	
Fam. GADIDAE				
Micromesistius australis Norman, 1937	+			
Fam. NOTOTHENIIDAE				
Notothenia (Gobionotothen) gibberifrons Lönnberg, 1905	+	+	+	+
Notothenia rossii marmorata (Fischer, 1885)	+	+	+	+
Notothenia (Notothenia) neglecta Nybelin, 1951	+	+	+	+
Notothenia (Lepidonotothen) kempi Norman, 1937	+	+	+	
Notothenia (Lepidonotothen) squamifrons Günther, 1880				+
Nototheniops nybelini (Balushkin, 1976)	+	+	+	+
Nototheniops nudifrons (Lönnberg, 1905)	+	+	+	+
Pagothenia hansoni (Boulenger, 1902)	+	+	+	
Pagothenia bernacchii (Boulenger, 1902)	+		+	
Trematomus eulepidotus Regan, 1914	+	+		
Trematomus scotti Boulenger, 1907	+		+	
Trematomus newnesi Boulenger, 1902	+		+	+
Trematomus loennbergi Regan, 1913				+
Dissostichus mawsoni Norman, 1937	+	+	+	+
Pleuragramma antarcticum Boulenger, 1902	+	+	+	+
Fam. BATHYDRACONIDAE				
Gerlachea australis Dollo,1900		+		
Parachaenichthys charcoti (Vaillant, 1906)	+		+	+
Psilodraco breviceps Norman, 1938			+	
Gymnodraco acuticeps Boulenger, 1902	+	+	+	+
Fam. CHANNICHTHYIDAE				
Champsocephalus gunnari Lönnberg, 1905	+	+	+	+
Chaenocephalus aceratus Lönnberg, 1906	+	+	+	+
Chionodraco rastrospinosus De Witt and Hureau, 1979	+	+	+	+
Chaenodraco wilsoni Regan, 1914	+	+		
Cryodraco antarcticus Dollo, 1900	+	+	+	+
Dacodraco hunteri Woite, 1916	+			
Neopagetopsis ionah Nybelin, 1947	+		+	+
Pagetopsis macropterus (Boulenger, 1907)	+		+	+
Pseudochaenichthys georgianus Norman, 1937	+	+	+	+
Fam. ZOARCIDAE				
Ophthalmolycus bothriocephalus (Pappenheim, 1912)	+		+	
Ophthalmolycus concolor (Roule and Despax, 1911)	+	+	+	
Lycodichthys antarcticus Pappenheim, 1911				+
Fam. LIPARIDIDAE				
Paraliparis sp.				+

*syn.: *Raja rakusai* Rembiszewski, 1981

In control catches, the greatest percentage was comprised of three species of Chaennichthyidae: *Champsocephalus gunnari, Chionodraco rastrospinosus* and *Chaenocephalus aceratus* as well as *Notothenia (Gobionotothen) gibberifrons* and *Notothenia (Notothenia) neglecta* from the Nototheniidae family (Table 2). In 1979 and 1980 a significant contribution of *Chionodraco rastrospinosus* was observed. *Notothenia (Gobionotothen) gibberifrons* was common in all the catches each year. Species composition varied with water depth; in shallow waters *Champsocephalus gunnari* was the most common.

Comparative studies of species composition were carried out in 1979 outside the investigated region. *Champsocephalus gunnari* was predominant in hauls which were carried out on the shelf between Livingston, Snow and Deception isles. A relatively high contribution came from *Chaenocephalus aceratus* and *Chionodraco rastrospinosus* (Fig. 2). A completely different species composition was characteristic in a haul which was carried out in the southern part of the Bransfield Strait on the Graham Land shelf. *Chaenodraco wilsoni* dominated here, but this species was rather sporadic on the King George Island shelf (Fig. 2).

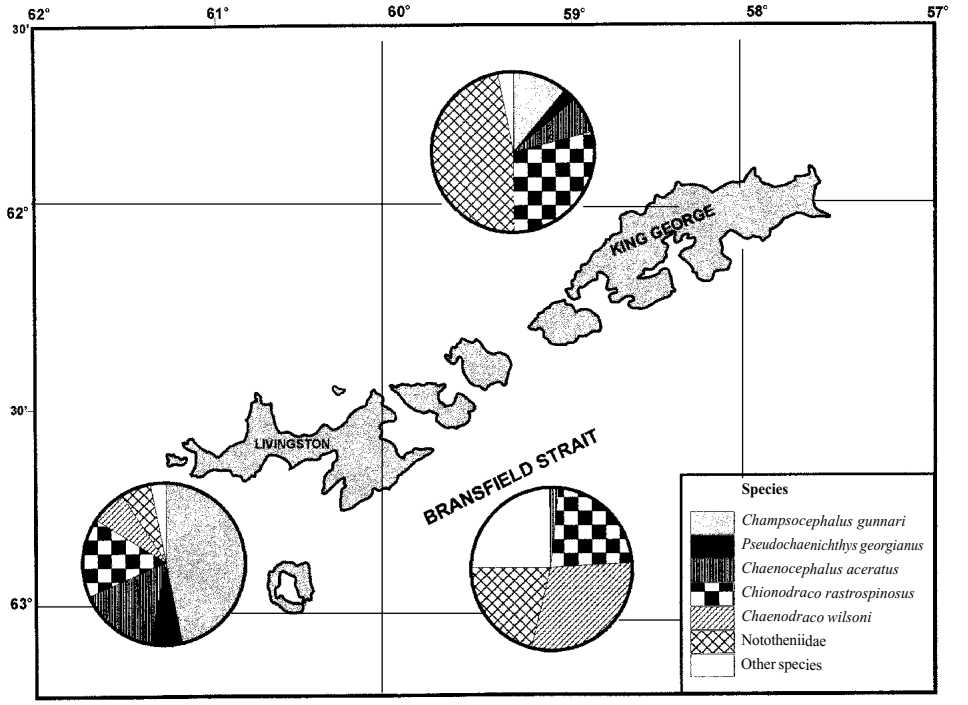

Fig. 2. Species composition of commercial fish in R/V PROFESOR SIEDLECKI surveys during January-March 1979

