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Comparison of fecundity of pikeperch (*Stizostedion lucioperca* [L.]) in three lagoons in the southern Baltic Sea

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Abstract. This paper presents the results of pikeperch fecundity estimates made using materials collected in the pre-spawning season of 2000. Pairs of ovaries were collected from fish inhabiting the Polish zones of the Szczecin and Vistula lagoons and the Russian zone of the Curonian Lagoon.

It was confirmed that the dependencies of absolute fecundity on age, length and gutted weight of fish which reproduce in the Szczecin Lagoon and the Vistula Lagoon are similar, but they vary significantly in those which reproduce in the Curonian Lagoon. The corresponding increases of absolute fecundity with total length and weight were the slowest in the Curonian Lagoon females. The relative fecundity of females from the Szczecin and Vistula lagoons increased along with total length, gutted weight and age. In the Curonian Lagoon, a dependence between relative fecundity and length and age was not confirmed, but as weight increased, relative fecundity decreased. Length at sexual maturation was determined based on the smallest females caught which had gonads in maturity stage IV on the Maier scale; in the Szczecin and Vistula lagoons it was 36 cm and 42 cm, respectively. After reaching a length of 42.9 cm, 50% of the females in the Szczecin Lagoon began to reproduce; in the Vistula Lagoon this figure was 43.9 cm.

Key words: Baltic Sea, Szczecin Lagoon, Vistula Lagoon, Curonian Lagoon, pikeperch (*Stizostedion lucioperca* [L.]), absolute fecundity, relative fecundity, length at sexual maturation.

INTRODUCTION

Pikeperch is a species which was originally endemic to the Ponto-Caspian basin (Berg 1949), but it now inhabits lakes, lower reaches of rivers, lagoons and brackish sea bays in Central Europe (Staff 1950). Brylińska *et al.* (1991) presents the current locations of pikeperch habitats in Eurasia. To the west, the pikeperch habitat extends to the rivers and lakes of France, and to the east it inhabits waters as far the Ural Mountains. The northern border of the pikeperch habitat are Scandinavian lakes and Baltic coastal waters and the waters of Karelia, extending even as far as the White Sea.

In Poland, the greatest numbers of pikeperch inhabit the northern lakes, lagoons and lowland dam reservoirs as a freshwater and semi-migratory species. It has adapted to lagoon waters, which include both river mouths and the lagoons proper, where reproduction conditions are advantageous. After spawning, the pikeperch from the Szczecin (Wiktor, 1954; Vistula (Filuk, 1955, 1962; Wilkońska, 1998; Borowski *et al.*, 1997) and Curonian lagoons (Samohvalova *et al.* 1987) migrate to the bays and coastal waters of the Baltic Sea to feed. According to Lehtonen *et al.* (1996), increasing eutrophication in the coastal areas of the Baltic Sea is advantageous for the spread of pikeperch habitats.

In Poland, pikeperch has long been the subject of studies and investigations and many publications regarding the age structure, growth, feeding patterns, migrations, seasonality of catches, etc. of this species have been published. However, only a few works have addressed the fecundity of pikeperch.

In publications regarding pikeperch inhabiting the Szczecin Lagoon, Wiktor (1954) discusses feeding patterns, growth rates, the age structure of the spawning stock and identifies spawning ground locations. In 1976-1977, Węgrzyn (1986) studied pikeperch fecundity with regard to age. This author also noted that the area of the spawning grounds decreased in comparison to that of the 1950s, and that excessive exploitation had influenced a decrease in fish stocks.

Studies of pikeperch in the Vistula Lagoon were conducted by Filuk (1955, 1962); he described the hydrological conditions of the basin and identified the spawning locations and periods as well as female fecundity. He also described the age structure of the spawning stock. Filuk (1967) also discussed issues concerned with pikeperch sexual maturity. Lugowaja (1991) presented information regarding the absolute fecundity of pikeperch which was estimated based on materials collected from 1977 to 1988 in the Russian part of the Vistula Lagoon.

Studies of the pikeperch from the Curonian Lagoon have focused on fecundity in relation to body length and weight (Apołłowa 1965) and selected biological issues, such as sexual maturity, spawning and nest locations, fecundity and fisheries (Virbickas *et al.* 1974), feeding patterns (Samohvalowa 1982), the dynamics of pikeperch stocks (Golubkova 1998), and fecundity in relation to body length (Samohvalova *et al.* 1987).

There are no works concerning the reproductive potential of pikeperch. If fecundity indices have been addressed at all, it has been in relation to such variable female characteristics as length, weight and age. The data presented for various ranges cannot, in fact, be compared. No studies have addressed the variations of reproductive potential measured in terms of population fecundity over time; not even the parameters of such a population are available. Variations in individual or population fecundity is one of the effects that can be registered when a population or stock adapts to changing environmental conditions.

The topic of the individual fecundity of pikeperch from northern Poland was undertaken in three doctoral dissertations that estimate the fecundity of this species in various basins. Terlecki (1976) estimated the fecundity of pikeperch from the following lakes in northern Poland: Wielimie; Jeziorak; Omólew; the Vistula dam reservoir near Włocławek.

The dissertation by Węgrzyn (1986) only includes selected data regarding the individual fecundity of pikeperch from the Szczecin Lagoon such as the average fecundity in age groups, age of females and males at sexual maturation, and the size of eggs at gonad maturity stage VI on the Maier scale. A review of the literature revealed a lack of studies dedicated to pikeperch fecundity in the German part of the Szczecin Lagoon.

The review of the available literature indicated that the fecundity of pikeperch in other Baltic states has also not been the subject of many studies. There are a number of interesting works dealing with migrations, growth, mortality, and recruitment (Lehtonen

1979; Lehtonen and Taivonen 1988, Lappalainemn *et al.* 1996). However, only the work by Lehtonen *et al.* (1996) includes a section which discusses the results of published data regarding such topics as sexual maturity, age at female and male sexual maturation (Virbickas *et al.* 1974, Winkler *et al.* 1989), the proportions of pikeperch spawning in the Pärnu Bay (Erm 1981), and the spawning season (Gaygalas *et al.* 1974). These authors, however, did not list the results of pikeperch population fecundity estimations from the Baltic Sea catchment area.

Of the authors who have discussed the fecundity of pikeperch of various European basins, Zivkov and Petrova (1993) must be mentioned. They analyzed variations in the dependencies between absolute fecundity and the length, weight and age of pikeperch from ten basins in Russia, Czechoslovakia, Bulgaria, Lithuania, Ukraine and Finland.

Raikova-Petrova and Zivkov (1998) studied spawning stocks of pikeperch inhabiting basins in Bulgaria. They analyzed the age at first maturity, the sex structure of the schools and the influence of temperature on spawning.

The aim of this work was to:

1. estimate the absolute fecundity of females which reproduce in the Szczecin, Vistula and Curonian lagoons;

2. compare the absolute fecundity of females from the three lagoon ecosystems of the southern Baltic Sea;

3. determine the individual female fecundity in the areas of their occurrence and the age when they reach sexual maturity.

MATERIALS AND METHODS

Materials were caught using trawls, fyke-nets and gill-nets in the spring of 2000 in the Polish zones of the Szczecin and Vistula lagoons and in the Russian zone of the Curonian Lagoon (Fig. 1). The eight-degree Maier scale was used to determine the gonad maturity stage (Maisner 1947). The analyses were made on pikeperch females whose gonads were, according to the Maier scale, in the IV stage (developed). Each female was measured to the nearest 1 cm in total length (l. t.). Their total and gutted weights were recorded to the nearest 10 g, the weight of both ovaries was recorded to the nearest g, and scales were collected to determine fish age. A total of 882 pairs of ovaries were collected (Table 1).

The ovaries were preserved according to the method described by Bleil and Oberst (1993). The gonads were frozen at a temperature of –20°C, and then defrosted and preserved in 80% ethylene alcohol. The subsequent procedures were similar to those used in the traditional methods. After the gonads had been removed from the alcohol, they were crushed, cleaned of tissues and dried. When this phase of preparation was complete, the gonads were weighed and three subsamples were weighed out for each gonad. These portions were counted using a binocular microscope.

Separate data bases were prepared for each lagoon; they include data which describes the absolute fecundity of females in relation to their length, weight and age. In order to determine female fecundity in relation to body weight, gutted weight was used, since the stomach contents varied, as did the weight of the gonads (Table 1).

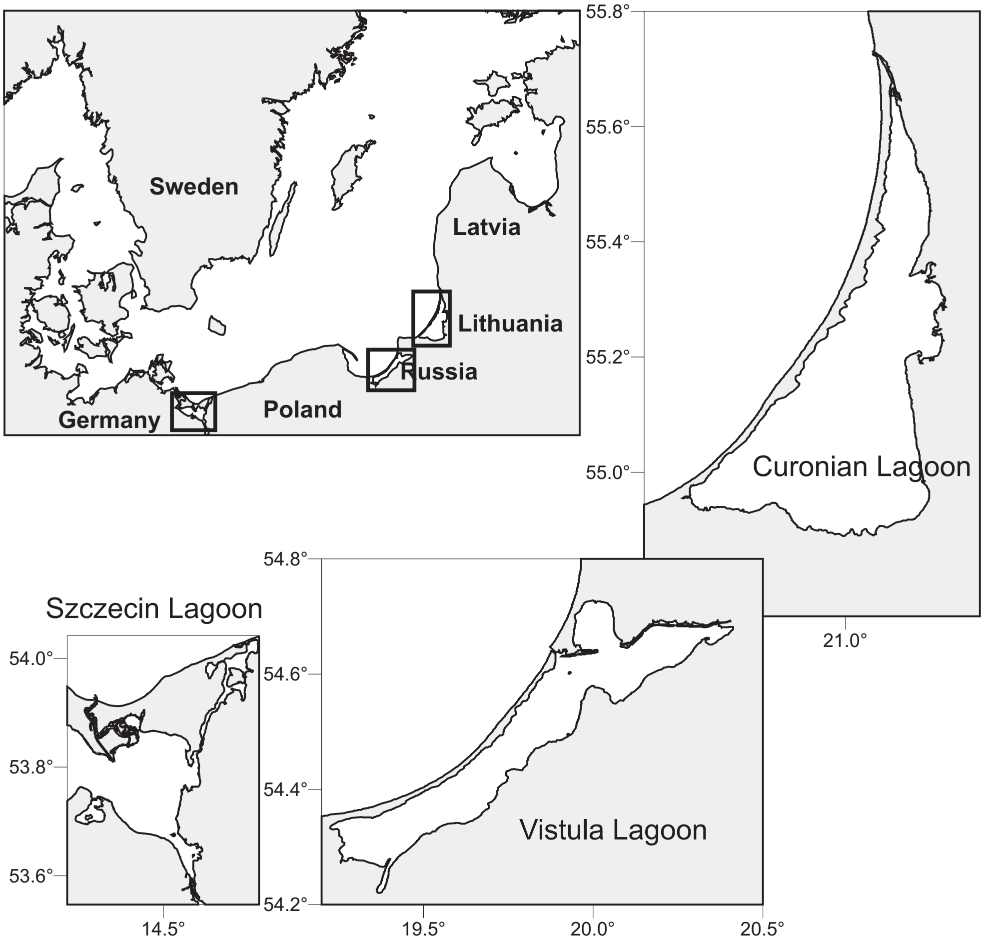

Fig. 1. Map of the southern Baltic Sea showing the locations of the Szczecin Lagoon, the Vistula Lagoon and the Curonian Lagoon

Table 1. Material collected in 2000

Lagoon	Females			Number of gonads		
	length ranges [cm]	weight ranges [g]	age groups	collected	analyzed	disregarded
Szczecin	39 – 91	485 – 6,715	3 – 14	334	312	22
Vistula	42 – 84	560 – 4,920	4 – 14	324	304	20
Curonian	48 – 81	1,010 – 5,130	3 – 11	224	217	7
Total				882	833	49

The fecundity was determined as the product of the number of eggs in the subsample and the index of the proportion between the weight of both ovaries and the weight of the subsample. The dependence of fecundity on length and weight was determined using regression analysis.

The dependence between the total length, gutted weight and age of a fish and absolute fecundity was described using the following exponential function:

$$F_a = a\, X^b$$

where:
F_a – absolute fecundity;
X – age, total length or gutted weight; *a, b* – parameters.

A linear relationship was obtained after the logarithm was obtained for both sides:

$$\log F_a = \log a + bX$$

The dependence between age, total length, and gutted weight and relative fecundity was described using the following linear relationship:

$$F_w = a + bX$$

where:
F_w – relative fecundity expressed as gutted weight [F_w(GW)];
X – age, total length, gutted weight; *a*, *b* – parameters.

The relationships obtained for three lagoons were compared using a series of tests described by Zar (1984).

After the parameters for the equations which describe the dependencies between length and the absolute female fecundity had been derived, the theoretical fecundity of 50, 60, and 70 cm long females was determined. This permitted comparing increases in the fecundity of the female pikeperch from the three lagoons with length.

The length at sexual maturation was determined. The criterion was the total length at which 50% of the specimens had gonads that had achieved at least stage III of maturity - developing on the Maier scale. Females with gonads in stages I and II were disregarded since it was assumed that they would not begin spawning in the 2000 spawning season. The smallest female whose gonads were in the developing stage was 36 cm long in the Szczecin Lagoon and 42 cm long in the Vistula Lagoon.

Using empirical data, i.e. the percentage of fish which reached sexual maturity according to length classes, frequency curves of females which had begun spawning were made. These data were used to determine the functional dependence between the features compared. It was assumed (Rickey 1995) that such a dependence is described by the logistic curve that follows:

$$P_L = 1 / (1 + e^{(a+b)\,L)})$$

where:
P_L – maturity at length L;
a and b – coefficients derived from empirical data;
L – fish length.

The length at which 50% of the fish reach sexual maturity was determined using the Delta method (Seber 1982).

$$L_{50\%} = -a/b$$

STUDY AREAS

The hydrographic conditions in these three lagoons (Fig. 1) are shaped by geographic and climatic factors. It follows that the fecundity in the basins may vary in response to the various hydrographic conditions prevailing in them.

The Szczecin Lagoon

This lagoon formed as an overflow-arm of the Oder River mouth. It is separated from the sea by the Uznam and Wolin islands, and is connected to the sea by the Dziwna, Świna and Piana straits. This basin, which lies parallel to latitudinal lines, is a proper lagoon divided at a narrowing into the Large Lagoon (Zalew Duży) and the Small Lagoon (Zalew Mały) and their adjacent waters. The lagoon falls under the jurisdiction of both the Polish and German governments. The Polish portion is comprised of the Large Lagoon, including its bays and straits, the Kamieński Lagoon, Dziwna River, Wicko Lake, Świna River, Piastowski Canal, Warpnieńskie Lake and Odrzańska Brook. It covers an area of 410 km^2, and at its widest point it measures 22.5 km. The German portion is comprised of the Small Lagoon, which has a surface area of 277 km^2 and has a maximum width of 16 km. According to Majewski (1980), the shoreline of the Large Lagoon is not very diverse. The bottom of the lagoon is even and flat and it is surrounded by sandy shoals. The average depth of the Szczecin Lagoon is 3.8 m. The water salinity varies with periodic inputs of water from the Pomeranian Bay, and is, on average, about 0.4 psu.

The water exchange between the Szczecin Lagoon and the Pomeranian Bay occurs in both directions through the Dziwna, Świna and Piana straits. As the lagoon is near a river mouth, it is influenced by the waters of the Oder River and the Baltic Sea. Fresh water from the Oder prevails alternately with saline water from the Baltic that is forced into the lagoon by northerly winds. According to Pęczalska (1973), the high trophic level of the water results from the lagoon’s geographical location. Relatively frequent and rapid changes in water level and salinity mainly occur in the northern and central parts of the lagoon, while the thermal conditions of the expansive, shallow waters mainly depend on atmospheric and not hydrological conditions, which only have a slight influence. The Szczecin Lagoon is one of the most productive near-sea bodies of water due to the diversity of its ichthyofauna and the abundance of some of the species which inhabit it.

Vistula Lagoon

The Vistula Lagoon is situated along the eastern coast of the Gulf of Gdańsk. Although it is the second largest lagoon in the Baltic Sea, it is almost two times smaller than the Curonian Lagoon. It is a long, narrow, rectangular lagoon that stretches from the south-west to the north-east. It is separated from the sea by the Vistula Spit and the Sambia Peninsula. The lagoon is connected with the Baltic Sea in the north-west through the Bałtyjsk Furrow, which is 400 meters wide and 8-12 meters deep. The Polish-Russian border runs through the lagoon above the Pasłęka River delta. The area of the lagoon is 838 km^2. The south-west part of the lagoon, with an area of about 328 km^2, belongs to Poland (Łomniewski 1958). The Vistula

Lagoon is shallow and narrow; both of these factors influence its thermal and salinity conditions. The salinity varies from 0.8 to 4.5 psu during the year. The average depth does not exceed 2.5 m, and the maximum depth is 4.5m. The maximum width is 11 km, and it is 90 km long. Hydrological conditions in the eastern part of the lagoon differ from those in the western part. According to Piechura (1961), interactions between the lagoon's two different water regimes, marine and inland, are continuously taking place. After the Nogat River had been cut off in 1916, the impact of river waters decreased and marine waters began to prevail. Salinity variations occur mainly in the central part of the lagoon. The Vistula Lagoon is highly productive.

Curonian Lagoon

The Curonian Lagoon is located in the eastern part of the Baltic Proper, north of the Vistula Lagoon, and falls under the jurisdiction of Russia and Lithuania. It is the largest of the three lagoons described in this paper with an area of 1,584 km^2. It is 98 km long and 46 km wide. It is separated from the sea by the Curonian Peninsula which is 611.8 km long. It is connected with the Baltic Sea through a narrow, 18 m deep strait located in its northern part near Klaipeda. The lagoon's depth reaches 6.5 m. The narrow connection with the Baltic Sea means that the water salinity is varied. According to Dubra *et al.* (1998), it ranges from 1.6 psu near Klaipeda to 0.03 psu in the south.

RESULTS

Szczecin Lagoon

The absolute fecundity of the females studied varied from 73.7 thousand to 2 024.1 thousand eggs. The fecundity of females 45 cm long was estimated at 12.8 to 234.9 eggs (Tab.2). Absolute fecundity increased along with length up to 80 cm; fecundity decreased at lengths greater than this. The length-fecundity dependence was curvilinear (Fig. 2a).