Fish density

Fish density, expressed as either catch in kg per hour of trawling or as biomass in kg per km^2 of sea bottom area (CPUE), varied in different years. It also varied with depth, just as the species composition of the catches did. The results of investigations, including data which describes

Table 2. Fishing results of Polish survey cruises on King George shelf area

Season vessel name dates	Gear type (horizontal opening of trawl) (m)	Stratum [m]	No of hauls	Average trawling speed [knots]	Duration of trawls [min]	Catches [kg]	Mean CPUE		Percentage by species [%]									
							[kg/h]	[kg/km^2]	1	2	3	4	5	6	7	8	9	10
1978/79 r/v Prof. Siedlecki 28.01-25.03.1979	WD 32/36 19	150-250	4	4.0	200	444	133	946	35	5	12	14	6	+		22	+	6
		250 <	17		1,350	19,700	876	6,225	13	2	6	28	+	2	+	44	1	4
		Σ	24		1,550	20,144	780	5,544	13	3	7	27	+	2	+	43	1	4
1979/80 m/t Libra 12-21.02.1980	WD 32/36 18	250 <	11	3.2	1,995	22,400	674	6,315	2		6	64		4		24		
1980/81 r/v Prof. Siedlecki 26-28.03.1981	WD 26/30 17	250 <	7	3.8	695	1,893	163	1,366			2	5	+		4	63		26*
1986/87 r/v Prof. Siedlecki 18.02.1987	WD 32/36 19	250 <	2	3.0	230	2,953	770	7,297	+		15	9				73		3
1987/88 r/v Prof. Siedlecki 05-06.02.1988	WD 32/36 19	< 150	3	3.5	180	35	12	95	37		20			14	3	6	3	17
		150-250	3		180	385	128	1,042	7	1	32	2		1	36	19	1	1
		250 <	2		120	298	149	1,210	1	2	12	5		1	2	76		1
		Σ	8		480	718	90	729	6	2	23	3		1	20	42	1	2

Species:

1. *Champsocephalus gunnari*
2. *Pseudochaenichthys georgianus*
3. *Chaenocephalus aceratus*
4. *Chionodraco rastrospinosus*
5. *Chaenodraco wilsoni*
6. *Notothenia rossi marmorata*
7. *Notothenia (Notothenia) neglecta*
8. *Notothenia (Gobionotothen) gibberifrons*
9. *Dissostichus mawsoni*
10. *Pisces nei*

* including 20% *Gymnoscopelus (Gymnoscopelus) nicholsi*

Table 3. Estimated fish biomass on King George Island shelf

Dates	Square*	Stratum						Total	
		0-150 m		150-250 m		250-500 m		Sea area covered [km^2]	Biomass [t]
		Sea area covered [km^2]	Biomass [t]	Sea area covered [km^2]	Biomass	Sea area covered [km^2]	Biomass [t]		
01-03.1979	13 + 23			1,020	971	3,601	22,416	4,627	23,387
02.1980	13					2,952	18,642	2,952	18,642
03.1981	13					2,952	4,032	2,952	4,032
02.1988	2 +13	2,200	09	661	689	3,002	3,632	5,863	4,530

*Everson [1984]

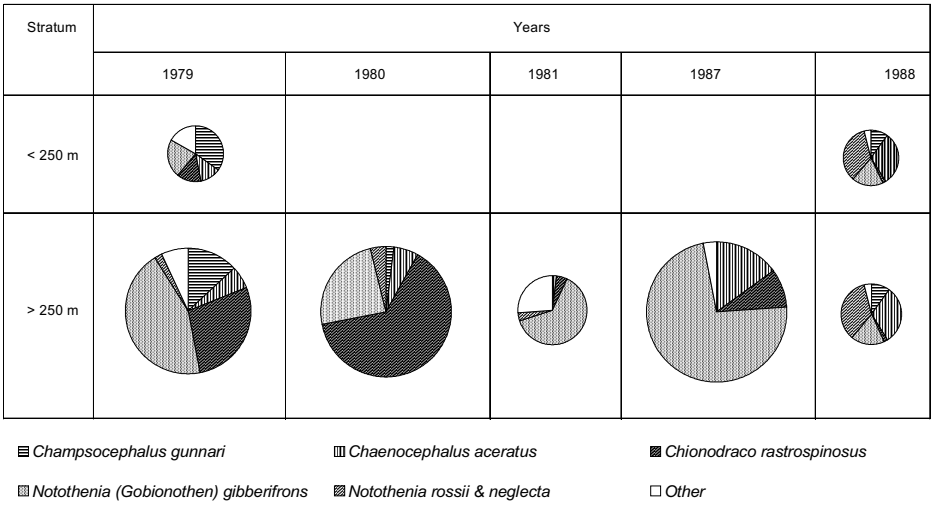

Fig. 3. Species composition and density of fish in King George Island shelf

the fishing gear, are presented in Table 3 and Figure 3, where the area of the graphs is proportional to the fish density.

The data in Table 2 were used to calculate the biomass of fish from the northwestern shelf of King George Island. It was calculated only for the depth strata in the sub-areas [according to the Everson scale (1984)] in which control catches were carried out. Table 3 presents the results obtained for the estimated fish biomass per area which the calculations refer to. The fish biomass which was obtained in particular years refers to areas from 3 to 5.9 thousand km^2, which is about 15 to 30% of the shelf area (up to 500 m depth) of the entire South Shetland area.

The total shelf area near South Shetland, including sub-areas 1-3, 5-7, 13, 14, 21-26 and 31, is 20,109 km^2 according to the Everson scale (1984).

The area of particular depth strata is as follows:

0-150 m – 8,324 km^2,

150-250 m – 2,803 km^2,

250-500 m – 8,982 km^2.

The biological characteristics of useful fish

Champsocephalus gunnari Lönnberg, 1905
The length of the majority of specimens caught varied from 30 to 48 cm (Fig. 4), while their mass varied from 190 g to 600 g. The investigated populations were characterized by either an equal contribution of both sexes or male domination. During the investigations fish were maturing for spawning. In general, males were more mature than females. The fish preyed (Table 4) on krill.

Chaenocephalus aceratus Lönnberg, 1906
The length of the specimens investigated varied significantly from 25 cm to 60 cm (Fig. 5). Their mass also varied significantly from 140 g to 1,700 g. Both immature specimens and those maturing for spawning occurred (Table 4). The sex ratio was very unstable, since specimens longer than 55 cm were mostly females. The stomachs were most often empty; this is due to the vomiting reflex which is characteristic of fish which are caught.

Pseudochaenichthys georgianus Norman, 1937
Fish length did not vary significantly (Fig. 6). The most common were specimens ranging from 37 to 53 cm in length and from 400 to 1,600 g in mass. The sex ratio was 1:1. During the investigation period most fish had maturing gonads, although some fish already had mature gonads (Table 4).

Chionodraco rastrospinosus De Witt and Hureau, 1979.
The length distribution curves have only one peak. Length varied from 30 to 45 cm (Fig. 7) and mass varied from 220 g to 900 g. Most fish had maturing gonads, but in 1979 some fish were

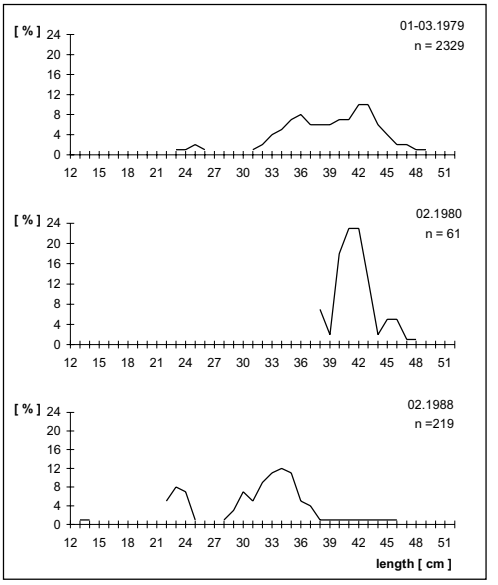

Fig. 4. Length distribution of *Champsocephalus gunnari* in different years

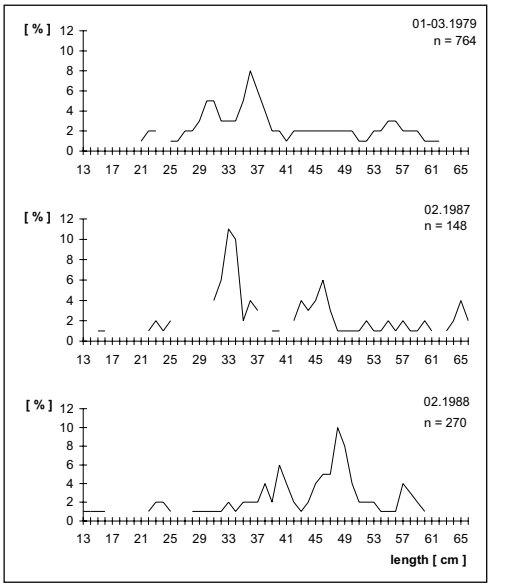

Fig. 5. Length distribution of *Chaenocephalus aceratus* in different years

Table 4. Maturity and stomach fullness of fish species on King George Island shelf (%)