The absolute fecundity in relation to body weight (gutted fish) was estimated from the distribution of this feature in 43 classes from 401 g to 6,800 g. The average fecundity increased in subsequent weight classes from 73.8 thousand eggs at 485 g to 1 844.7 thousand eggs in the heaviest class at a weight of 6,715 g. The highest fecundity, 2 024.1 thousand eggs, was estimated for a female which weighed 4,195 g. Absolute fecundity increased along with body weight and the dependence was linear (Fig. 2 b). This figure demonstrates that a significant fecundity distribution was observed in classes above 3,000 g.

The studied material contained females from eleven age groups (from III to XIV). The absolute fecundity estimated for these age groups varied from 73.8 thousand to 1 844.7 thousand eggs. The highest maximum fecundity (2 024.1 thousand eggs) was estimated for age group X. The most common was age group VI (101 ovaries) in which fecundity varied from 318.1 thousand to 1 235.3 thousand eggs, with an average of 624.6 thousand eggs. The data indicate a high of absolute fecundity in subsequent age groups, as well as from age group IX and older (Fig. 2c).

The relative pikeperch female fecundity in the Szczecin Lagoon (the number of eggs per g of gutted weight) estimated for the length classes varied from 152 eggs at 39 cm to 643 eggs

Table 2. Absolute fecundity *Fa* according to total length clases

l.t. [cm]	Szczecin Lagoon				Vistula Lagoon				Curonian Lagoon			
	min.	max.	average	*n*	min.	max.	average	*n*	min.	max.	average	*n*
39	73799	73799	73799	1								
41	167504	167504	167504	1								
42					116137	116137	116137	1				
43	150923	262809	200997	3								
44	166784	236538	192694	3								
45	122821	234900	179327	3	189101	227425	204792	6				
46	201403	268300	243360	4								
47	104225	498040	250733	10	172273	295135	218508	6				
48	188236	388835	257061	11	241014	258408	252040	3	214620	361398	294220	8
49	199540	361769	275192	13	196358	342133	260557	11	243820	502729	325974	7
50	234381	484398	325521	14	235666	397296	290230	18	295881	387457	336887	8
51	231916	461457	322633	13	198465	327582	281191	11	277454	404955	346778	8
52	205539	438217	309232	18	231348	412425	328787	11	302927	452523	365095	9
53	276967	514913	364594	10	277410	498071	380000	10	326974	416026	391014	8
54	266270	402976	336906	10	347595	493983	403185	11	336569	566782	420173	8
55	410158	468149	439153	2	285895	579162	393023	16	344050	441133	390885	8
56	423104	450753	436929	2	379828	570791	456518	16	363981	544337	456823	8
57	297446	630920	463501	6	331748	637663	482331	9	382047	615411	499762	8
58	418832	586823	494722	7	443440	627089	514571	20	276024	669832	457771	7
59	386624	633555	484510	10	375168	657866	512037	18	400766	527924	478256	8
60	426423	650413	533920	16	392063	713714	578596	13	408208	790938	537009	8
61	336569	784714	557617	19	470810	774498	591534	18	363833	762908	559273	8
62	476993	1026476	649079	16	430570	736979	624608	15	485860	793714	600633	8
63	426419	1015760	626685	18	412163	822059	597975	8	547845	737698	643829	8
64	562310	867871	701059	16	476015	806998	662527	11	578794	856270	664126	8
65	318184	1202570	718439	16	494651	951500	771210	12	521332	826199	673276	8
66	596576	1235365	858445	12	609681	1005193	780936	8	596613	796758	682440	8
67	734504	1561784	1035752	10	564251	1035501	743960	4	666569	891582	769412	8
68	667512	1174082	902189	10	771788	1217711	965967	8	600708	919240	762263	8
69	722100	1131339	949124	7	984216	1158604	1071410	2	626623	986258	773842	8
70	1281442	1281442	1281442	1	990861	1212938	1100344	6	628196	927243	806405	8
71	686276	1248236	1010434	9	1036418	1269001	1141128	5	525778	1154959	819659	8
72	803085	803085	803085	1	1061208	1494255	1321976	3	633186	975957	833599	7
73	816113	1225030	1020571	2	1045009	1654165	1293308	6	887767	1081686	958247	3
74	1109527	1311996	1220705	3	916353	1458923	1170234	7	742550	1099576	909375	4
75	1167265	1323255	1245260	2	1121540	1623175	1341304	4	784522	1066062	961898	5
76					1618490	1618490	1618490	1	770163	1134983	953636	3
77	1410347	1927199	1668773	2	1649219	1649219	1649219	1	1107288	1107288	1107288	1
78	1314332	1446844	1380588	2	1458928	1798212	1588833	3	1112955	1307436	1210195	2
79	1901591	2024152	1962871	2	1788596	1788596	1788596	1				
80	1343213	1343213	1343213	1								
81	1126252	1735237	1497978	3					1164502	1164502	1164502	1
82	1168863	1168863	1168863	1								
84	1378896	1378896	1378896	1	1852823	1852823	1852823	1				
91	1844707	1844707	1844707	1								
Total	73799	2024152	594507	312	116137	1852823	595767	304	214620	1307436	593262	217

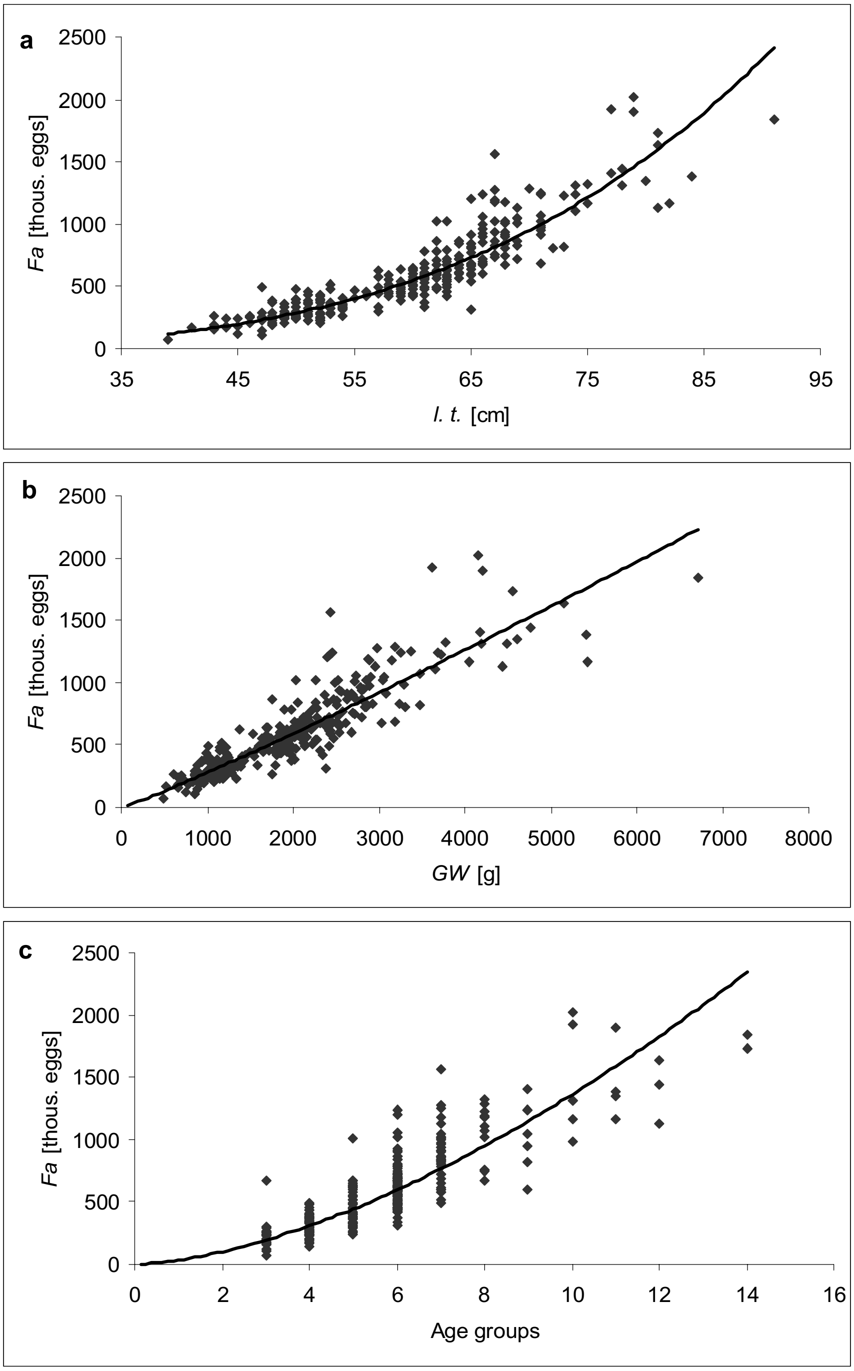

Fig. 2. Dependence of absolute fecundity on fish length (a), gutted weight (b) and age (c) in the Szczecin Lagoon

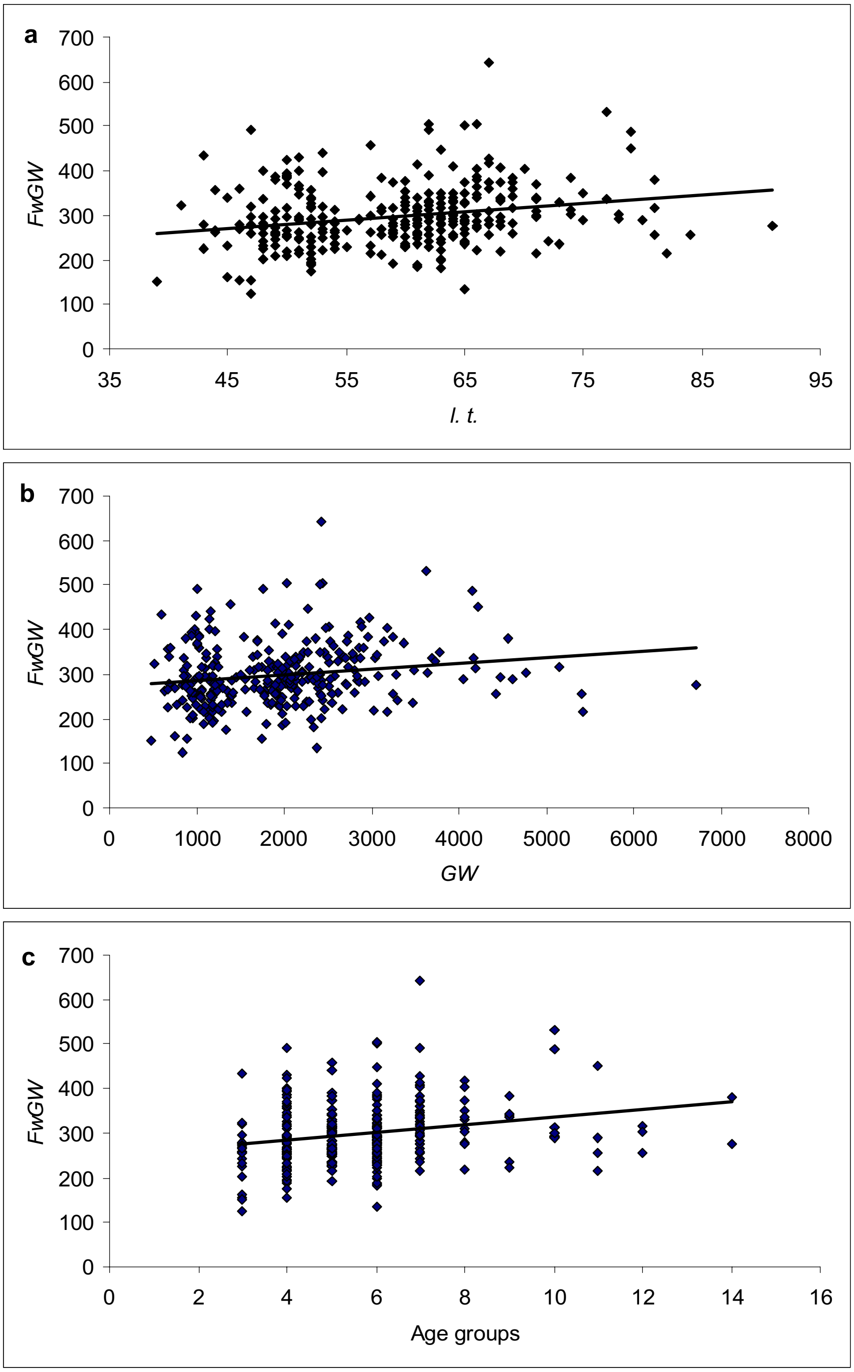

Fig. 3. Dependence of relative fecundity on fish length (a), gutted weight (b) and age (c) in the Szczecin Lagoon

at 67 cm. A female measuring 91 cm had a relative fecundity of only 275 eggs. The data confirm various values of fecundity in the different length classes (Fig. 3a).

The relative fecundity in the weight classes ranged from 152 eggs at 485 g to 643 eggs at 2,500 g. However, females weighing 6,715 g had only 275 eggs per gram of body weight. The highest fecundity was observed among females from the 1,500- 4,500 g classes. The data reveal significant differences in the fecundity of females from the same weight classes (Fig. 3b).

The lowest relative fecundity according to age group was 123 eggs for age group III females, while the highest was 643 eggs for age group VII females. The fecundity of females from age group XIV varied from 275 to 381 eggs (Fig. 3 c). The average relative fecundity for the entire sample was 299 eggs per g of female body weight.

Vistula Lagoon

The estimated fecundity of the smallest female (42 cm) was 116.1 thousand eggs, and that of the longest female (84 cm) was 1852,8 thousand eggs. The latter had the highest absolute fecundity of the study sample. The fecundity of females from the 45 cm length class ranged from 189.1 to 227; 204.8 eggs was the average (Table 2). The data obtained revealed that absolute fecundity in the Vistula Lagoon females increased along with length increase. The dependence was curvilinear (Fig. 4a).

Absolute fecundity in relation to body weight was estimated for 39 classes. The average fecundity varied from 116.1 thousand to 1852,8 thousand eggs. The data indicated that the absolute fecundity increased uniformly as body weight increased. This is confirmed by the linear character of the increase (Fig. 4 b).

There were females from eleven age groups in the sample from this lagoon. The absolute fecundity of the females in subsequent years of life from age group IV to XIV ranged, on average, from 260.3 thousand to 1655.8 thousand eggs. The most specimens in the sample belonged to age group V. The average, estimated fecundity was 364.6 thousand eggs. As was the case with length and body weight classes, absolute fecundity in the females increased with age. Beginning with age group VIII, there is a high distribution of empirical data points; this resulted from the small number of older females studied (Fig. 4c).

The relative fecundity estimated for the smallest length class studied, 42 cm, was 207 eggs, while for the longest class, 84 cm, it was 377 eggs. The lowest fecundity, barely 172 eggs, was confirmed for females 51 cm long. The relative fecundity increased with length (Fig. 5a).

When relative fecundity was classified according to gutted weight (Fig. 5b), females weighing 1,210 g from age group IV had the lowest at 172 eggs, while a female weighing 1,000 g from the VI age group had 503 eggs. The data reveal that the relative fecundity in weight classes increased as weight increased. Similar tendencies were also observed in the age groups (Fig. 5c). The average relative fecundity estimated for the entire sample of females was 304 eggs per g of body weight.

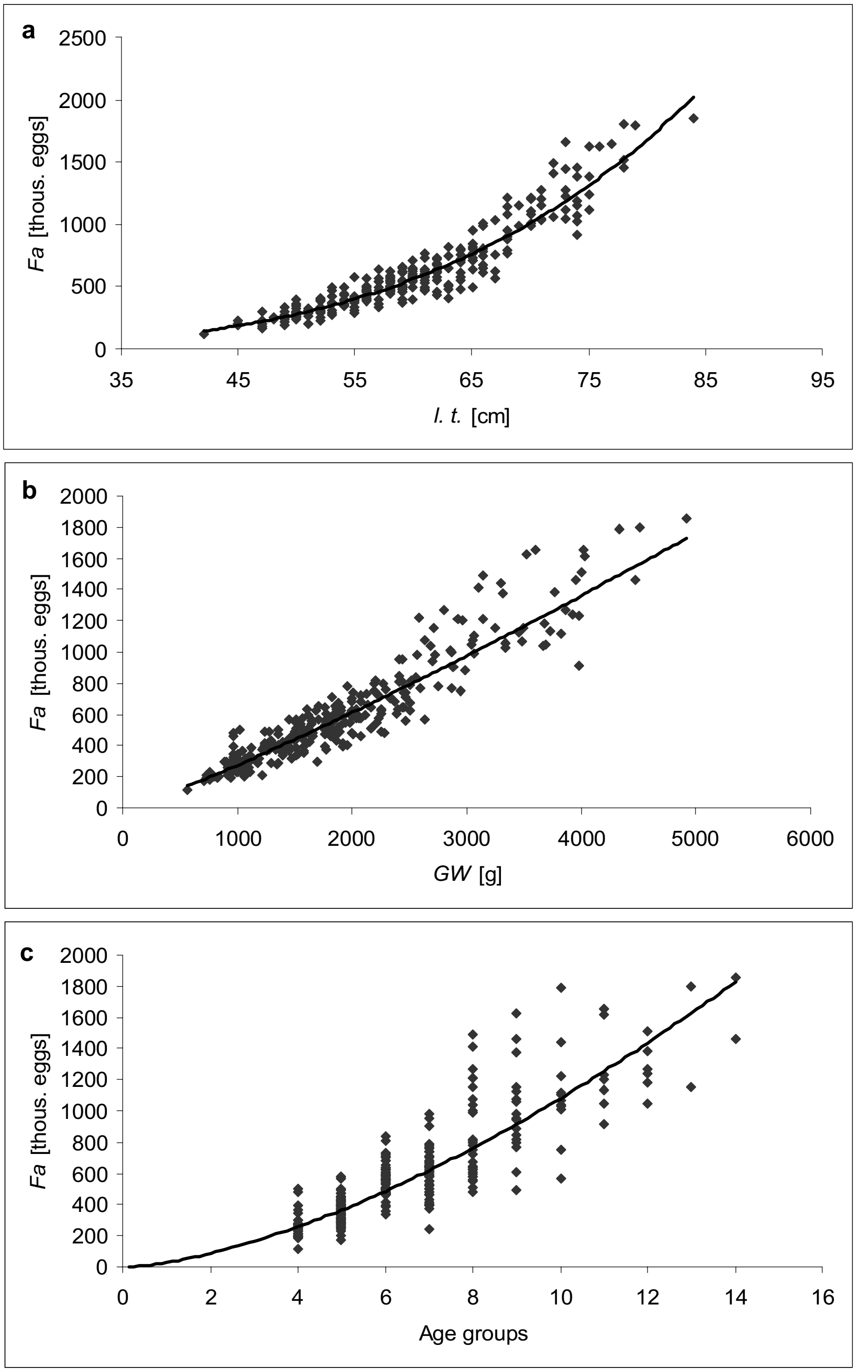

Fig. 4. Dependence of absolute fecundity on fish length (a), gutted weight (b) and age (c) in the Vistula Lagoon

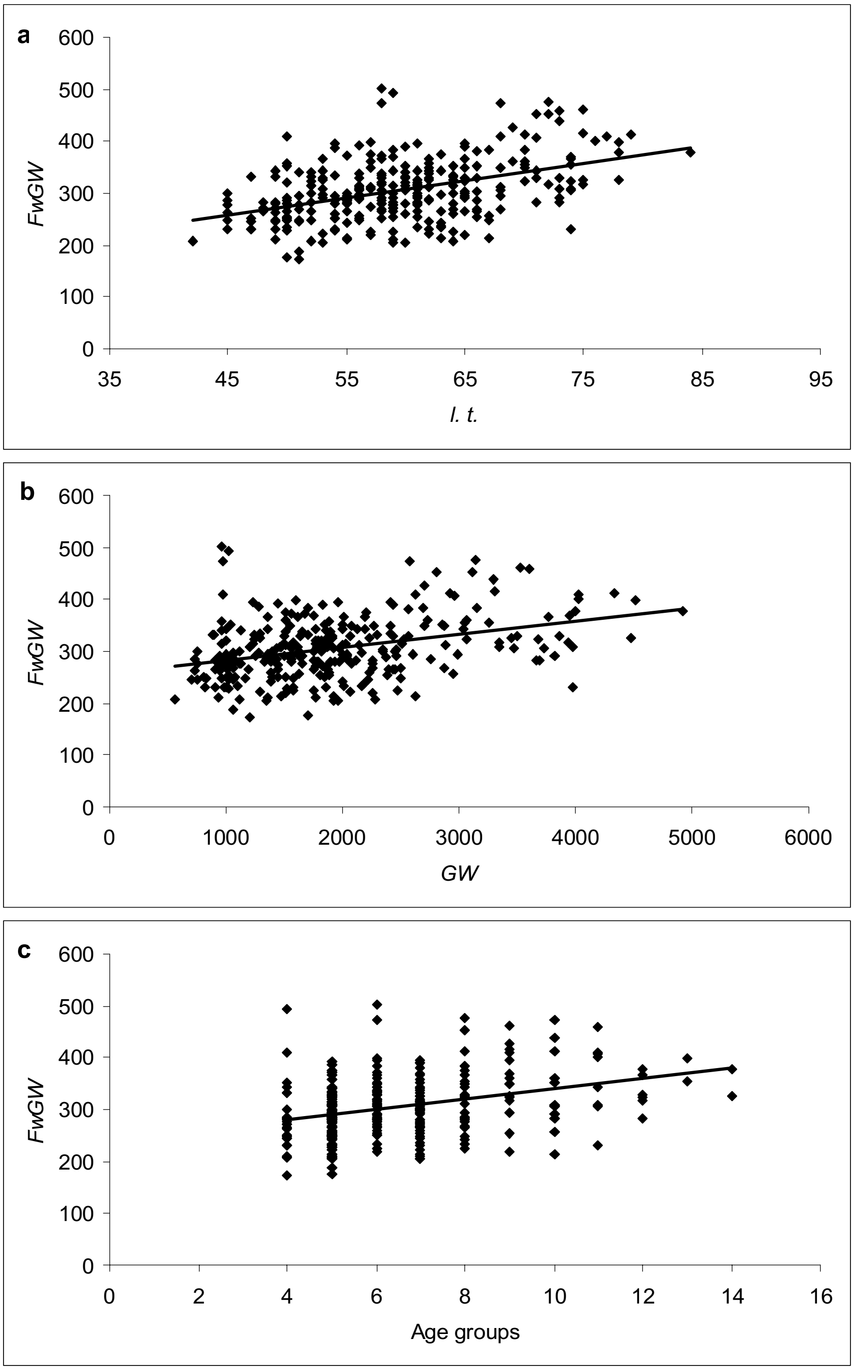

Fig. 5. Dependence of relative fecundity on fish length (a), gutted weight (b) and age (c) in the Vistula Lagoon

Curonian Lagoon

The absolute fecundity of pikeperch females in the Curonian Lagoon was estimated for 32 length classes. The lowest fecundity was noted in a female 48 cm long at only 214.6 thousand eggs, while a female 81 cm long had 1164.5 thousand eggs (Table 2). The data revealed that the absolute fecundity of females which inhabit the Curonian Lagoon increased as their length increased and that the dependence is curvilinear (Fig. 6a).

Absolute fecundity was classified according to 31 weight classes. The average fecundity estimated from the ovaries of five females varied from 318.4 thousand eggs at a body weight of 1010 g to 1164.5 thousand eggs at a body weight of 5130 g. The absolute fecundity of females from the Curonian Lagoon increased along with weight. The increase was linear (Fig. 6b). An increasingly greater distribution of fecundity values was observed as weight increased.

Absolute fecundity was estimated for ten age groups. Age group VII was the most numerous, and its fecundity varied from 276.0 thousand eggs to 566.6 thousand eggs. The average fecundity in subsequent age groups was related to the increase of eggs (Fig. 6c).

When relative fecundity was recalculated for gutted weight, the lowest value, 138 eggs, was found in the ovary of a 58 cm female weighing 1 930 g from age group VII. The highest relative fecundity, 449 eggs, was noted for a 49 cm female which weighed 1200 g from age group VI. Relative fecundity showed significant diversity in subsequent length classes. The average relative fecundity of the entire sample in age groups was 268 eggs. The empirical data revealed that the relative fecundity both in length and weight classes, as well as age groups, was very diverse. However, in general, as length, body weight and age increased, relative fecundity decreased (Fig. 7a, b, c).

Differences between lagoons

Exponent *b* in the dependence between total length and absolute fecundity varies from 2.7 to 3.8 (Table 3). Significant differences were confirmed between the values of coefficient *b* between the Curonian and the Vistula lagoons and between the Curonian and the Szczecin lagoons. No significant differences were confirmed between the Vistula and Szczecin lagoons.

Table 3. Parameters of the power dependence $F_a = a\ (l.\ t.)^b$ between total length, *l. t.*, and absolute fecundity, F_a

Lagoon	Parameter		n	R^2
	a	b		
Curonian	7.79	2.71	217	0.85
Vistula	0.10	3.81	304	0.91
Szczecin	0.26	3.56	312	0.85

Statistical analysis		
H_0: exponent *b* equal for the three lagoons	$P < 0.0001$	
Multiple comparisons	Line inclination	Line height
Curonian – Vistula	$P < 0.0001$	
Vistula – Szczecin	$P > 0.05$	$P > 0.25$
Curonian – Szczecin	$P < 0.0001$	

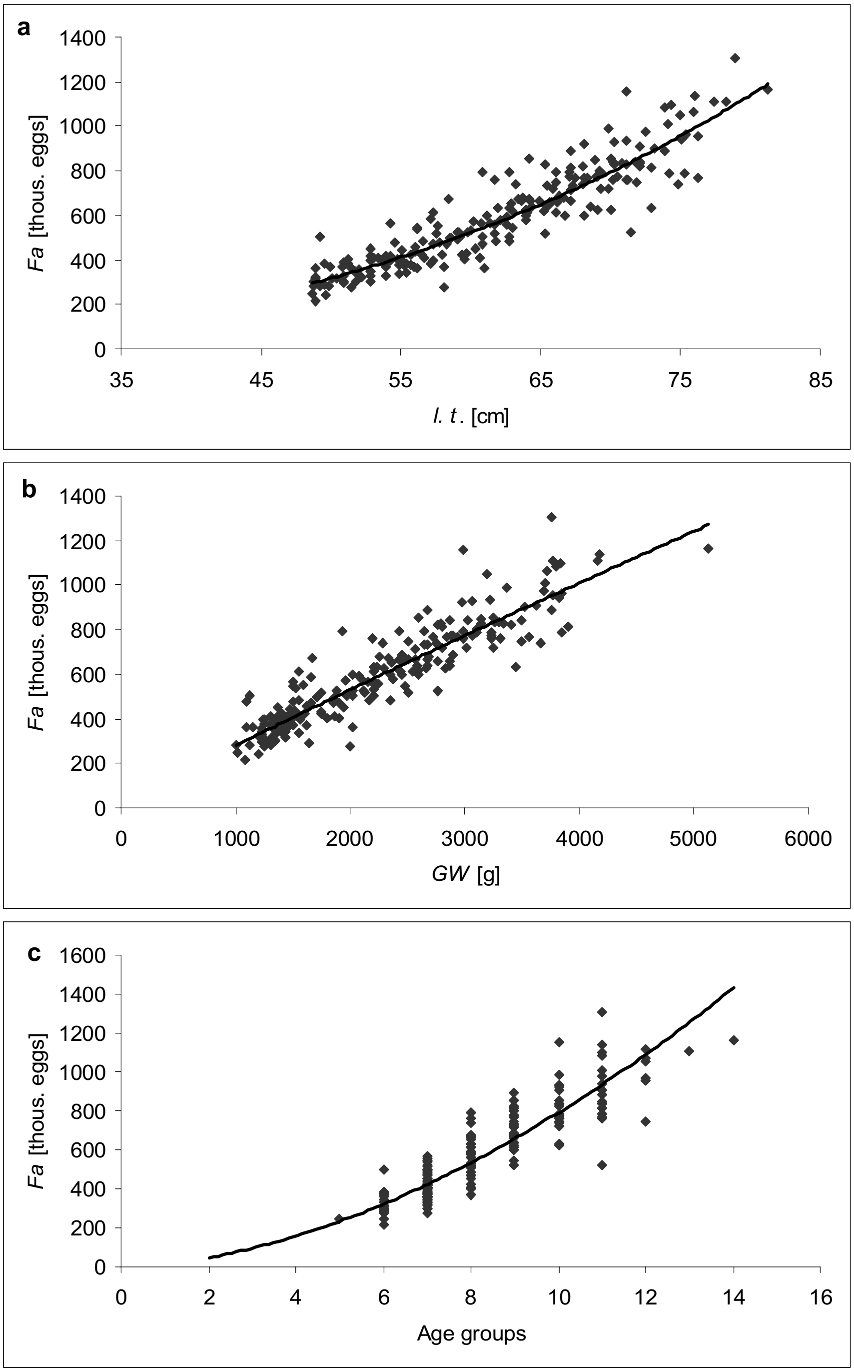

Fig. 6. Dependence of absolute fecundity on fish length (a), gutted weight (b) and age (c) in the Curonian Lagoon

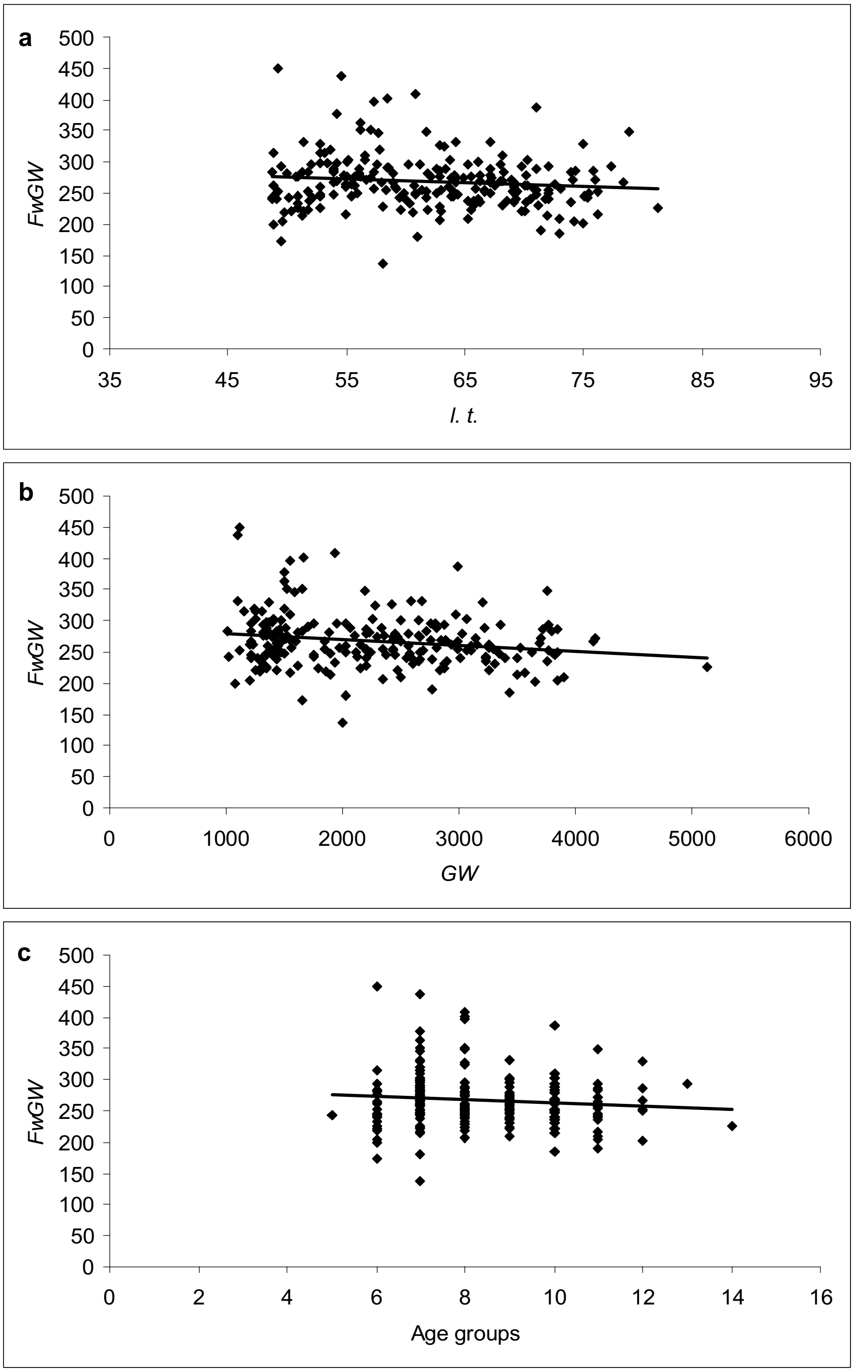

Fig. 7. Dependence of relative fecundity on fish length (a), gutted weight (b) and age (c) in the Curonian Lagoon

Parameter b in the dependence of gutted weight and absolute fecundity varied from 0.9 to 1.2 (Table 4). In the cases described, exponent b varied significantly from 1, which indicated the lack of a linear dependency. Pikeperch absolute fecundity increased more slowly in the Curonian Lagoon and more rapidly in the Vistula and Szczecin lagoons than did gutted weight. Significant differences in exponent b were confirmed between the Curonian and Vistula lagoons and between the Curonian and the Szczecin lagoons. No significant differences were confirmed between the Vistula and Szczecin lagoons.

Exponent b in the dependence between age and absolute fecundity (i.e. coefficient of line inclination) varied from 1.6 to 1.8 (Table 5). The dependencies obtained for the three basins were compared using the series of tests described by Zar (1984). No differences in exponent b were confirmed among the three basins, and its common value was 1.6. Significant differences were confirmed for the line height among all three lagoons based on multiple equations (pairs) and the Tukey test (Zar 1984).

Table 4. Parameters of power dependence $F_a = a\,(GW)^b$ between gutted weight, GW, and absolute fecundity, F_a

Lagoon	Parameter		n	R^2
	a	b		
Curonian	460	0.93	217	0.84
Vistula	95	1.15	304	0.89
Szczecin	140	1.10	312	0.85

Statistical analysis		
H_0: exponent $b = 1$		
Curonian	$P < 0.01$	
Vistula	$P < 0.0001$	
Szczecin	$P < 0.0005$	
H_0: exponent b equal for the three lagoons	$P < 0.0001$	
Multiple comparisons	Line inclination	Line height
Curonian – Vistula	$P < 0.0001$	
Vistula – Szczecin	$P > 0.1$	$P > 0.1$
Curonian – Szczecin	$P < 0.00025$	

Table 5. Parameters of power dependence $F_a = a\tau^b$ between age, A, and absolute fecundity, F_a

Lagoon	Parameter		n	R^2
	a	b		
Curonian	13 819	1.76	217	0.81
Vistula	29 387	1.56	304	0.75
Szczecin	32 833	1.62	312	0.75

Statistical analysis		
H_0: exponent b equal for the three lagoons	$P > 0.1$	
H_0: Line height equal for the three lagoons	$P < 0.0001$	
Multiple comparisons	Line inclination	Line height
Curonian – Vistula		$P < 0.0001$
Vistula – Szczecin		$P < 0.0001$
Curonian – Szczecin		$P < 0.0001$

In the dependence between total length and relative fecundity recalculated into gutted weight, exponent *b* varied from 0.6 to 3.3 (Table 6). The relative fecundity of pikeperch $F_w(GW)$ in the Vistula and Szczecin lagoons increased, but in the Curonian Lagoon it did not show any clear dependence on total length. Significant differences were confirmed for exponent *b* among all three lagoons.