Species	Date	Sex ratio	Maturity stages					Stomach fullness					$W = K \cdot L^n$		*n*
		♂ : ♀	1	2	3	4	5	0	1	2	3	4	*K*	*n*	
Champsocephalus	01-03.1979	50 : 50	3	68	29	0	0	-	-	90		-	0.0234	2.6440	1102
gunnari	02.1980	64 : 36	0	34	66	0	0	11	26	31	26	6			61
Chaenocephalus	01-03.1979	49 : 51	43	47	10	0	0	80	-	-	-	-	0.0028	3.2196	834
aceratus	02.1987	50 : 50	60	29	11	0	0	82	5	5	5	3			100
	02.1988	56 : 44	23	74	2	1	0	85	6	5	3	1			161
Pseudochaenichthys	01-03.1979	50 : 50	2	74	23	1	0	-	-	-	-	-	0.0014	3.5121	260
georgianus															
Chionodraco	01-03.1979	44 : 56	13	63	21	2	1	12	22	18	30	18	0.0021	3.3989	999
rastrospinosus	02.1987	-	12	85	3	0	0	45	20	15	20	0			100
	02.1988	66 : 34	15	85	0	0	0	mean 1.3							46
Chaenodraco	02.1979	50 : 50	0	100	0	0	0	feeding					0.0057	3.1223	618
wilsoni															
Notothenia	01-03.1979	50 : 50	31	68	1	0	0	weak feeding					0.0011	3.6559	1507
(Gobionotothen)	02.1980	51 : 49	0	97	3	0	0	2	20	56	20	2			100
gibberifrons	03.1981	43 : 57	31	66	3	0	0	20	67	6	2	5			100
	02.1987	50 : 50	58	42	0	0	0	24	51	22	3	0			100
	02.1988	43 : 57	6	75	18	1	0	28	45	19	5	3			201
Notothenia rossii	02.1979	50 : 50	0	71	29	0	0	14	47	20	19	0			49
marmorata	02.1980	46 : 54	0	66	34	0	0	3	4	47	40	6			100
Notothenia	01-03.1979	50 : 50	0	36	64	0	0	feeding					0.0072	3.2314	118
(Notothenia)															
neglecta	02.1988	50 : 50	0	100	0	0	0	8	32	20	35	5			40
Dissostichus	01-03.1979	50 : 50	15	85	0	0	0	13	31	29	25	2	0.0032	3.3022	48
mawsoni															

(-) no data

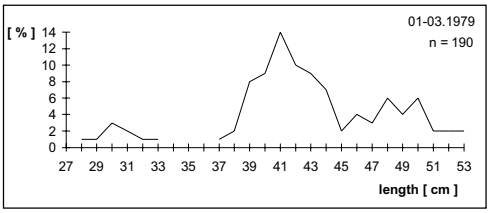

Fig. 6. Length distribution of *Pseudochaenichthys georgianus* in 1979

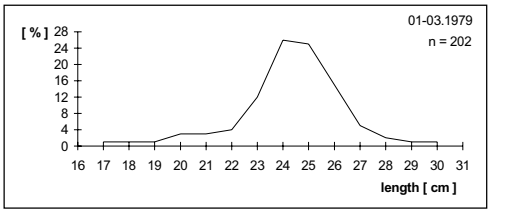

Fig. 8. Length distribution of *Chionodraco wilsoni* in 1979

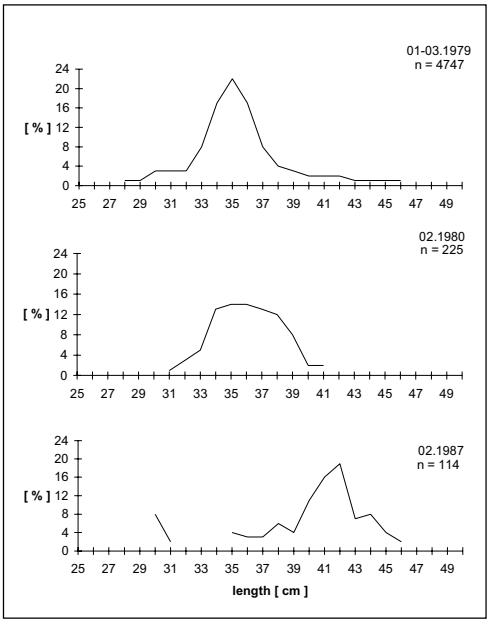

Fig. 7. Length distribution of *Chionodraco rastrospinosus* in different years

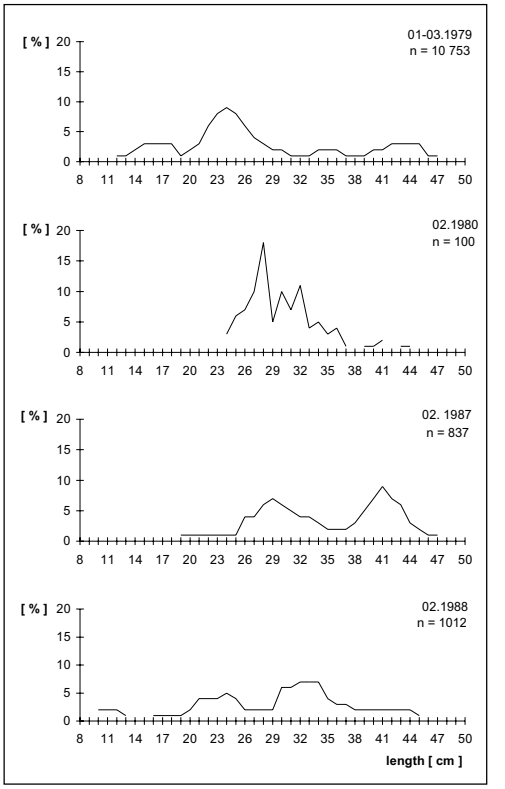

Fig. 9. Length distribution of *Notothenia (Gobionotothen) gibberifrons* in different years

mature for spawning (Table 4). Among the fish which were investigated, some had fed on krill and some had empty stomachs.

Chaenodraco wilsoni Regan, 1914

The stock which was investigated in 1979 was homogeneous in terms of specimen length and maturity. The length of most specimens varied from 22 to 28 cm (Fig. 8), while their mass varied from 90 to 200 g. Their gonads were maturing (Table 4) and they fed on krill.

Notothenia (Gobionotothen) gibberifrons (Lönnberg, 1905)

Their length varied significantly from 17 to 47 cm (Fig. 9), as did their mass which ranged from 60 to 1,500 g. On average, the sex ratio was as 1:1. The stock consisted of both immature and maturing specimens (Table 4). The fish investigated did not prey extensively and about 25% of them had empty stomachs.