Exponent *b* in the dependence of gutted weight and relative fecundity recalculated into gutted weight varied from 0.01 to 0.03 (Table 7). In each case, the exponent varied significantly from 0. The pikeperch relative fecundity $F_w(GW)$ in the Curonian Lagoon decreased with gutted weight, but in the Vistula and Szczecin lagoons it increased. Significant differences

Table 6. Parameters of linear dependence $F_w(GW) = a + b\ (l.t.)$ between total length, *l.t.*, and relative fecundity recalculated into gutted weight, $F_w(GW)$

Lagoon	Parameter		*n*	R^2
	a	*b*		
Curonian	305	-0.60	217	0.01
Vistula	109	3.30	304	0.20
Szczecin	187	1.88	312	0.06
Statistical analysis				
H_0: exponent $b = 0$				
Curonian		$P > 0.1$		
Vistula		$P < 0.0001$		
Szczecin		$P < 0.0001$		
H_0: exponent *b* equal for all three lagoons		$P < 0.0001$		
Multiple comparisons		Line inclination		
Curonian – Vistula		$P < 0.0001$		
Vistula – Szczecin		$P < 0.05$		
Curonian – Szczecin		$P < 0.00025$		

Table 7. Parameters of linear dependence $F_w(GW) = a + b\ (GW)$ between gutted weight, *GW*, and relative fecundity recalculated into gutted weight, $F_w(GW)$

Lagoon	Parameter		*n*	R^2
	a	*b*		
Curonian	289	-0.010	217	0.03
Vistula	256	0.025	304	0.13
Szczecin	273	0.013	312	0.03
Statistical analysis				
H_0: exponent $b = 0$				
Curonian		$P < 0.01$		
Vistula		$P < 0.0001$		
Szczecin		$P < 0.0025$		
H_0: exponent *b* equal for all three lagoons		$P < 0.0001$		
Multiple comparisons		Line inclination	Line height	
Curonian – Vistula		$P < 0.0001$		
Vistula – Szczecin		$P > 0.05$	$P > 0.25$	
Curonian – Szczecin		$P < 0.00025$		

Table 8. Parameters of linear dependence $F_w(GW) = a + b\tau$ between age, A, and relative fecundity recalculated into gutted weight, $F_w(GW)$

Lagoon	Parameter		n	R^2
	a	b		
Curonian	290	–2.71	217	0.01
Vistula	238	10.20	304	0.13
Szczecin	249	8.64	312	0.05

Statistical analysis		
H_0: exponent $b = 0$		
Curonian	$P > 0.1$	
Vistula	$P < 0.0001$	
Szczecin	$P < 0.0001$	
H_0: exponent b equal for all three lagoons	$P < 0.0001$	
Multiple comparisons	Line inclination	Line height
Curonian – Vistula	$P < 0.0001$	
Vistula – Szczecin	$P > 0.5$	$P > 0.1$
Curonian – Szczecin	$P < 0.0005$	

of exponent b were confirmed between the Curonian and Vistula lagoons and between the Curonian and Szczecin lagoons. No significant differences were confirmed between the Vistula and Szczecin lagoons.

Exponent b in the dependence of age and relative fecundity recalculated into gutted weight varied from 2.7 to 10.2 (Table 8). In both the Vistula and Szczecin lagoons, exponent b varied significantly from 0. The pikeperch relative fecundity $F_w(GW)$ in the Vistula and Szczecin lagoons increased, while in the Curonian Lagoon there were no clear dependencies on age. Significant differences of exponent b were confirmed between the Curonian and Vistula lagoons and between the Curonian and Szczecin lagoons. No significant differences were confirmed between the Vistula and Szczecin lagoons.

Length at sexual maturation was determined based on the smallest female specimens that were collected in the catches. Their gonads were in maturity stage IV in spring. In the Szczecin Lagoon, the smallest female was 36 cm long and in the Vistula Lagoon it was 42 cm long. There were no data available for the Curonian Lagoon. The empirical data reveal that 50% of the females began reproducing after they had reached a total length of 42.9 cm in the Szczecin Lagoon and 43.9 cm in the Vistula Lagoon (Fig. 8).

DISCUSSION

The material collected in the pre-spawning season allowed a variety of information to be assembled regarding the fecundity of female pikeperch which spawn in the Vistula, Szczecin and Curonian lagoons. Simultaneous sampling and the unified analyses methodology permitted the evaluation and reliable comparison of the fecundity of female pikeperch in all three basins. Just as Załachowski (1961), Brylińska and Bryliński (1972), Terlecki (1976) and others, the author of the present study decided that eggs from gonads in maturity stage IV are developed

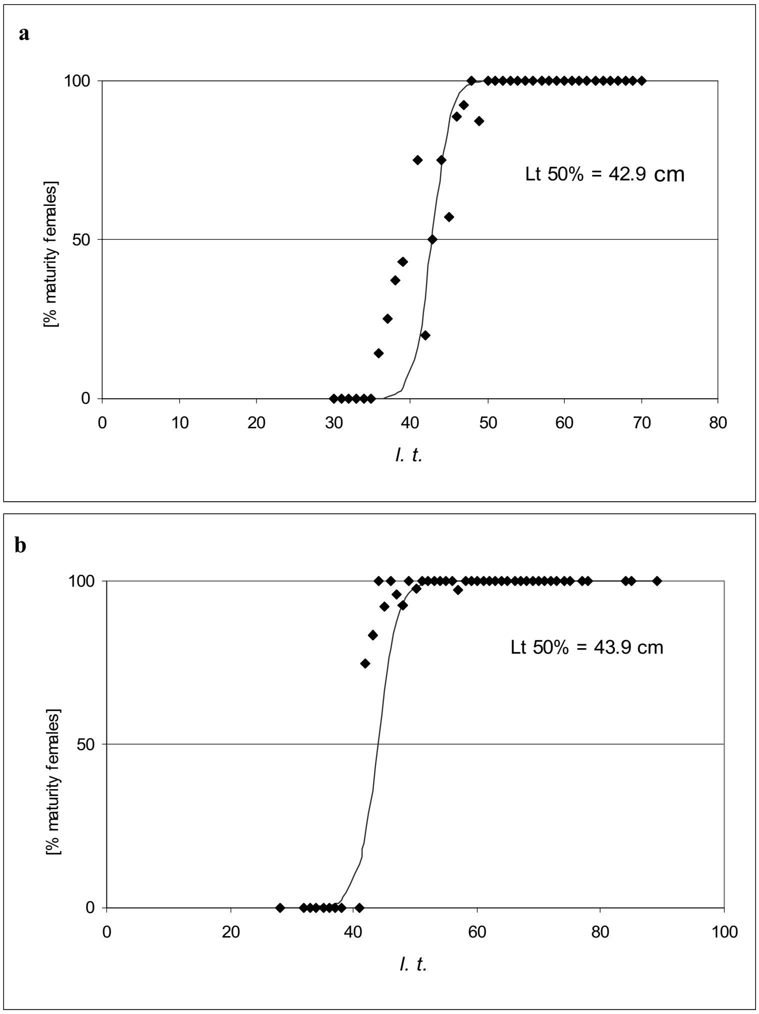

Fig. 8. Ogive of female maturity in the Szczecin Lagoon (a) and the Vistula Lagoon (b)

enough so that their number can be determined. Other researchers estimated pikeperch female fecundity based on gonads in maturity stage VI (Węgrzyn 1986) and yet others in stage V (Filuk 1962).

The results of the present study indicate that absolute fecundity is independent of the length, gutted weight or age of the spawning females, and are the same in both the Szczecin and Vistula lagoons. Only in the case of individuals longer than 70 cm and heavier than 3 500 g was the fecundity of females in the Vistula Lagoon slightly higher than that of females in the Szczecin Lagoon. However, significant differences were confirmed between the fecundity of females which spawn in the Szczecin and Vistula lagoons and the absolute fecundity of those in the Curonian Lagoon. In comparison to the other basins, increases in the absolute fecundity of females from the Curonian Lagoon with respect to increases in total length, body weight and age were the slowest. Changes were observed in the case of the dependence of absolute fecundity and age; the absolute fecundity of females from the Szczecin Lagoon was higher than in the Vistula Lagoon. The absolute fecundity in relation to fish length and weight was the highest in females from the Vistula Lagoon.

Relative fecundity in the Szczecin and Vistula lagoons increased along with the increase of total length, gutted weight and age. In the Curonian Lagoon, no dependence between relative fecundity and total length and age was confirmed, and relative fecundity decreased as weight increased.

A review of the ichthyological literature revealed that, to date, no data on pikeperch fecundity in the Szczecin Lagoon has been published in either Polish or international publications.

The variability of individual absolute fecundity in relation to age is less apparent and its increase with age is related to the increase of the female's weight (Załachowski 1961, Brylińska 1972). Additionally, the reliability of determining age, especially in older fish, can be questionable due to the subjective criteria of annual ring divisions. The small number of the older female specimens studied is also significant. These factors may have an influence on the magnitude of the estimated absolute fecundity in the subsequent years of life.

The fecundity of pikeperch females in the Vistula Lagoon was investigated by Filuk (1962) and Lugowaja (1991). The comparison of the results of these two works indicated that despite the high empirical data distribution, the tendencies they show are similar.

Lugowaja (1991) estimated the absolute fecundity in relation to fish age (from age groups III to XVII) to range from 162.3 thousand to 1 690.5 thousand eggs. These data revealed that individual absolute fecundity increased with age. The current study material included estimations of the absolute fecundity of females only from age groups V to XIV. The average fecundity varied from 247.4 thousand to 1 164.5 thousand eggs, respectively. The comparison of these data with those obtained by Lugowaja, i.e. 233.8 thousand and 1528.5 thousand eggs, respectively, revealed that the fecundity estimated in this study was higher for younger fish and lower for older fish. This indicates an increase in fecundity as age increases.

The absolute fecundity of females in the Curonian Lagoon was estimated by Apołłowa (1965), Virbickas *et al.* (1974) and the author of the present study in 2000. Apołłowa estimated the fecundity of pikeperch with total lengths from 33 to 63 cm to be 54.3 to 848.2 thousand eggs, respectively. Virbickas estimated the fecundity of females with total lengths from 33 to 54 cm at 24 to 898 thousand eggs, respectively. The results for various length classes obtained by these two authors are difficult to compare with those presented in this paper, as they refer to 1 cm length classes (Table 2).

Following the example of Lehtonen *et al*. (1996), in order to compare the fecundity of pikeperch in various basins, the absolute fecundity data for pikeperch females with a total length of 45 cm were used (Table 9). The absolute fecundity estimated for 45 cm females was comparable in all three basins, with the exception of the data presented by Filuk (1962) whose values were much lower than the others. The results obtained by Winkler *et al.* (1989) were similar to those obtained in the present study for the Vistula and the Szczecin lagoons. The fecundity of 45 cm long females from the Curonian Lagoon was similar to that of females from the Pärnu Bay.

Analyses of ichthyological literature data regarding the absolute fecundity of pikeperch females from various basins and different study periods indicate that in the majority of cases it is impossible to compare the data (Samohvalova 1987 – graph only). The remaining authors reported absolute fecundity in various total length or weight ranges (Erm 1961, Apołłowa 1965, Virbickas *et al*. 1974, Lugowaja 1991). Additionally, the various numbers of fish in the study samples yielded different values for the estimated relationships of absolute fecundity and

Table 9. Absolute (*Fa*) and relative (*Fw*) fecundity of pikeperch females from various basins

Basin	Length [cm]	*Fa* [thou. eggs]	*Fw* [eggs/g]	Author
Pärnu Bay	40.0 – 70.0	62.3 – 1,436.2	162 – 467	Erm 1961
Peipsi Lake	40.0 – 74.0	119.4 – 1,214.1	141 – 212	
Võrtsjärves Lake	40.0 – 65.0	135.2 – 831.1	109 – 214	
Ähijärves Lake	39.0 – 60.0	141.8 – 370.5	156 – 176	
Wielimie Lake	37.0 – 64.5	140.8 – 1,173.4	110 – 570	Terlecki 1976
Jeziorak Lake	35.5 – 63.5	21.5 – 780.4	39 – 371	
Omulew Lake	34.0 – 60.0	71.1 – 727	178 – 510	
Vistula near Włocławek	34.0 – 54.5	26.6 – 429.7	44 – 365	
Pärnu Bay	41.0 – 62.0	154 – 1,110	-	Erm 1981*
Curonian Lagoon	34.1 – 64.0	54.3 – 848.2	-	Apołłowa 1965
Curonian Lagoon	39.0 – 79.0	24 – 1,227	-	Vibrickas *et al.* 1974
Vistula Lagoon	43.0 – 88.0	94.4 – 2,498	-	Filuk 1962
Vistula Lagoon	38.0 – 85.0	64.4 – 2,957.4	-	Lugowaja 1991
Vistula Lagoon	42.0 – 72.0	126.4 – 1,186.4	126 – 503	Wilkońska 1996
Szczecin Lagoon	39.0 – 91.0	73.8 – 2,024.1	123 – 643	author's own data
Curonian Lagoon	48.0 – 81.0	214.6 – 1,307.4	138 – 449	author's own data
Vistula Lagoon	42.0 – 84.0	116.1 – 1,852.8	172 – 503	author's own data

* after Lehtonen *et al.* 1996

Table 10. Calculated theoretical absolute fecundity for females from three lagoons

Lagoon	*L .t.* [cm]		
	45	60	70
Szczecin	196,890	548,126	948,732
Vistula	187,851	561,330	1009,154
Curonian	239,157	522,131	793,377

total length. This is characteristic for many fish species and not only for pikeperch. Bagenal (1978) stated that it is possible to compare results by estimating the theoretical absolute fecundity by using an appropriate equation to describe the fecundity-length or fecundity-weight relationships. Table 10 presents the estimated values for three lengths which were based on the author's own materials. The data revealed that at a length of 45 cm the highest theoretical fecundity was confirmed for females from the Curonian Lagoon, while the highest fecundity was observed for fish from the Vistula Lagoon that measured 60 and 70 cm in length.

Relative fecundity is independent of length, mass and age; as such, it should be used as an indicator to compare female fecundity values in various basins. According to Bagenal (1978), relative fecundity is a suitable way to describe the fecundity of various fish populations. However, of the pikeperch females which inhabit the three lagoons in question, only data on female fecundity values in relation to age were found for fish from the Szczecin Lagoon (Węgrzyn 1986). Węgrzyn reported that the relative fecundity estimated for age group III was 132 eggs, it was the highest in age group VI at 296 eggs and it decreased in subsequent groups. In age group IX, it was 246 eggs. The relative fecundity of females from various length classes in the Curonian Lagoon was estimated by Apołłowa (1965); however, her data cannot be compared with those discussed in the present study.

The analyses data from various studies regarding age at sexual maturation revealed that in 1951 in the Szczecin Lagoon (Wiktor 1954) only 10% of the females in age group III and 40% in age group IV had gonads in the pre-spawning stage. Kraczkiewicz (1969) reported that 20% of females 41-45 cm long and 75% of females 46-50 cm long which were sexually mature belonged primarily to age groups IV and V. Węgrzyn (1987) reported that in the 1970s, 50% of pikeperch females began spawning after they had reached a length of 42.2 cm. By employing the age-length relationship, Węgrzyn estimated the average age of female maturation to be 3.2 years. Based on the author's own data, 50% of the females began spawning after they had reached a length of 42.9 cm.

According to Filuk (1962), pikeperch females in the Vistula Lagoon which began spawning in 1951-1952 belonged primarily to age groups III and IV, and only a small number, up to 5%, belonged to age group II. Filuk estimated that the three year old females with an average length of 43.9 cm constituted about 31% of females which began spawning. According to the present author's own data from 2000, 50% of the females began spawning after they had reached a length of 43.9 cm.

According to Apołłowa (1965), pikeperch females in the Curonian Lagoon achieved sexual maturity in their third year. According to Virbickas *et al.* (1974), three and four year old females began spawning after they had reached lengths of 30-35 cm. Females measuring from 38 to 53 cm were the most abundant at spawning grounds.

Winkler (1989) reported that primarily three and four year old females begun spawning in the Greifswalder Bay and Darss-Zingster Bay.

The studies quoted above indicate that pikeperch females in the southern Baltic Sea reach sexual maturity at ages three to four. However, the percentages of females from these age groups varied in different basins.

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Structure of benthic fish assemblages under intense exploitation in the Gulf of Gdańsk

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Abstract. The results of experimental fish catches using a benthic trawl in the Gulf of Gdańsk in 1985-1999 were analyzed using multivariate statistical methods. These analyses provided the basis for discerning two stable benthic fish assemblages which, on a regional scale, are characteristic of the Gulf of Gdańsk. The ranges of occurrence of the assemblages varied and intersected. Geography occurred to be more influential with regard to assemblage location than depth was. The analysis of the multivariate structure of the collected material was facilitated by applying several statistical techniques simultaneously. This also limited the choice of the subjective criteria used while interpreting the results of particular methods.

Key words: Baltic Sea, Gdańsk Bay, fish assemblages, community composition, multivariate analysis

INTRODUCTION

The Gulf of Gdańsk is under constant, strong fishing pressure. Landings from ICES Subarea 26, in which the Gulf of Gdańsk plays an important role, constitute about 20% of the total Baltic Sea catches (an average of 150-200 thousand tons annually). Increasing fishing effort and improving methods of fish location result in a greater number of fish being caught and influence changes in the exploited stocks.

The lower salinity of Baltic waters is a barrier for many ocean species, while species with lower salinity needs are subjected to stress reflecting in size differences between organisms of the same species in the Baltic and the North seas. Freshwater species are an important element of the Baltic ichthyofauna. However, their distribution range is also limited by salinity levels. Due to the fact that there are very few species inhabiting the Baltic Sea, this basin is considered to be a unique example of an ecosystem which functions at low levels of biodiversity.

The dynamics of variations in commercial fish resources in the Baltic Sea have been under evaluation for more than 20 years. Analysis has been done using mathematical models which take into consideration the following: stock age structure, food availability, indexes of the rate of fish growth, population fecundity, natural mortality, predatory pressure and catch effort and rate. The possibility of applying them to several fish stocks simultaneously is limited due to the high variance in determining the values of the model parameters. However, these models do not include biomass or indexes of the variability of stocks of non-commercial fish species.

Since the second half of the nineteenth century, scientists have made attempts to determine the number of species in the Gulf of Gdańsk. Typically, their works are descriptive and comparative, and the authors simply recorded information that either a species does in fact occur in the region being described or that it was observed there. Segestrålle (1957) related the variations in the number of sea fish species from Kattegat (75 species), through Arkonia Basin (30) to Bothnia Bay (22 species) salinity. Strzyżewska (1990) reports a list of 49 species occuring in the Gulf of Gdańsk, while Skóra (1996) expands the list to 71 species by using both current and historical data in the literature, his own observations and personal communications. In the majority of these works, the authors do not describe the criteria they used to confirm the presence of one or more individuals of a particular species in a given area.

Scientists have used descriptive and comparative methods, biodiversity indexes, and the numbers of fish per unit area to analyze fish assemblages (Ojaveer 1996, Draganik *et al.* 1996, Repečka 1995), but analyses of their occurrence and variability in time using multidimensional statistical methods has not been carried out until now. This approach is recognized as the most appropriate for the description of fish species assemblages, and has been used widely in other sea areas (Fargo and Tyler 1991, Gomes *et al.* 1992, Koslow 1993).