Notothenia rossii marmorata (Fischer, 1885)

These fish are relatively large. Their length varied from 35 to 55 cm, while their mass ranged from 600 to 2,900 g. Specimens up to 71 cm in length and 4,700 g in mass were noted (Fig. 10). During the investigations, the fish had gonads in maturity stages 2 and 3 (Table 4).

Notothenia (Notothenia) neglecta Nybelin, 1951

In terms of body size (Fig. 11) and body mass, these fish were very similar to *Notothenia rossii marmorata*. The sex ratio was also 1:1. The fish were maturing for spawning (Table 4).

Dissostichus mawsoni Norman, 1937

These fish occurred sporadically in the catches. Their length varied from 32 to 50 cm (Fig. 12), and body mass ranged from 300 to 1,100 g. One specimen occurred measuring 143 cm in length and weighing 43,000 g. The fish were either immature or maturing (Table 4). Most often these fish had other fish in their stomachs.

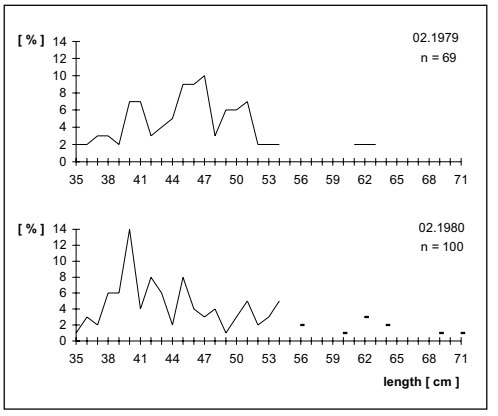

Fig. 10. Length distribution of *Notothenia rossii marmorata* in different years

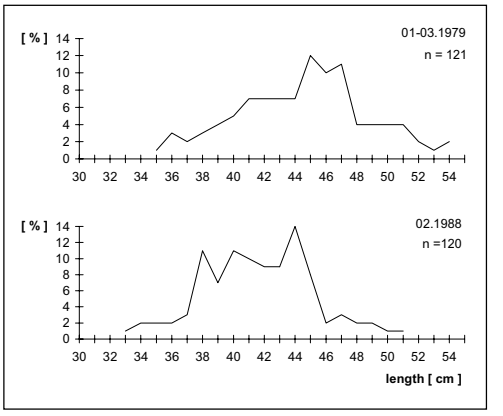

Fig. 11. Length distribution of *Notothenia (Notothenia) neglecta* in different years

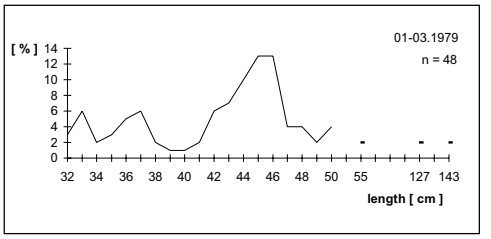

Fig.12. Length distribution of *Dissostichus mawsoni* in 1979

DISCUSSION

In comparison with other regions of the world, there are fewer fish species in Antarctic waters. The ichthyofauna of the Southern Ocean consists of 275 species from 49 families (Kulesz, 1998). The majority of these species (168) occurs in West Antarctica. Of five distinct regions (including South Georgia, the South Sandwich Islands, the South Shetland Islands, the South Orkney Islands and the Antarctic Peninsula) the South Shetland Islands have the greatest ichthyofauna diversity with 104 species of 20 families confirmed. This relatively numerous ichthyofauna, in terms of the number of species, is connected with the presence of various water masses which come from the Weddell Sea, the southeastern Pacific and the Bellingshausen Sea.

The fish species which are described in this work were observed at locations shown in Figure 1. They were caught mainly in the benthic layer of the northern shelf of King George Island. The location of the investigations was determined by the ease of hauling with benthic equipment. The presence of 39 species of 9 families was confirmed in this limited area and species occur here which had not been observed in the area of the South Shetland Islands (Kulesz, 1998). These include*: Notothenia (Lepidonotothen) squamifrons* (Günther, 1980) from the Nototheniidae family; *Psilodraco breviceps* Norman, 1938 from the Bathydraconidae family and *Ophthalmolycus bothriocephalus* (Pappenheim, 1912) and *Ophthalmolycus concolor* (Roule and Despax, 1911) from the Zoarcidae family.

King George Island has a relatively large shelf on its northwestern side, while on the southern side there is a steep slope. The southern coast is composed of large bays, among which Admiralty Bay, with an area of 122.08 km^2, is the largest (Rakusa-Suszczewski 1980). It is wide-open to the Bransfield Strait and the input of Bellingshausen Sea waters undoubtedly influences its ichthyofauna, which has been well described through the efforts of scientists from the Henryk Arctowski Antarctic Station. A detailed list of fish taxa which inhabit Admiralty Bay was published by K. E. Skóra and A. V. Neyelov (1992). This list, supplemented with data obtained by C. Żukowski, K. Zdzitowiecki and T. Zadrożnego, was also presented by J. Kulesz [1998].

A comparison of this list with the data presented in Table 1 shows many similarities between the ichthyofauna composition of Admiralty Bay and that of the northwestern shelf of the island. There are 27 common fish species from 7 families. The most common in both basins are Nototheniidae and Channichthyidae. However, some differences were also confirmed between the ichthyofauna of the two basins. This may result from different catch methods, but environmental influence must also play an important role. Fish from three families which occurred in the bay were absent on the shelf, including: Artedidraconidae, Harpagiferidae and Gempylidae. Specimens of two families, Gadidae and Paralepididae, which were not present in Admiralty Bay occurred on the shelf.