The aim of this work was to identify the benthic fish assemblages in the Gulf of Gdańsk using the method of locating repeatable species systems in time and space through the application of multivariate statistical analyses.

MATERIALS AND METHODS

The material used to evaluate species assemblages was collected during 37 research cruises from 1985 to 1999. Two vessels were used in the investigations: from 1985 to 1993 it was the B 25-S cutter GDY-30 (24 m long, 240 KM engine) and from 1993 to 1999 it was the R/V BALTICA (41 m in length, 1,500 KM engine). The hauls were made with a P 20/25 benthic herring trawl with the following specifications: trawl length – 55.9 m; vertical opening – 3.9 m on average; horizontal opening – 10 m; mesh bar length in the codend bag – 6 mm. The greater power of the R/V BALTICA required the trawl gear to be reinforced, and the new fishing gear was calibrated in December 1993. The effective time of the catch, measured from the moment the trawl was positioned on the bottom to the moment hauling in began, was 30 minutes. The trawling speed was about 3 knots (ranging from 2.7 to 3.1). The catches were carried out between October and March only during the day. The sampling stations were grouped into five cross-sections. Their names reflect the existing geographical names, Krynica Morska, Wisłoujście, and Zatoka Pucka, or the local names of fishing grounds, Bromka and Władysławowo. The location of subsequent stations was related to the 10 m isobath. Figure 1 presents the location of sampling stations. Differences in the location of the beginning of hauls in subsequent years did not exceed 3 minutes of latitude.

Additional hydrological data describing the water layer above the bottom, i.e. temperature, salinity, and oxygen content, were collected during three cruises.

Data available in the literature regarding differences in feeding and the choice of location in the Gulf of Gdańsk by groups of different-sized fish of one species (Mulicki 1947, Popiel 1951, Załachowski 1985, Szypuła *et al.* 1997) were used to divide the four most common fish species, namely herring, sprat, cod and flounder, into categories according to total length (Table 1).

Fig 1. Map of the Gulf of Gdańsk with trawling locations

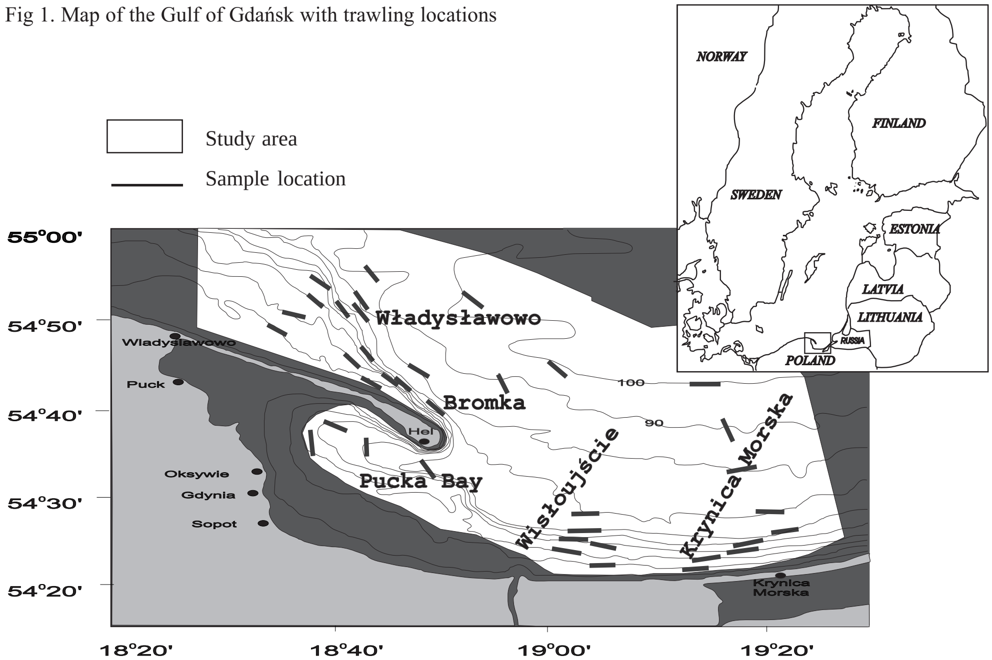

Table 1. Fish division according to size category

Species	Size category	Category code*	Fish lenght range [cm TL]
Herring	1	Herr1	≤15
	2	Herr2	16-25
	3	Herr3	>25
Sprat	1	Spart1	≤9,5
	2	Sprat2	>10
Cod	1	Cod1	≤12
	2	Cod2	13-25
	3	Cod3	26-55
	4	Cod4	>55
Flounder	1	Floun1	≤10
	2	Floun2	11-17
	3	Floun3	18-30
	4	Floun4	>30

* Use of category codes was necessitated by the use of computer programs

Data used for cluster analysis and multivariate scaling were transformed using the root-root method in order to reduce the impact of random, large numbers of one or several species on the similarity of objects (Sneath and Socal 1973). The similarity matrix between the particular stations was created using the Bray-Curtis index (Bray and Curtis 1957). The similarity matrix was clustered using the UPGMA (unweighted group average linking) method (Sneatch and Socal 1973). The outliers that were detected during the first cluster analysis caused the station distribution to be asymmetric, so that they were removed from the raw data table and then the dissimilarity matrix was recalculated. The dendrogram arms were divided according with the criterion of intra-group similarity at a similarity level of 55%. A similarity matrix, calculated using data that excluded non-fitting objects, was used for non-metric multidimensional scaling (MDS) (Clarke and Warwick 1994a). Therefore, areas typical for a given assemblage were those in which the species composition of the catch allowed a location to be assigned to a specific assemblage in over 90% of the analyzed cruises.

Cluster analysis and multivariate scaling were done using PRIMER (*Plymouth Routines in Multivariate Ecological Research*) software (Clarke and Warwick 1994b).

Data used in ordination analyses were log-transformed. In order to determine the species system model, indirect analyses of the DCA ordination were carried out first to evaluate the length of the assembly variation gradient. Since the length of the gradient did not exceed four SD units in any case, the RDA method was then applied to analyze the interactions between species and the environment (Ter Braak and Šmilauer 1998). In order to determine species structure variability in relation to particular environmental parameters for each case, both total and partial analyses were done (Borcard *et al.* 1992). The significance of the impact of factors on the species system was tested using Monte Carlo permutation tests (unlimited permutations) at a confidence level of 5%. In order to illustrate the variability of the analyzed fish assemblages over time, additional RDA analyses were done for cruises made in January, March, October-November and December throughout the investigation period. Only in January and March was the continuity of investigations maintained, i.e. the cruises were repeated almost every year. Ordination analysis diagrams present only those species and categories for which statistically significant variability was confirmed in relation to any environmental factor.

The species responsible for object (station) clustering in cluster analysis were determined using the average contribution of each species versus the averaged dissimilarity between all pairs of clustered objects in accordance with the method of index species analysis (Clarke and Warwick 1994a).

Hypotheses regarding putative differences in fish assemblages in hauls made using various types of fishing gear were tested using ANOSIM tests (*ANalysis Of SIMilarities*) that is the nonparametric equivalent of multidimensional variance analysis (Clarke and Green 1988), at a confidence level of 5%. In order to verify the assumptions of the continuity of the investigation method, the zero hypotheses of a lack of differences in the species systems and their categories in cruises were tested.

RESULTS

Fish from eight orders, 22 families and 35 species were confirmed over the course of the investigations. The number of specimens registered and the frequency of occurrence of species throughout the entire investigation period are presented in Table 2.

The results of the ANOSIM tests show that there were no statistical differences between the two vessels used. The confidence level calculated from the comparison of the observed value r-statistics ($R = 0.029$) to the permutation distribution generated from a random sample (20,000 permutations) equaled 12.1%, thus exceeding the assumed confidence level value of 5%.

Table 2. Inventory of species recorded in catches

Common name	Latin name	Number of individuals	Frequency of occurrence [%]
Herring	*Clupea harengus membras* (Linnaeus, 1758)	2137,459	93.94
Sprat	*Sprattus sprattus balticus* (Schneider, 1904)	1613,275	77.37%
Eelpout	*Zoarces viviparus* (Linnaeus, 1758)	300,561	62.97
Smelt	*Osmerus eperlanus* (Linnaeus, 1758)	218,437	54.73
Flounder	*Platichthys flesus* (Linnaeus, 1758)	115,449	97.92
Cod	*Gadus morhua callarias* Linnaeus, 1758	91,111	87.03
Stickleback	*Gasterosteus aculeatus* Linnaeus, 1758	50,024	8.62
Rockling	*Gaidropsarus vulgaris* (Cloquet, 1824)	27,305	28.79
Round goby	*Neogobius melanostomus* Pallas, 1811	11,678	3.13
Bull-rout	*Myoxocephalus scorpius* (Linnaeus, 1758)	6,774	40.3
Gobies *	Gobidae	3,861	19.70
Pikeperch	Stizostedion lucioperca (Linnaeus, 1758)	1,944	17.05
Turbot	Psetta maxima (Linnaeus, 1758)	1,173	35.04
Plaice	*Pleuronectes platessa* Linnaeus, 1758	745	17.90
Lumpsucker	*Cyclopterus lumpus* Linnaeus, 1758	638	22.06
Greater sand-eel	*Hyperoplus lanceolatus* Le Sauvage, 1824	432	3.22
Hooknose	*Agonus cataphractus* (Linnaeus, 1758)	97	3.88
River lamprey	*Lampetra fluviatilis* (Linnaeus, 1758)	74	1.70
Sea snall	*Liparis liparis* (Linnaeus, 1766)	39	1.99
Perch	*Perca fluviatilis* Linnaeus, 1758	39	1.61
Twaite shad	*Alosa fallax* (Lacepede, 1803)	39	2.18
Lesser sand-eel	*Ammodytes tobianus* Linnaeus, 1758	29	1.89
Snake blenny	*Lumpenus lumpretaeformis* (Walbaum, 1792)	20	1.23
Whiting	*Merlangius merlangus* (Linnaeus, 1758)	19	1.52
Butterfish	*Pholis gunnellus* (Linnaeus, 1758)	15	1.04
Ruffe	*Gymnocephalus cernua* (Linnaeus, 1758)	9	0.85
Eel	*Anguilla anguilla* (Linnaeus, 1758)	7	0.66
Trout	*Salmo trutta* Linnaeus, 1758	4	0.19
Dab	*Limanda limanda* (Linnaeus, 1758)	3	0.28
Pike	*Esox lucius* Linnaeus, 1758	2	0.19
Mackerel	*Scomber scombrus* Linnaeus, 1758	2	0.19
Sichel	*Pelecus cultratus* Linnaeus, 1758	2	0.09
Salmon	Salmo salar Linnaeus, 1758	1	0.09
Vimba bream	*Vimba vimba* (Linnaeus, 1758)	1	0.09
Roach	*Rutilus rutilus* (Linnaeus, 1758)	1	0.09

*Gobiidae individuals below 5 cm LT were not identified. Most probably they were *Pomatoschistus minutus* Pallas, 1770 and *Pomatoschistus microps* Kroyer, 1838.

The application of cluster analysis facilitated the distinction of two to four groups of stations which included from two to 20 objects (Table 3). The results of the cluster analysis were plotted using multidimensional scaling. The results of both analysis indicated that the representation of multidimensional distance in two-dimensional space was acceptable. The value of the stress index varied from 0.07 to 0.19, depending on the cruise. The results of analyses indicated that depth gradient and region category played similar roles in the grouping of stations. With the exception of two cruises, two fish assemblages were identified in each

Table 3. Results of cluster analysis and multidimensional scaling

Research profile																																					
Region	Pucka Bay				Wisłoujście						Krynica Morska									Bromka									Władysławowo								
Depth / Date of survey	30	40	50	60	20	30	40	50	60	70	20	30	40	50	60	70	80	90	100	20	30	40	50	60	70	80	90	100	20	30	40	50	60	70	80	90	100
85, March																d	d	d	d					◆		d	d	d						d	d	d	d
85, December											s									s	s							◆	s	s	s						◆
87, March											s	s																									
87, December											s									s	s																
88, January					s						s	s						d		s	s								◆	◆					d	d	d
88, March					s	s					s									s	s								s	s							
88, December																										d	d	d									
89, January											s	s														d										d	◆
89, March											s	s								s									s	s							
90, January											s									s								d									d
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91, January																													s	s							
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91, December																		d	d									d									d
92, January																				s		s	s						◆								
92, October																	◆											◆									
93, January					s															s																	
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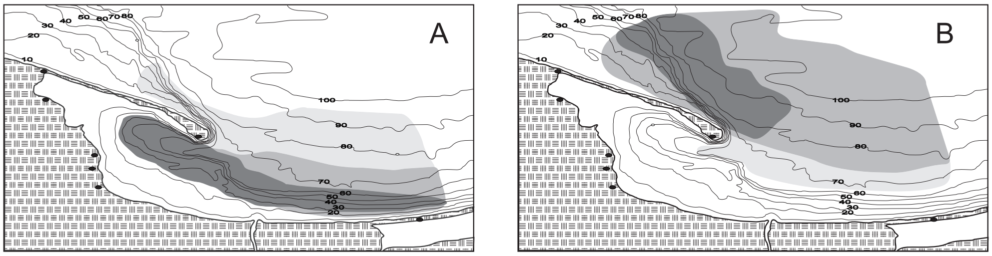
94, March											s	s						d	d			s						d	s	s							
94, December																	d	d																			
95, February		s			s						◆	s							◆	s	s						d									d	d
96, January					◆														d								d	d	s	s							
96, March					s			◆			s									s	s	s							s	s							
97, January		s			s						s								d	s	s						d	d	s	s						d	d
97, March					s	s	s				s							d									d	d	s							d	d
98, January								◆										d	◆								d	d			d					d	d
98, March																													s	s	s						
99, March																													◆								

* survey conducted with GDY-30 ** survey conducted with r/v BALTICA

	Station not present in survey		Station assigned to the location of inner bay fish assemblage		Station assigned to the location of open sea fish assemblage
s	Station assigned to the location of shallow water fish group	d	Station assigned to the location of deep water fish group	◆	Station excluded from cluster analysis

cruise on the basis of the analysis of the material collected. The first one, which most often covered hauls at stations in the Puck Bay, Wisłoujście and Krynica Morska, was named **the inner bay fish assemblage.** The second one, which most often encompassed the stations located near Bromka and Władysławowo, was named **the open sea fish assemblage**. The range of both assemblages varied in time and space. The zone of the greatest intersection of the fish assemblage was in the area delineated by the 70 and 80 m isobaths along the line from Hel to Krynica Morska. Figure 2 presents the location of each assemblage.



A. Inner bay fish assemblage

B. Open sea fish assemblage

Frequency of fish assemblage occurence
in the series of analyzed cruises

Over 90%
60-89%
30-59%

Fig. 2. Location of fish assemblages in the Gdańsk Bay

In addition to the two above-mentioned fish assemblages which were constantly present, there were also systems of species and categories at certain stations which could not be grouped with different assemblages. This phenomenon occurred most often in shallow hauls (20-30 m) and the deepest hauls (70-100 m), although it was not observed in every cruise. The range of occurrence of local-temporary species and category assemblages (further referred to as **coastal fish groups and deep water fish groups**), were similar to the assemblages as they also varied in time and space. During five cruises, the range of the coastal fish groups included hauls as deep as 60 m near Władysławowo. With the exception of one cruise at a depth of 40 m near Władysławowo, the limit for the deep water fish groups in which a similar species composition was observed was the 70 m isobath.

The average number of fish caught during cruises until 1994, expressed as the average number of individuals per haul, was similar varying from 9 500 to 15 000 individuals for both fish assemblages; the exceptions were the cruises in January and March 1991. Beginning with the cruise in December 1994, a stable increase was noted in the total number of fish caught in the location where the inner bay fish assemblage occurs. In both assemblages, the highest differences in numbers were characteristic for two pelagic species, herring and sprat. The highest abundance of these species was recorded in the region where the inner bay fish assembly occurs; the joint contribution of the two species in the 1994 catches was 98% of all the registered fish (Fig. 3A-B). Additionally, the contribution of particular clupeid categories was different. In the inner bay fish assemblage, the greatest number of fish were category 1 herring and sprat (further referred to as juvenile). The contribution of juvenile herring to this assembly,

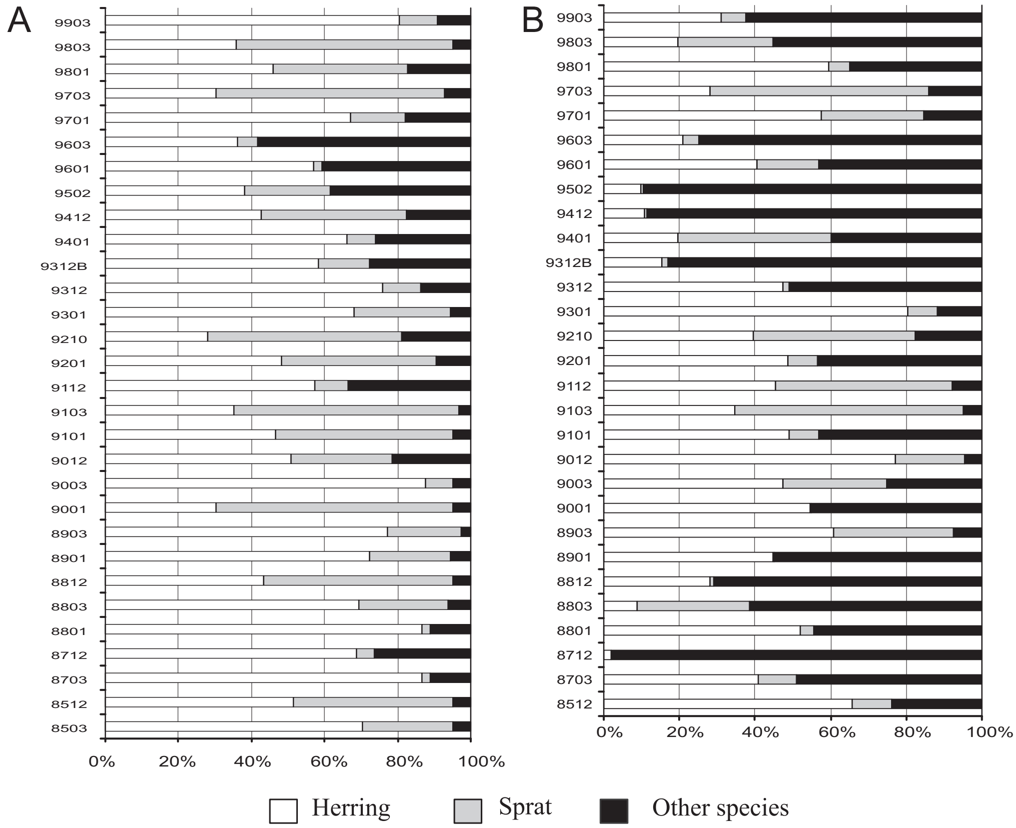


Fig. 3. Herring and sprat percentages of the total amount of fish caught in the areas of occurrence: A – inner bay fish assemlage, B – open sea fish assemblage

with the exception of cruises in March 1988 and 1991 and January 1991, varied from 23 to 83% of all the registered clupeid fish. The contribution of juvenile sprat was relatively high, although time-dependant, and their abundance in the assemblage varied from 0 to 43%. Smelt was also a stable element among the clupeid fish in the inner bay assemblage. Its contribution, with the exception for the series of cruises between December 1988 and March 1989 and in March 1996, varied from 4 to 15% of the recorded numbers of clupeid fish. The significance of category 1 herring in the open sea assemblage was rather small, with the exception of the four cruises in January and March 1990 and 1996. Category 2 herring made the greatest contribution to the catches with percentages varying from 25 to 87% of the clupeids in the catches. The occurrence of sprat of both categories varied between 0 and 40% of all the clupeids.