Among families which occurred in both basins, 8 fish species were observed only on the King George Island shelf and not in Admiralty Bay. It must be emphasized that, although fish of the deep water family Zoarcidae occur in both basins, their species composition is completely different.

Greater fish concentrations in Antarctica which serve as a resource base for fisheries usually occur above shelves which surround islands and which are up to 500 m deep (Andriashev 1965). Taking into consideration the magnitude of fish resources and the ease of fishing, re-

gions which are especially important for fisheries have been identified. In the Atlantic sector of Antarctica these regions are: South Georgia, the South Orkneys, Elephant Island, Joinville Island and King George Island. These fishing grounds are relatively small.

Just as in other regions of the Atlantic sector of Antarctica, the following fish species are commercially significant on the shelf of King George Island: *Champsocephalus gunnari*, *Chaenocephalus aceratus, Pseudochaenichthys georgianus, Notothenia rossii marmorata* and *Notothenia (Gobionotothen) gibberifrons*. Additionally, *Chionodraco rastrospinosus* makes a significant contribution to the catches, just as it does in the region of the South Orkneys (Sosiński, 1994). However, this species does not occur in the fishing grounds of South Georgia which belongs to the South Georgian Province. *Chionodraco rastrospinosus* is a species which typically inhabits the Continental Province of the zoo-geographical Region of Antarctica (Andriashev, 1965). In control catches which were carried out in 1979 by the R/V PROFESOR SIEDLECKI, *Chionodraco rastrospinosus* constituted 25%, 15% and 10% in the regions of the South Shetlands, Elephant Island and the South Orkneys, respectively (Sosiński and Skóra 1979).

Chaenodraco wilsoni, the most abundant species caught at the fishing ground near Joinville Island, is sporadic in the region of the South Shetland Islands. It was relatively more abundant in the control catch which was carried out in a place similar to Joinville Island in the Bransfield Strait (Fig. 2).

Density varied in different years (Table 2). This resulted from specimen biomass fluctuations and the seasonal character of their concentrations. It was also influenced by the number and effectiveness of the control catches. Repeatedly during the investigations, greater concentrations of fish occurred near the bottom (at depths below 250 m) than in shallow waters.

The concentrations, expressed as the mass of caught fish per fishing effort unit or per trawled unit area, are comparable to those obtained from the other regions of the Atlantic sector of Antarctica which have been reported by different authors for different seasons (Table 5).

The estimated fish biomass was derived based on the average concentration of fish in particular depth strata (Table 2) in the sub-areas investigated. This figure varied from about 4,000 to about 23,000 tons in an area from 3,000 to 5,900 km^2 (Table 3). The total area of the South Shetland shelf, which spreads mainly to the northwest of King George Island and Livingston Island, is about 20,000 km^2.

During the 1975-1976 and 1977-1978 seasons the total biomass of five basic fish species which occur near South Shetland amounted to approximately 123,000 tons (K. H. Kock *et al.* 1985 – Table 51).

The results presented in Table 4 and in Figures 4 to 12 refer to the biological state of the fish species investigated. A common feature of these species was usually the generally equal proportion of both sexes (1:1) in the stocks investigated. It must be noted, though, that the investigations were carried out only during the Antarctic summer.

Table 5. Mean bottom density of fish in Atlantic Antarctic Area

Sub-area	Season	Mean CPUE								Cruise type[a)]	Source
		[kg/hour]				[kg/km]^2					
		Stratum [m]									
		< 150	150-250	250 <	mean	< 150	150-250	250 <	mean		
South Georgia	1976/77						34,800	17,700		C. C.	Ślusarczyk *et al.* 1985
	1977/78						5,700	5,800		C. C.	
	1978/79						1,500	1,700		S. C.	
	1980/81					19,200	9,400	5,700		C. C.	
	1981/82					14,700	9,100	12,900		C. C.	
	1984/85					5,554	3,501	924		S. C.	Kock 1986
	1986/87	300	1,092	378	790	1,153	3,069	1,489	2,298	S. C.	Sosiński, Szlakowski 1992
	1987/88	184	594	76	388	689	2,085	360	1,336	S. C.	
	1988/89	276	584	268	432	1,078	2,410	833	1,734	S. C.	
South Orkney	1978/79				1,100					C. C.	Sosiński 1994
	1978/79				1,090					S. C.	
	1979/80				1,990					C. C.	
	1983/84				180					S. C.	
	1984/85					350	851	1,207		S. C.	Kock 1986
Elephant	1984/85					2,443[1]	6,822[2]	1,741[3]	146[4]	S. C.	Kock 1986
King George (South Shetland)	1978/79		133	876	780		946	6,225	5,544	S. C.	Table 2
	1979/80			674				6,315		C. C.	
	1980/81			163				1,366		S. C.	
	1986/87			770				7,297		S. C.	
	1987/88	12	128	149	90	95	1,042	1,210	729	S. C.	

[a)]Cruise type
S.C. - survey
C.C. - commercial

1) stratum 0-100 m
2) stratum 100-300 m
3) stratum 300-400 m
4) stratum 400-500 m

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A study of polymorphism within growth hormone gene 2 in sea trout from Polish coastal rivers using heteroduplex analysis

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Abstract. Polymorphism within growth hormone gene 2 (GH2), which is 1,489 bp in length and includes both introns and exons, was investigated in populations of sea trout from six Polish coastal rivers. The GH 2 fragment was amplified by PCR, and digested with the restriction enzyme *Hin*fI. It was then analyzed using the heteroduplex method. Two alleles were identified and no significant differentiation in their frequency among the investigated populations was observed. Differentiation in the frequency of the heterozygotes was found. No deviation from the Hardy-Weinberg rule was observed in the investigated populations; this reveals that no mixing of genetically isolated populations occurs (the Wahlund effect).