Eelpout played an important role in both assemblages. This species became common in the inner bay fish assemblage in 1994. From that time, a significant increase in the eelpout contribution to both assemblages was observed comprising up to 70% of the fish (excluding clupeids) in the open sea assemblage in March 1994 (the inner Gulf of Gdańsk assemblage was not observed during this cruise), and up to 79% of the fish in the inner bay assemblage. The greatest eelpout contribution was observed in samples collected during the cruises in January and March 1997 in the inner bay assemblage, when its contribution reached 95% of the all the fish, excluding herring and sprat (Fig. 4 A-B)

The joint occurrence of cod and flounder in the catches of nearly all the cruises is a characteristic feature which diversifies the species composition of both assemblages. The contribution of particular flounder categories in the inner bay assemblage was higher than that of the cod categories. The opposite was observed in the open sea fish assemblage with regard to two size categories; in nearly every cruise the number of category 1 and 2 cod exceeded the number of flounder of the same categories. The numbers the intensively exploited category 3 fish of each species, i.e. cod from 26 to 55 cm. *l. t.* and flounder from 18 to 30 cm *l. t.*, was higher in the open sea assemblage in comparison with that in the inner bay.

The remaining fish species present in both assemblages were put into two groups – that of species which diversified the assemblage and whose contribution to both assemblages was different and that of stable species whose contribution to both assemblages was similar. In the open sea assemblage, plaice, four-bearded rockling, sculpin, sand launce and sand eel were the species that determined the assemblage dissimilarity. In the inner bay assemblage these species were pikeperch, stickleback, Gobiidae and brook lamprey. The non-diversifying (stable) spe-

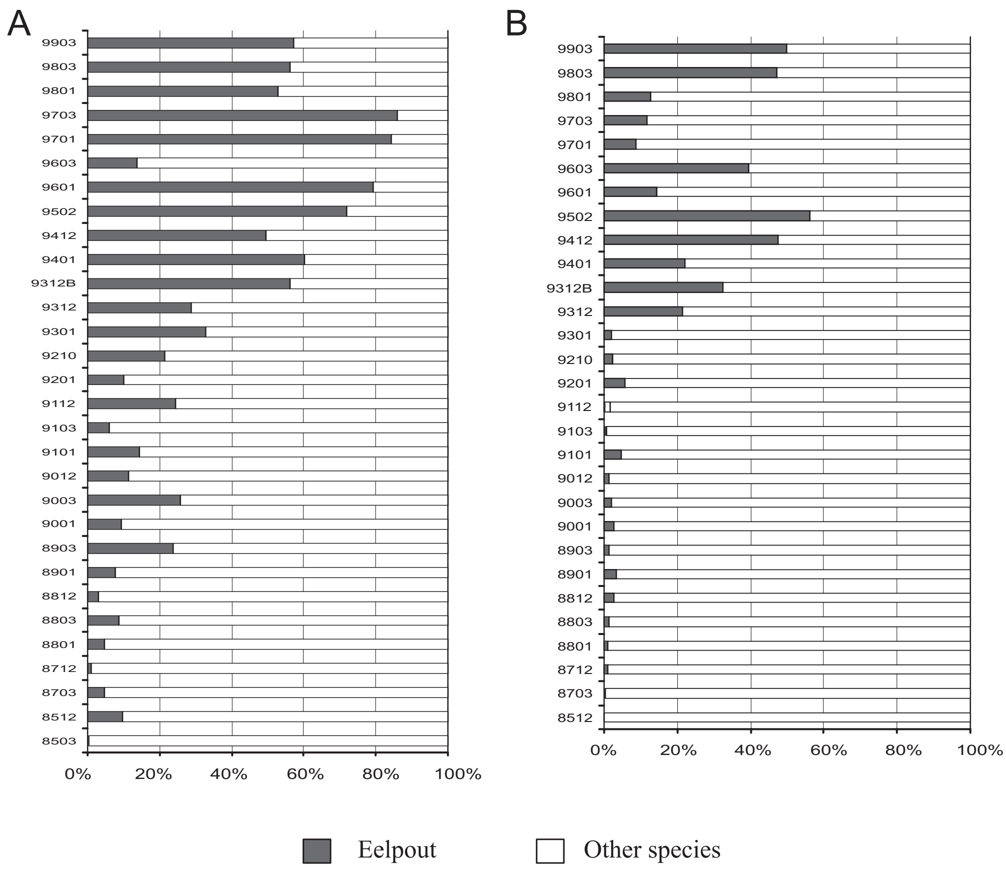


Fig. 4. Eelpout percentages of the total amount of fish caught in the areas of occurrence:
A – inner bay fish assemlage, B – open sea fish assemblage

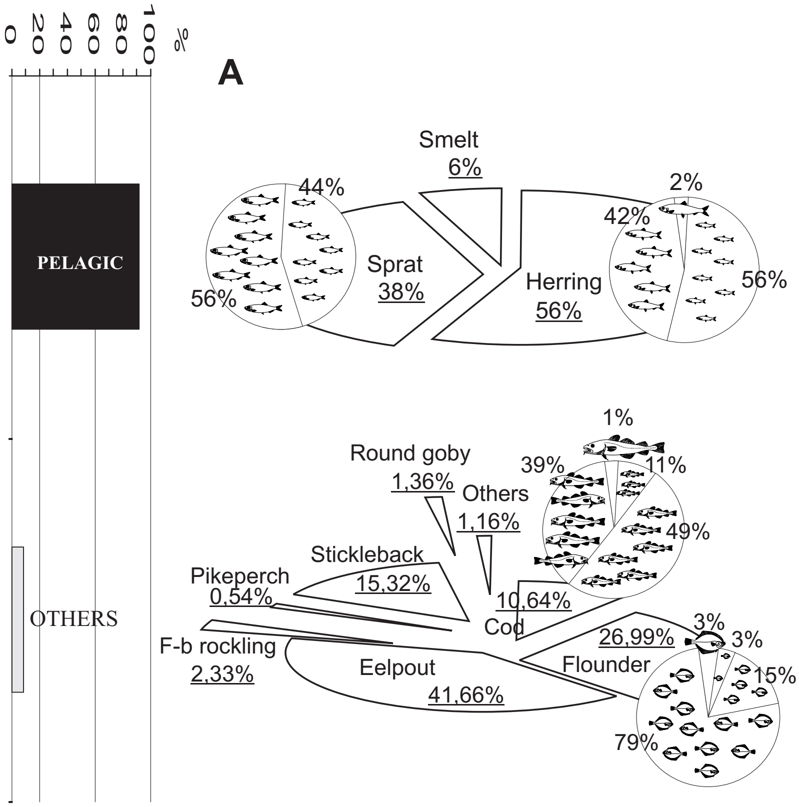


Fig. 5A. Percentages of species and their categories in the inner bay fish assemblage

cies consisted of all species whose frequency of occurrence did not exceed 3% during the investigations and sculpin, lumpfish, hooknose, and brill which were observed on a similar proportions in both fish assemblages. The average contribution of species and their categories in the distinguished fish assemblages are presented in Figs. 5A and 5B.

The length of the axis of the gradient of fish assemblage variability in DCA varied from 1.42 to 3.05 SD units, depending on the cruise, while the length of the variability axis was 2.13 SD for the entire investigation period. With regards to the data set of all the cruises, the first two canonic axes of RDA analyses explained 28.5% of the variability of the species assemblages and categories. The environmental factors most responsible for variances were geographical location (regions), depth at which the haul was made, month and year of the cruise. Partial analyses, in which only one environmental factor was taken into consideration, revealed that the impact of each of them was systematically significant at the level of alfa = 0.05 (Fig. 6). Geographical location had the greatest impact on the variability of fish assemblages. Other factors, considered independently, were much less important. Depth, which explained 7.6% of the variance, explained only 2% of it after the portion of combined depth with geographic location was excluded. This was true of the time factor (month and year of cruises) to an even greater extent; the month and year factors independently explained 0.9 and 0.6% of the variability, respectively, and their impact was statistically significant.

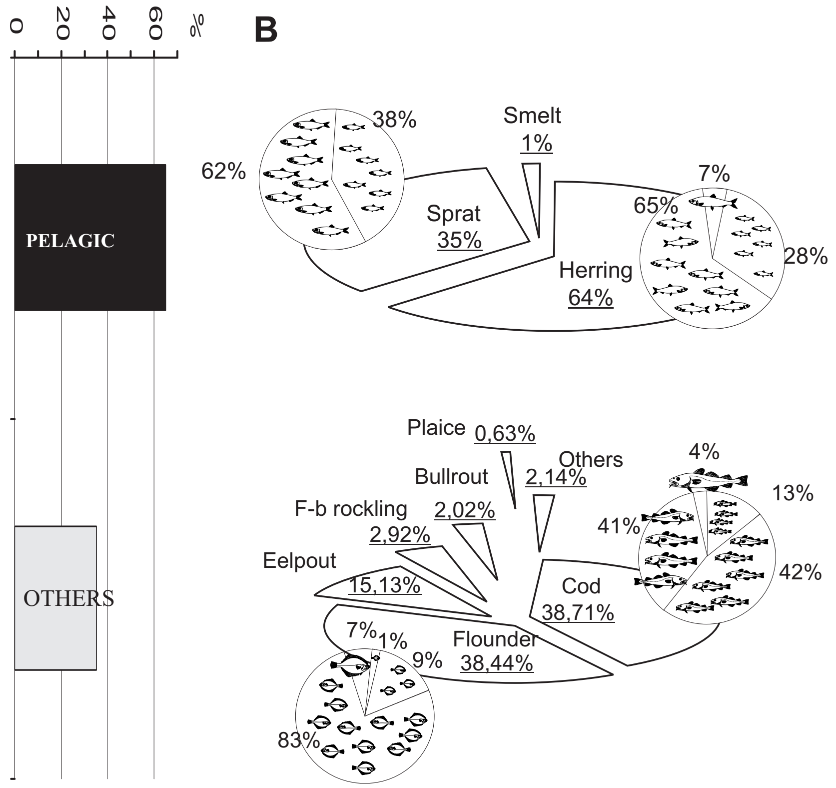
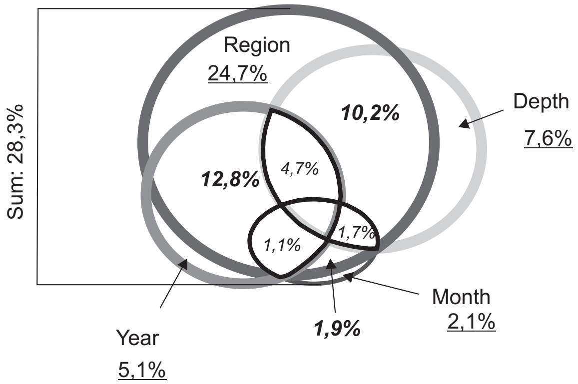


Fig. 5B. Percentages of species and their categories in the open sea fish assemblage

The results of RDA analyses of different cruises are diversified with regards to the degree which they explain variability. This value varied from 22.5% in March 1997 to over 60% for the cruises in January 1986 and 1987 with an average level of about 35%. The high level of the explained variance in the above mentioned cruises resulted from the small number of hauls. The geographic region factor on average determined about 28% of the explained variability. The level of the explained variance by the depth factor was more variable with an average value of about 15%. With the exception of three cruises, geographical location appeared to be a better factor for explaining fish assemblage variability in the area investigated (Fig.7 A-B). The degree of variance explained by the depth factor alone (i.e. that which cannot be explained jointly with the geographical location factor) varied from 2 to 13%, with an average of about 5.5%.

The results of RDA analyses for particular cruises allowed detection of repeatable patterns of variability for species systems in the context of environmental factors. The grouping of nominal geographical factors was characteristic. In the majority of cruises they constituted a polar system of two location groups: the region of Bromka with Władysławowo and that of Wisłoujście with Krynica Morska and the Puck Bay. This system was distorted in some cruises, e. g. when no hauls were made in one of the regions and in March 1987 (the Puck, Władysławowo and Bromka regions group), in March 1989, December 1991 and 1993 and in January 1997

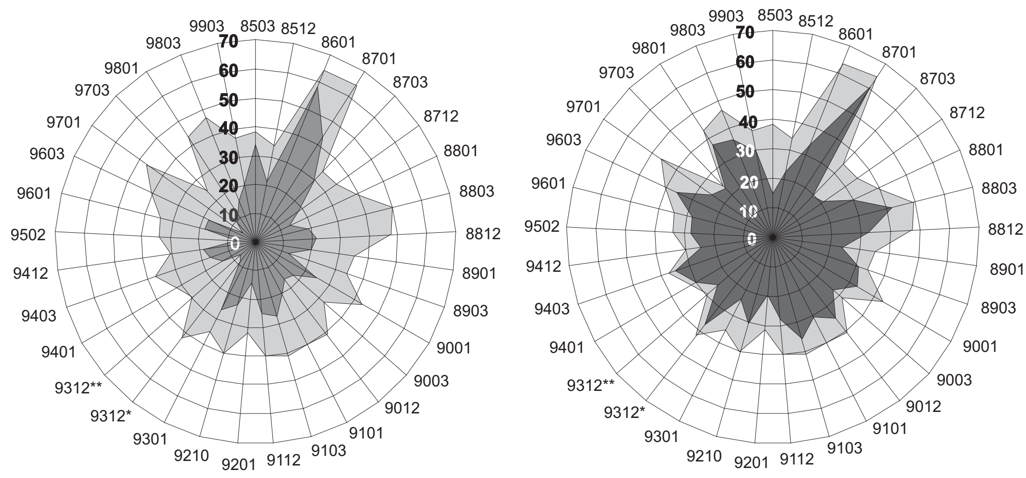


7,6% - Variability explained by one factor

12,8% - Variability explained by two factors

4,7% - Variability explained by three factors

Fig. 6. Variations in species systems explained by the two first canonic axes in RDA ordination for the entirely of the investigation period using partial analyses



Variability explained by the first two axes of total RDA ordination

Variability explained by partial RDA ordination - depth factor

Variability explained by partial RDA ordination - geographical region factor

Fig. 7. Variability explained by analyzing environmental factors

(the Krynica, Władysławowo and Bromka regions group). On the assignment diagrams the Krynica region was often located near the center of the coordinates, which means that in such cruises this factor was rather insignificant in comparison to the remaining parameters with regard to the variability of species composition. The depth factor was strongly correlated with the geographical location of the Bromka and Władysławowo regions in almost in all analyses. The species system and their categories revealed the presence of stable elements, species assigned to a particular environmental factor, that were independent of the cruise. As depth increased, so did the four-bearded rockling numbers in every assignment diagram. In the majority of cases, a similar relation was observed for the largest cod (cod 4) and more infrequently for cod in the 26-55 cm *l. t.* (category 3) range, the largest flounder (floun. 4) and the largest herring (herr. 3). An increase of the contribution of other species and their categories (e.g. cod 1, cod 2, sprat 2, plaice) could only be associated with depth increase in some cruises. Since the depth factor in the majority of RDA diagrams correlated with the location of the Bromka-Władysławowo group, this variability could be related to the combined impact of both depth and geographical location factors. The increase in the numbers of cod to 12 cm *l. t.* (cod 1) and from 13 to 25 cm *l. t.* (cod 2) and plaice was most often in agreement with the group of geographical location factors (assuming nominal variables) Bromka – Władysławowo, and, also in some cruises, Krynica Morska or the Puck Bay. Brill, sculpin and Gobiidae were more infrequent and observed to a lesser extent in these geographical locations. Increases in the numbers of flounder to 10 cm *l. t.* (floun. 1) and from 11-17 cm *l. t.* (floun. 2), herring to 15 cm *l. t.* (herr. 1), sprat up to 9.5 cm *l. t.* (sprat 1) and pikeperch, smelt, and stickleback were most common in the Wisłoujście – Puck Bay – Krynica geographical location group. During the cruise in October 1992, the increase in numbers of brook lamprey was strongly connected with the region of Krynica and Wisłoujście, while at the beginning of January 1994 a stable relation between the increase of the contribution of Gobiidae and the Puck Bay geographical location was observed. Eelpout had a characteristic place in the series of assignment diagrams. The increase of its contribution most often coincided with the Wisłoujście – Puck Bay – Krynica location, however, the vector of the fish number increase was often located between the two geographical location groups. In the majority of the cruises, this species had a negative relation with depth.