Key words: sea trout, heteroduplex, growth hormone gene, heterozygosity, population genetics

INTRODUCTION

Due to its potential importance in aquaculture for the growth hormone, its gene in fish has been under investigation for over 10 years. At the end of the 1980s it was learned that if recombinant growth hormone (GH) was given to cultivated rainbow trout, it increased their growth (Agellon *et al*. 1988a). In the following years, the structure and sequence of the growth hormone gene were determined for various fish species, such as seabream (Funkenstein *et al*. 1991), rainbow trout (Agellon *et al.* 1988b) and Pacific salmon (Devlin, 1993). Salmonids are characterized by two types of GH gene (1 and 2) due to genome duplication (tetraploidy) (Devlin, 1993). Among some specimens the occurrence of a GH2 type pseudogene was confirmed (Nakayama *et al.* 1999). The application of the PCR technique allowed the GH gene sequence to be used to investigate genetic polymorphism in populations, e.g. by means of restriction analysis (Gross and Nielsson, 1999) or heteroduplex analysis (Gross *et al.* 1996).

The genetic investigations of sea trout (*Salmo trutta*) populations revealed a low level of polymorphism of allozymic loci. Over two-thirds of the 33 loci investigated for populations of sea trout in Polish rivers were monomorphic with one allele (Łuczyński *et al.* 1997, Wenne *et al.* 2000). Two alleles were confirmed at every other loci. In order to investigate the genetic polymorphism of a sea trout population, including heterozygosity, it is necessary to apply more polymorphic chromosome markers, such as microsatellite DNA or other sequences for coding or non-coding DNA. Gross and Nilsson (1995) described a method using heteroduplex analy-

sis for finding polymorphism in a single copy of the GH gene 2 for sea trout. The basic assumption in the method is that the lack of full compatibility of sequences in DNA heteroduplexes causes changes in the three dimensional helix structure. Due to spatial deformations, heteroduplex molecules migrate during electrophoresis in the polyacrylamide sequencing gel slower than molecules which are fully complementary. Heteroduplexes are obtained through the denaturation and then renaturation of PCR products from the matrix of the diploidal locus of a heterozygotic specimen. Heteroduplexes are not created for homozygotic specimens, since identical allele do not vary by sequences.

The aim of this work was to identify genotypes for the GH2 gene sequence and to determine their frequency and heterozygosity in the sea trout populations of six Polish coastal rivers. The possible confirmation of heterozygote deficiency could indicate that isolated reproduction populations of sea trout mix (the Wahlund effect).

MATERIALS AND METHODS

The sea trout spawner samples were collected from four rivers in Pomerania, the Vistula River and its tributary, the Drwęca River, from September to December 1996 (Fig. 1). Fish in the Parsęta River were collected by electrofishing 40 km above the river mouth. Fish in the Rega, Wieprza, Słupia and Drwęca rivers were caught in traps and used in artificial reproduction during the annual fish stocking program carried out by the Polish Anglers' Union. The traps were located at the following distances above the river mouths: in the Rega – 14 km, in the Wieprza – 3 km, in the Słupia – 28 km and in the Drwęca near Lubicz near Toruń. Fish from the Vistula River were caught in the river or at the distance of 1 km from the river mouth. For the investigations, pieces of caudal fins were collected from about 40 specimens of each sample. The pieces of tissue were preserved in 95% ethanol and kept at a temperature of 4°C. The DNA genome was isolated by the mini-column method using Genomic DNA Prep Plus sets (A&A Biotechnology, Gdynia) according to the manufacturer's instructions.

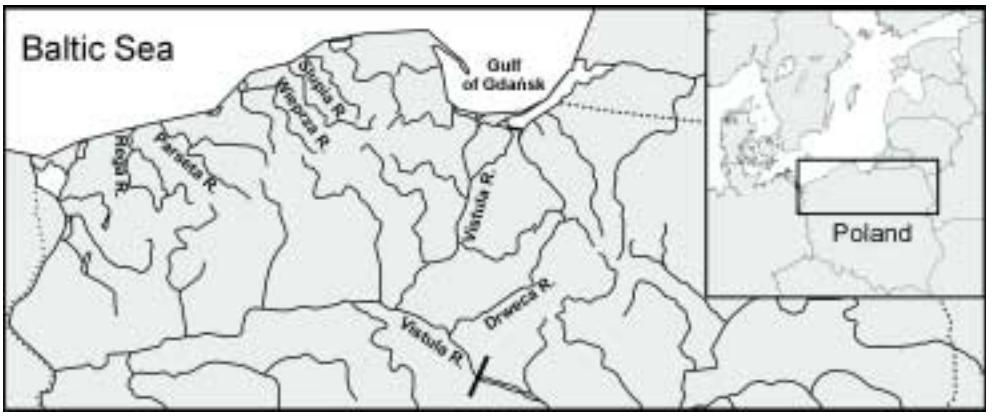

Fig. 1. Map presenting six rivers from which migrating sea trout samples were collected