The results of RDA analyses using the data from the three cruises during which the influence of temperature, salinity and oxygen contents on the depth of catches was included (Table 4) indicated that there was a significant dependence between these three factors and those described earlier. In 1998, none of the additional factors was statistically significant in relation to

Table 4. Variability in species systems explained by five environmental factors through partial RDA analysis

Survey code	9603		9701		9803	
Factor	[%]*	p**	[%]*	p**	[%]*	p**
Depth	18.2	< 0.05	5.5	< 0.05	15.7	< 0.05
Region	36.2	< 0.05	25.4	< 0.05	35.5	< 0.05
Temperature	8.4	0.03	13.3	0.01	4.7	0.26
Salinity	3.8	0.38	1.9	0.76	6.2	0.13
Oxygen	2.2	0.76	12.6	0.01	3.7	0.40

*variability explained by single environmental factor (independetly from another factors)
**significance coefficient

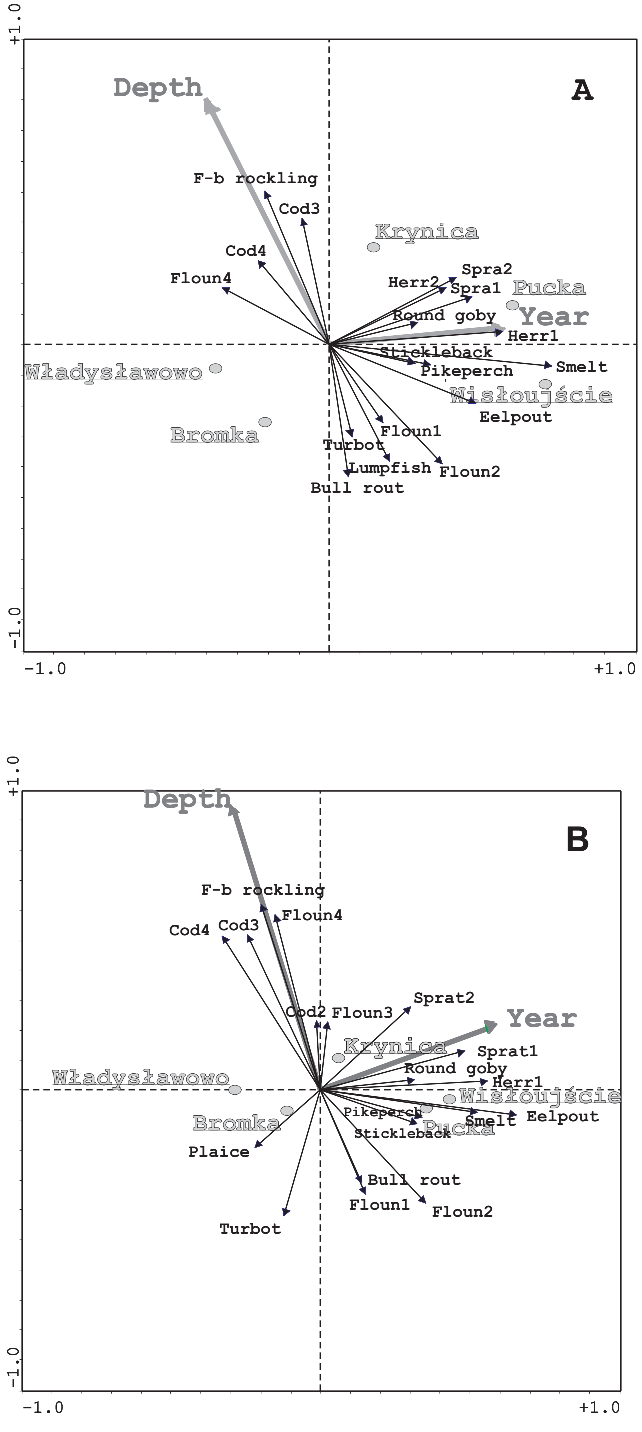


Fig. 8. RDA diagrams of cruises carried out in: A – January-February, B – March

species variability. Furthermore, salinity and temperature showed a very strong positive correlation (from 0.91 to 0.97, depending on the cruise) with depth, while the oxygen contents showed a very clearly negative value (in the range of r = –0.83 to –0.91). This indicates a significant dependence between the environmental factors and allows only those factors which had the greatest impact on the variability in the species system to be taken into consideration.

RDA analyses based on data from the series of cruises in a single month over the course of the investigation years, revealed that, beside such species as four-bearded rockling, category 3 and 4 cod and category 4 flounder whose numbers increased along with depth, the other species and their categories were connected with the passing years (Fig. 8 A-B). The increase in the numbers of fish in accordance with the time gradient was most common for eelpout, clupeids of all categories, Gobiidae, stickleback, and pikeperch. A decrease in numbers with the time gradient over the years was characteristic for species such as brill and plaice. In the diagram of RDA analysis for the results of the set of cruises from subsequent months, the groupings of stations reflected the geographical location factor; the Władysławowo area was correlated with Bromka (r = 0.9) and Puck Bay with Wisłoujście (correlation coefficient r varied from 0.7 to 0.9). The time factor turned out to have a negative correlation with the first group of regions (geographical location) and a positive correlation with the second group. This must have resulted from the higher variability in fish numbers in the Puck Bay – Wisłoujście – Krynica fishing grounds group and the low sensitivity to changes of the fish numbers in the Bromka – Władysławowo fishing grounds.

DISCUSSION

Fishing exploitation complicates the relations between evolutionarily developed fish assemblages and the environment (Mahon and Smith 1989). The results of investigations during which it was possible to compare assemblages of non-commercial fish in relation to fish assemblages under fisheries pressure reveal that exploitation has a significant impact on the variability of these assemblages (Koslow *et al.* 1988, Dufour *et al.* 1995). No information is available regarding Gulf of Gdańsk fish assemblages prior to exploitation. In order to determine the potential effect of fishing pressure on fish assemblages, it is necessary to monitor them and to include species which are not commercially fished. This rule had also been applied in determining changes in the fish assemblages of the North Sea. Based on a series of investigations from the 1930s, Greenstreet and Hall (1996) confirmed that changes in fish assemblages are indisputable, however, they concerned mainly species under fishing pressure. The numbers of non-commercial species varied only slightly over this period of time. Similar results were obtained by Aldebert (1997) who used research cruise data and landing statistics to confirm that over a 40 year period a decrease in the number of commercial species occurred, while the number of species not under fishing pressure remained basically unchanged. Based on the analyses of data series regarding the contribution of non-commercial species which had the highest numbers in standardized research hauls over a period of 23 years, Heesen and Daan (1996) state that the majority of them exhibited an increase in numbers in accordance with the time gradient. Using the same material, Heessen (1996) observed the tendency for the numbers of a majority of fish species under fishing pressure to decrease. The current investigations revealed an increase in the numbers of a majority of non-commercial species such as Gobiidae, stickleback, smelt and eelpout in accordance with the time gradient. The highest increase was observed for eelpout for which the density index increased from 0.3 kg/hour of haul in 1985 to 373 kg/hour of haul in 1999.

According to Pimm and Hyman (1987), because of their decreasing numbers commercially exploited species may be replaced by species which have similar ecological requirements but whose populations are under less fishing pressure. This situation may cause changes in the exploited system, thus resulting in the transition from one stable level to another (Beddington 1984). This process may be of significant economic importance if the replacement species at the new ecosystem stability level has either a low commercial value or none at all (Brown *et al.* 1976, Sherman 1991).

The boundaries for the location of fish assemblages determined in this work have not been strictly determined. It was assumed that if the frequency of occurrence of a particular fish assemblage at a station throughout the analyzed years is 90%, then this station can be regarded as its location. The ranges of occurrence of the inner bay and the open sea fish assemblages varied in subsequent research cruises. As a result of this time-space variability, a pulsing picture of the inner bay fish assemblage was created. Its basic feature is the intersection of the ranges of occurrence of the determined fish assemblages which depends on the probability of a given assemblage occurring in a given location. Through analyses, two of the most probable causes of the inner bay fish assemblage pulsations were determined. The first must be related to the limited possibilities of randomly locating sampling stations as a result of the limited catch abilities of the applied fishing gear (vessel and fishing gear). As is stated in the Introduction, sampling in the sea is a factor which limits drawing conclusions about determining the ranges of occurrence of fish assemblages. A review of the literature indicates that due to high investigation costs, data from materials obtained for other purposes have often been used for analyses of fish assemblages in sea waters. Tyler *et al.* (1984), Rickey and Lai (1990), Rogers and Pikitch (1992) all used materials from commercial cruises and fisheries statistics. Gabriel and Tyler (1980), Gomes *et al.* (1995), Heessen (1996), and Rätz (1997) based their investigations on material from cruises whose goal was to collect information regarding selected commercially important species. In all cases, the authors had to accept the limitations resulting from the specifics of the set of materials available. The selectivity of the fishing gear has a decisive impact on the effect of the investigations in the case of commercial catches as does the non-random choice of investigation stations.

The set of factors that are inherent in the marine environment was the second cause of the pulsations of the inner bay fish assemblages over the investigation years. Unlike plant assemblages, fish are not bound to one particular location. They migrate according to either their spawning or feeding needs within an area that presents optimum conditions. This is an open system and it is problematic to strictly define the permanent geographical location of an assemblage as a distinct ichthyocenosis (Mahon and Smith 1989).

The existence of distinct biotic assemblages is one of the fundamental questions in assemblage ecology (Mills 1969). On the one hand, some researchers maintain that species are distributed independently within an assemblage, along with the gradient of environmental factors. Changes in environmental parameters cause changes in fish species composition. On the other hand, some researchers believe that the species in an assemblage are interdependent. If one of the species reaches its range limits, then the assemblage looses its integrity and is replaced by a new assemblage. If so, then assemblage structure would be determined by one or several species whose absence causes assemblage succession. In investigations of fish assemblages, changes in their structure are almost never rapid, nor do the assemblages themselves have strictly determined ranges of occurrence. These investigations usually indicate the existence of species associations that depend on physical parameters but lack any strict limits of occurrence (Mahon and Smith 1989). The gradients which were the most influential in many investigations of the distribution and structure of fish assemblages were geographic location, depth, salinity, temperature, and, to a lesser extent, oxygen contents and sedimentation type. The results of many investigations confirm that environmental parameters are also interdependent, e.g. the type of sedimentation is determined by the depth gradient (Scott 1982), and temperature and salinity influence the oxygen contents and the distribution of organisms which constitute fish food (Perry and Smith 1994). In the majority of the investigations, the interdependence of two or more environmental parameters was observed. Colvocoresses and Musick (1984) and Musick *et al.* (1985) confirmed the existence of segregated fish assemblages in the Central Atlantic Basin according to depth and temperature gradients; the latter was regarded as the decisive factor for determining fish distribution. Overholtz and Tyler (1985) report that the fish assemblages in the Georges Bank region (north-west Atlantic) were organized along the depth gradient and the salinity which it was correlated with. Rätz (1997) confirmed that the distribution of fish assemblages in the waters around Greenland depends on geographic location and depth.

The small numbers of fish and the low species diversity registered in hauls at depths of 20-30 meters combined with the fact that information regarding the occurrence of characteristic species system in the coastal area was not recorded in every cruise, requires careful interpolations of fish systems in the shallowest waters (20-30 m), as well as their comparison with assemblages from deeper areas. It must be noted that the majority of the material was collected in the winter months, and it was observed that fish migrate deeper in order to adjust to thermal conditions in the coastal zone of the Gulf of Gdańsk. This is due to the low temperatures in shallow waters; the deeper layers maintain higher temperatures and salinity (Cyberska 1994, Piechura 1993). The 20-30 m zone is probably of a transitional character, and it may be influenced by factors other than those described in this paper.

The results of the investigations presented in this work are based on material collected from a smaller area (2,600 km^2) than those of the investigations cited above. The length of the axis of the assemblage variability gradient from DCA was 2.13 SD units. This means that the variability of the environmental gradients does not cause a total exchange of species composition between two of even the most different locations. When taking into consideration the low species diversity and the domination of clupeids in both assemblages, the question arises if the two fish assemblages are in fact integrated, local fish assemblages characterized by the repeatability of the species composition. This question is concerned with the problem of scale in ecological investigations. On a global scale, the two assemblages identified in the Gulf of Gdańsk are almost identical; however, they may be distinct on a regional scale (Austin 1987, Levin 1992). Mahon and Smith (1989) state that conclusions regarding marine organism assemblages must be based on subjective investigation criteria due to the impossibility of collecting totally random samples.

Initially, cluster analysis was regarded as the proper method for defining fish assemblages in a given geographical area (Tyler *et al.* 1982). The area of assemblage occurrence had been defined as the geographical area in which a fish assemblage with species composition repeatability occurs. Determining regions of assemblage occurrence was justified by other authors because of the need to determine ecological bases for resource management in a given area (Murawski and Finn 1988, Sinclar *et al.* 1984) or to define the effects which fishing exploitation has on species composition (Koslow *et al.* 1988, Aldebert 1997, Rogers *et al.*

1999). The application of multidimensional statistical analysis techniques, as is stated in the Introduction, are often used in questions of assemblage ecology. A review of the available literature reveled that, to date, no information regarding the application of multidimensional analyses to the identification of fish assemblages in the southern Baltic Sea has been published. Methods like cluster analysis, multidimensional scaling and ordination are regarded as the most appropriate to illustrate the variability patterns and interactions which occur in the assemblages of living organisms (Clarke and Green 1988, Palmer 1993, Clarke 1993, Clarke and Ainsworth 1993, Ter Braak and Verdonchot 1995). On the other hand, multidimensional statistical methods are criticized because of the necessity of making subjective decisions during cluster analysis and multidimensional scaling, and the danger of directly interpreting processes and ecological connections using results obtained from transformations using ordination methods (Oksanen 1987, Wartenberg *et al.* 1987, James and McCuloch 1990). James and McCuloch (1990), in their work which summarizes both the advantages and disadvantages of particular multidimensional statistical methods, state that the role of the above mentioned techniques should be limited to descriptive studies which reveal interactions between the assemblages and the environment, and which will then be confirmed or rejected as a result of experiments and/or the application of one-dimensional statistical methods. Keeping in mind the limitations and the danger of over-interpreting results obtained using one method, three multidimensional statistical methods were used in the interpretation of the results presented in this paper. In light of the similarity of the conclusions of the various types of analyses presented in this paper, it can be stated that the results presented here summarize well the current knowledge of the distribution and coexistence of fish species in the Gulf of Gdańsk.

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Production and mineralization of organic matter in the Pomeranian Bay

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Abstract. The aim of this work was to estimate the influence of the Oder River on the biological production of the Pomeranian Bay and to identify the role of the local community in organic matter mineralization. The first problem was examined through the comparison of local nutrient resources and local primary production with nutrient loads and organic matter loads reaching the Pomeranian Bay from outside. The latter problem, concerning organic matter decomposition in the bay, was examined on the basis of measurements of oxygen consumption conducted in various seasons (March 1996, July 1996, May 1997 and October 1997).

It was calculated that 67% of nitrogen in the Pomeranian Bay came from the Oder River, 12% from the atmosphere and 21% was of marine origin. In the case of phosphorus, the marine and land-based shares were approximately even. As opposed to the open parts of the Baltic Proper, where nitrogen is the nutrient limiting primary production, phosphorus is a potentially limiting factor in the Pomeranian Bay. The annual organic matter load from the Oder River and atmosphere exceeded the annual "new" primary production by a factor of 2-3, but the amount of the biologically decomposable organic matter from these sources was close to the value of "new" primary production. Full decomposition of the degradable allochthonous organic material depends, however, on adequately high temperature and requires a longer period of time. The utilization of this material for bacterial production, and, thus, its inclusion into the trophic cycle was rather small and was concentrated around the river mouth area. Despite this the total community (dark) respiration appears to exceed (^{14}C) primary production by 30-50% throughout most of the vegetation period, thus suggesting an important contribution of the allochthonous organic material in the community energy budget. However, methodological uncertainties involved in primary production and community respiration measurements make this conclusion only hypothetical.

Key words: primary production, bacterial production, respiration, eutrophication, carbon budget, Baltic Sea, estuary

INTRODUCTION

The trophic status of the Baltic Sea has undergone dramatic evolution over the last century; it turned from an oligotrophic water body into a euthrophic one. This results from a rapid increase in pollution by nutrients, caused by demographic growth, urban development, intensive agriculture and industrial development in the countries located in the Baltic Sea catchment area (Elmgern 1989; Gerlach 1990). The negative effects of Baltic pollution, especially euthrophication, has affected all coastal countries with severe intensity. In order to prevent further degradation of the natural environment, these countries established the Helsinki Commission in 1974, an intergovernmental organization managing a common monitoring program and a number of environmental programs on a Baltic scale. A variety of regional research programs (e.g. the PELAG project in the northern part of the Baltic – Tamminen and Kuosa, 1998, the Gulf of Riga Project – Savchuk, 1998, Wassman and Tamminen, 1999) have been undertaken over the past few years, with the aim of better recognizing material flow processes in the ecosystem, as well as to assess the possibility of reversing unfavorable changes in the marine environment.

German and Polish scientists' attention has recently turned towards the Pomeranian Bay. In the period of 1994-1996, the German research project TRUMP was conducted with the aim of determining transportation and transformation processes of the substances discharged to the sea by the Oder River (Pollehne 1998). A Polish research program, supported by the Polish-German Cooperation Foundation, was conducted from 1996 to 1998, and was aimed at identifying the Oder's influence on the marine ecosystem in the Pomeranian Bay region. Results presented in this paper are part of the Polish program.

The Pomeranian Bay is a second-order estuary of the Oder River, which is the largest river entering the Western Baltic and one of the largest rivers within the entire Baltic catchment area. The annual water discharge of the Oder into the Baltic is estimated at about 18 km^3 of water that carries significant loads of nutrients, organic matter and other chemical pollutants. These substances originate from the river basin lying within the borders of three countries: Poland, the Czech Republic and Germany. The Polish part of the Oder basin comprises 35% of the total Polish territory. The Oder River basin area is highly developed with respect to agriculture, industry and urban development. Thus, the Oder contributes significantly to the high pollution of the Baltic Sea.

Pollutants reaching the Pomeranian Bay undergo initial transformation in the Szczecin Lagoon, a first-order estuary. The Pomeranian Bay, however, is not the final recipient of Oder discharges. The Pomeranian Bay is enclosed by land from the south and west, opens widely towards the north and east, and connects with the adjacent regions of the Baltic Proper (Arkona Basin and Bornholm Basin). The Pomeranian Bay is very shallow; its depth averages as little as 14 m (Majewski, 1974). The euphotic zone comprises almost the entire pelagial of the bay, therefore nutrients dissolved in the water are always available for phytoplankton and can easily be removed from the water column with sedimenting phytoplankton. However, because of the shallowness of the bay and its broad open boundary, water is mixed intensely and sediment can be resuspended. Thus, little organic material is sedimented on the bottom of the Pomeranian Bay and sandy sediments predominate. The Pomeranian Bay is, therefore, a transitional region, from which land-based pollution is transported, after partial transformation, to more distant, deeper parts of the Baltic Sea (Jost and Pollehne 1998).