A newly revised method of heteroduplex analysis, which allows for the identification of homozygotes types, was applied (Gross and Nilsson, 1995). The full GH2 sequence, which is 1,489 bp in length and includes introns and exons, was PCR amplified using the following primers: GH2-b: 5'-CACGTGAAGAATCATCCTT-3' and GH2-d: 5"-CCCTGGAGACAGGCTCTTGC-3'. The PCR products were separated by electrophoresis in 1% agarose gels and made visible by staining them with ethidium bromide under UV light. The PCR products obtained for the investigated samples of sea trout and the DNA indicative for salmon were digested with endonuclease *Hin*fI. Equal volumes of the digested PCR product of salmon and sea trout were combined to a total volume of 20 µl. EDTA was then added to the mixture to obtain the final concentration of 10 mM. The sample was then heated to 98ºC (denaturation), and then incubated at a temperature of 68ºC for one hour (renaturation). The aliquotes of mixtures, whose volumes varied from 10 to 20 µl, were placed on 8% (29:1) polyacrylamide gels and were electrophoresed in the TBE buffer. The gels were silver stained (Sambrook *et al* 1989). The X^2 and G tests were applied to evaluate the compliance of the observed genotype frequencies with the Hardy-Weinberg rule.

RESULTS

After the electrophoresis of PCR products digested with the enzyme *Hin*fI, the sea trout genotypes were identified by the presence of the heteroduplex band above the 193 bp restriction fragment (Fig. 2). Heterozygotes AB were identified after the electrophoresis of digested PCR products without adding the salmon DNA. The occurrence of two bands in the region of 193 bp indicated that the specimen was a heterozygote. The type of homozygote, AA or BB, was determined after electrophoresis of the mixture of sea trout and salmon DNA as follows: a single fragment 193 bp indicated homozygote AA, two fragments around 193 indicated homozygote BB. Table 1 presents the frequency of genotypes and alleles and the observed heterozygosity for investigated populations of sea trout from six rivers. Homozygotes AA dominated in all populations. The differentiation of heterozygotes AB frequencies was found. The BB homozygote did not occur in any population. Allele A was the most common in all populations. Frequencies of alleles and genotypes in populations from the Rega and Drwęca did not vary. The level of heterozygotes observed revealed differences among the investigated populations of sea trout and it was the highest in the Słupia River. No statistically significant differences between the observed (H_o) and expected (H_e) heterozygosity were observed. Therefore, no deviation from the Hardy-Weinberg rule was found in the studied populations. The average values of the population

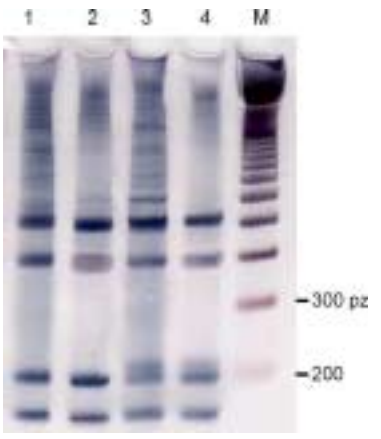

Fig. 2. DNA electrophoresis in 8% polyacrylamide gel silver stained. Restriction patterns of gene GH2 amplified with PCR and digested with *Hin*fI for sea trout. Occurrence of additional, less apparent band above intense band which reflects DNA fragment 193 bp in length identifies heterozygotes AB (lines 3 and 4). DNA fragments 200 and 300 bp in length are marked. M – molecular marker.

Table 1. Frequencies of genotypes and alleles of growth hormone GH2
and level of observed heterozygosity H_o in samples of sea trout from six Polish rivers
N – number of specimens in a sample. Number of specimens of particular genotype is given in parenthesis.

Population	N	Genotype frequency			Allele frequency		Observed Heterozygosity
		AA	AB	BB	A	B	H_o
Rega	36	0,944 (34)	0,056 (2)	0	0,972	0,028	0,056
Parsęta	38	0,816 (31)	0,184 (7)	0	0,908	0,092	0,184
Wieprza	36	0,833 (30)	0,167 (6)	0	0,916	0,084	0,167
Słupia	34	0,794 (27)	0,206 (7)	0	0,897	0,103	0,206
Wisła	40	0,875 (35)	0,125 (5)	0	0,938	0,062	0,125
Drwęca – Vistula tributary	36	0,944 (34)	0,056 (2)	0	0,972	0,028	0,056

differentiation coefficient F_{ST} for six investigated populations of sea trout were very low: 0.0023 for allele A and 0.0002 for allele B.

DISCUSSION

Investigations of a small number of specimens (7 and 14 respectively) revealed that two populations of sea trout from Sweden and Estonia varied in frequencies of allele and genotypes of the growth hormone gene (GH2) (Gross and Nilsson, 1995). The Swedish population was characterized by the occurrence of homozygote AA, while the Estonian population was characterized by the occurrence of mainly homozygote BB and common heterozygotes (43%). In the investigated populations of sea trout in Poland no homozygote BB was found. The results obtained indicate the similarity between the Polish and Swedish populations of sea trout.

The allozyme studies revealed that the average heterozygosity observed (H_0) for sea trout from the Vistula, Słupia, Parsęta and Rega rivers varied from 3.5 to 5.7 (Łuczyński *et al* .1997) and it was comparable with populations from other regions of Eastern Europe (Osinov, 1984; Paaver, 1989). The investigations of the gene GH2 polymorphism indicated that the value H_o for populations of sea trout in the Rega and Drwęca rivers was about 5.6%, while for populations from the Słupia and Parsęta rivers was about 20%. The values H_o for locus GH2 were higher than in the case of allozymic loci. The lack of a heterozygote deficiency indicates that in the investigated Polish populations of sea trout the genetic Wahlund effect does not occur. It suggests the lack of a genetic effect of reproductively isolated populations mixing.

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