An attempt was made in this paper to explain the importance of the Oder River to the primary production in the Pomeranian Bay, and to quantify the utilization of the organic material produced in the bay and brought into the bay from the land in the metabolism of the local community.

MATERIALS AND METHODS

Data for this paper were collected during four cruises of the R/V BALTICA, carried out in different seasons of the year, as follows: March 1996, July 1996, May 1997 and October 1997. The same stations were visited on each cruise (Fig. 1). The data on primary production and pelagic community respiration collected by the authors during a pilot cruise in September 1993 were also used in this paper.

Primary production measurements were made with the radioisotope method in light and dark bottles (Steemann-Nielsen 1952), using $NaH^{14}CO_3$. For the determination of the daily primary production, incubations were performed *in situ* in 100 cm^3 glass bottles at depths of 0.5, 2.5, 5, 10, 15 and 20 m, over a 4 h period around noon. Directly after incubation, 30-50 ml sub-samples were filtered through GF/F filters and placed in concentrated HCl fumes for 3-5 minutes. The sample activity was measured with a Beckman LS 6000 IC scintillation counter. A relatively short incubation time gives primary production values close to "gross" values. Following BMB recommendations (Ærtenberg, Nielsen and Bresta 1984), a correction factor of 1.06 was introduced in order to compensate for losses of organic ^{14}C due to phytoplankton

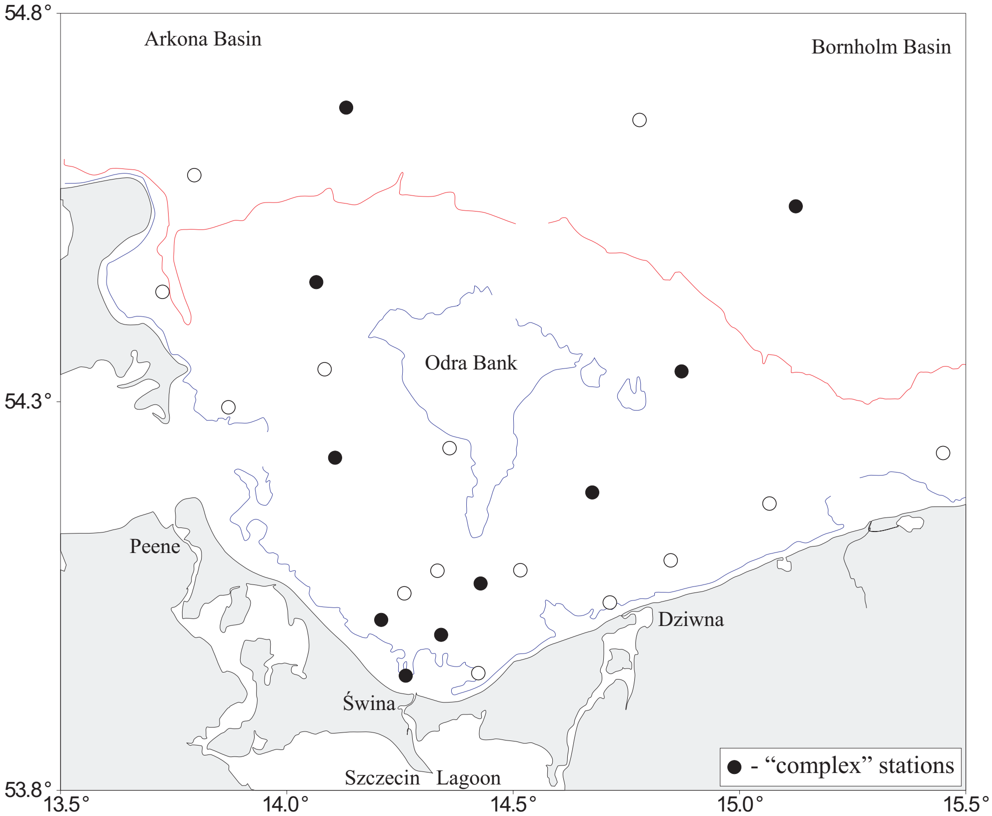

Fig. 1. Location of sampling stations in the Pomeranian Bay. "Complex stations" are stations arranged in a V-shaped transect, at which *in situ* measurements of primary production and sedimentation rate were performed, in addition to other measurements

respiration during incubation. Daily production was calculated taking into account the ratio of a daily dose of light to the dose of light during the *in situ* incubation period, both measured with a Kipp and Zonen pyranometer.

Pelagic community respiration was determined by measuring oxygen consumption during 24 h incubations of unfiltered seawater in 2 l glass bottles placed in darkness at *in situ* temperature. At shallow stations with the bottom depth below 13 m two samples were taken: 1 m below the sea surface and about 1 m above the bottom. At deeper stations samples were taken at 10 m depth intervals and 1 m above the bottom. For oxygen measurements (Winkler method), three 100 ml sub-samples were taken from the bottle, using a tube. In the September 1993 and March 1996 cruises, an ABU 12 autoburette was used for titration, with a visually determined titration endpoint. On subsequent cruises, an automatic Titrino 702 SM Metrohm titrometer equipped with a platinium electrode was used, with a potentiometrically determined titration endpoint.

To determine bacterial production, the rate of thymidine (/methyl-^{3}H/thymidine; specific activity 1,61 TBq · mmol^{-1}) incorporation was measured with the method described by Fuhrman and Azam (1980). The incubation was performed over 1 hour (in March 1996 over 2 hours) at the *in situ* temperature. Activity measurements were made with the Beckman LS 6000 IC scintillation counter. Conversion factors of 1.1 · 10^6 cells · pmol^{-1} thymidine (Rieman *et al*. 1987) and 0.35 pg C ·μm^{-3} of bacteria cells volume (Bjørnsen 1986) were applied for the calculation of bacterial production.

For the biochemical oxygen demand (BOD) samples were taken at 10 m depth intervals and incubated in 100 ml or 250 ml glass bottles. Oxygen concentration measurements were made with the Winkler method or with a WTW probe equipped with a potentiometric electrode. Three variants of measurements were carried out during the cruises, all using 21-day incubation times, ensuring the almost complete mineralization of the accessible carbohydrates at 20°C (Starmach *et al*. 1976):

– unfiltered samples, incubated at a temperature of 20°C (total potentially biodegradable organic matter, BOD_{21}-$TOM_{20°C}$);

– unfiltered samples, incubated at *in situ* temperature (total, biodegradable in actual thermal conditions, organic matter, BOD_{21}-TOM);

– samples prefiltered through 0.2 μm Sartobran capsule, incubated at *in situ* temperature (dissolved, biodegradable in actual thermal conditions, organic matter, BOD_{21}-DOM).

Sediment oxygen consumption was measured in deck experiments. Samples of bottom sediment were collected with a Raineck-type box corer. One or two boxes with undisturbed sediment cores and overlying water layer were incubated at *in situ* temperature in the dark. Oxygen consumption in the overlying water was measured in bottomless BOD-type bottles, driven into the sediment to a depth of 5 cm (2 bottles in each box). Oxygen concentration was checked every 2- 4 hours with a WTW probe. The bottles were tightly capped between measurements. The overlaying water was mixed only during the measurements. Incubation lasted from 8 to 24 hours.

RESULTS

Primary production

Seasonal and spatial variability of the primary production in the Pomeranian Bay, within the period of time considered here, have been described in detail by Ochocki *et al*. (1995, 1999). Figure 2 presents the seasonal variability of daily primary production in the Pomeranian Bay, presented against a background of the results from the Gulf of Gdańsk (Witek *et al*. 1999). The lowest values in the Pomeranian Bay were noted in March 1996, the highest in July 1996 and September 1993. In March, relatively high values also occurred, which accompanied the local phytoplankton bloom. Investigations in the Pomeranian Bay in July 1996 and in May 1997 were conducted directly after research was completed in the Gulf of Gdańsk, as part of the same research cruise. In July 1996, primary production in the Pomeranian Bay on average amounted to 65% of the average production in the Gulf of Gdańsk, and in May 1997 it amounted to 86%.

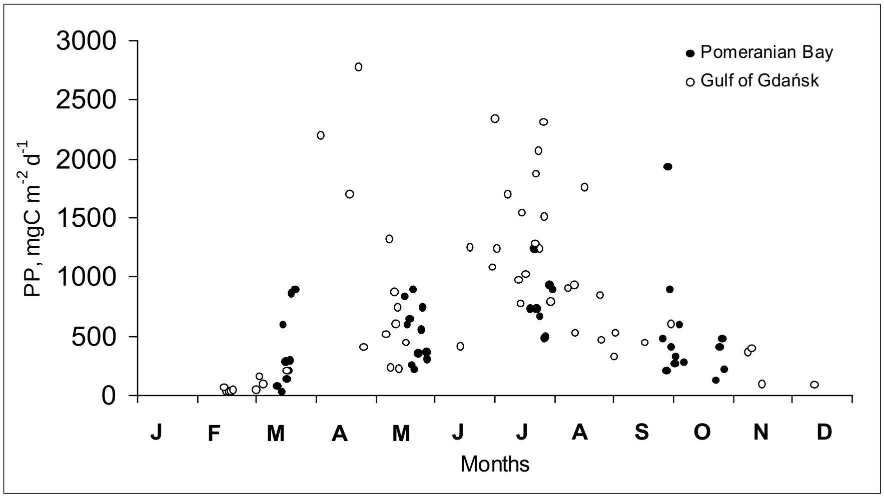

Fig. 2. Depth-integrated primary production in the Pomeranian Bay and in the Gulf of Gdańsk in years1993-1997

Pelagic community respiration

Respiration values of the pelagic community were distributed in accordance with the yearly distribution pattern of sea water temperature (Fig. 3). In March 1996, values were very low, unmeasurable by the method employed at that time to determine oxygen concentrations (the end of titration was visually assessed with an accuracy of approximately 0.02-0.03 ml $O_2 \cdot dm^{-3}$. The highest respiration values in the surface layer were recorded in July 1996, ranging from 0.06 to 0.57 ml $O_2 \cdot dm^{-3} \cdot d^{-1}$ (on average 0.18 ± 0.11 ml $O_2 \cdot dm^{-3} \cdot d^{-1}$). In May 1997 and September 1993, the average value at the surface amounted to 0.11 ± 0.07 ml $O_2 \cdot dm^{-3} \cdot d^{-1}$ and 0.14± 0.08 ml $O_2 \cdot dm^{-3} \cdot d^{-1}$, ranging from 0.03 to 0.31 ml $O_2 \cdot dm^{-3} \cdot d^{-1}$ and 0.07 to 0.27, respectively. In October 1997 the average value amounted to 0.05 ± 0.03 ml $O_2 \cdot dm^{-3} \cdot d^{-1}$, ranging from 0.01 to 0.12 ml $O_2 \cdot dm^{-3} \cdot d^{-1}$. Respiration was noticeably higher in regions where estuarine waters were found. The highest values were usually noted in the region of the Świna

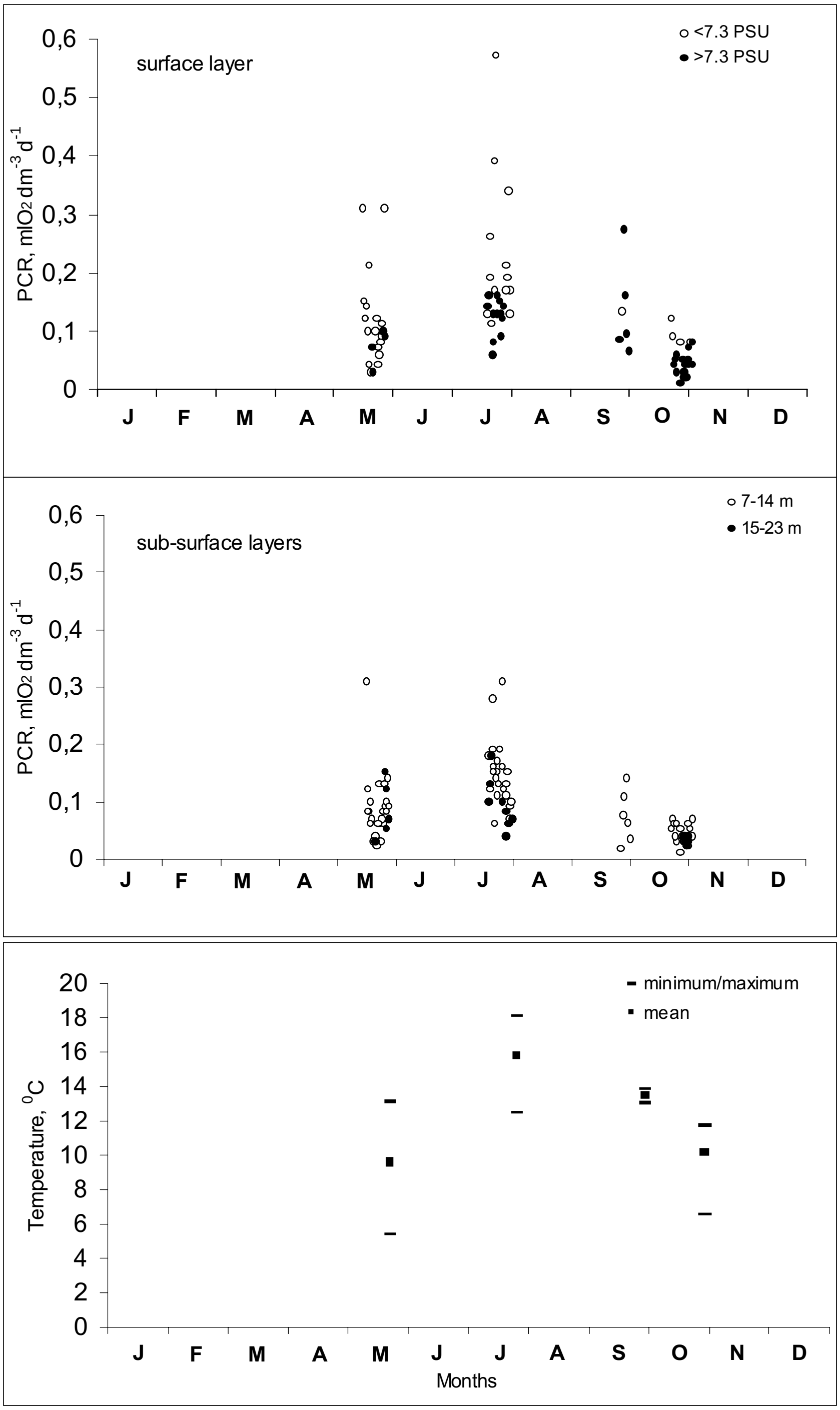

Fig. 3. Pelagic community respiration (PCR)

mouth. In the presence of the strong salinity stratification developed in this region, the vertical variability of respiration was significant, with surface values exceeding those recorded at the bottom by severalfold. In other regions there was little vertical variability of respiration.

Bottom sediment oxygen consumption

Similarly to the pelagic community, oxygen consumption by bottom sediments followed the yearly temperature distribution pattern (Fig. 4). The lowest average oxygen consumption rate (equal to 109.6 ml $O_2 \cdot m^{-2} \cdot d^{-1}$) was found in March 1996, and the highest (452.7 ml $O_2 \cdot m^{-2} \cdot d^{-1}$) rate in July 1996. During all the cruises, the maximum oxygen consumption rate was found in the proximity of the Świna mouth; the minimum rate was typical in the central part of the Pomeranian Bay. Oxygen consumption by the bottom sediments was not measured in the northern parts of the Pomeranian Bay due to methodological difficulties related to greater bottom depths.

By calculating pelagic community respiration values within the entire water column from the surface to the bottom, and adding oxygen consumption by bottom sediments, it is possible

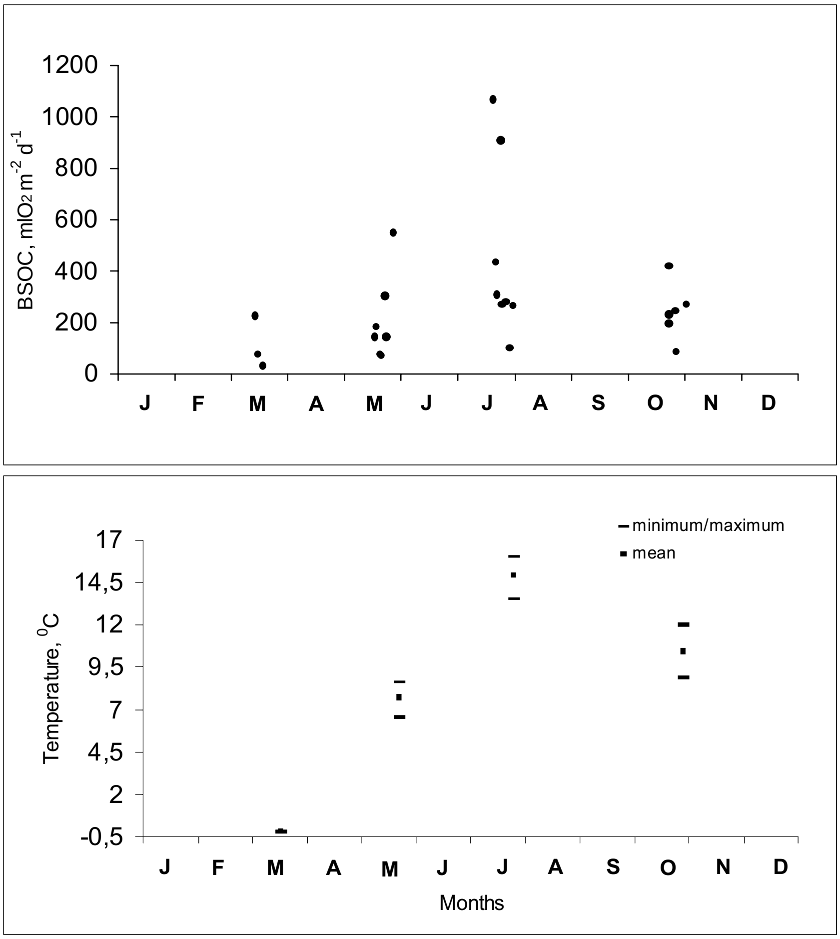

Fig. 4. Bottom sediment oxygen consumption (BSOC)

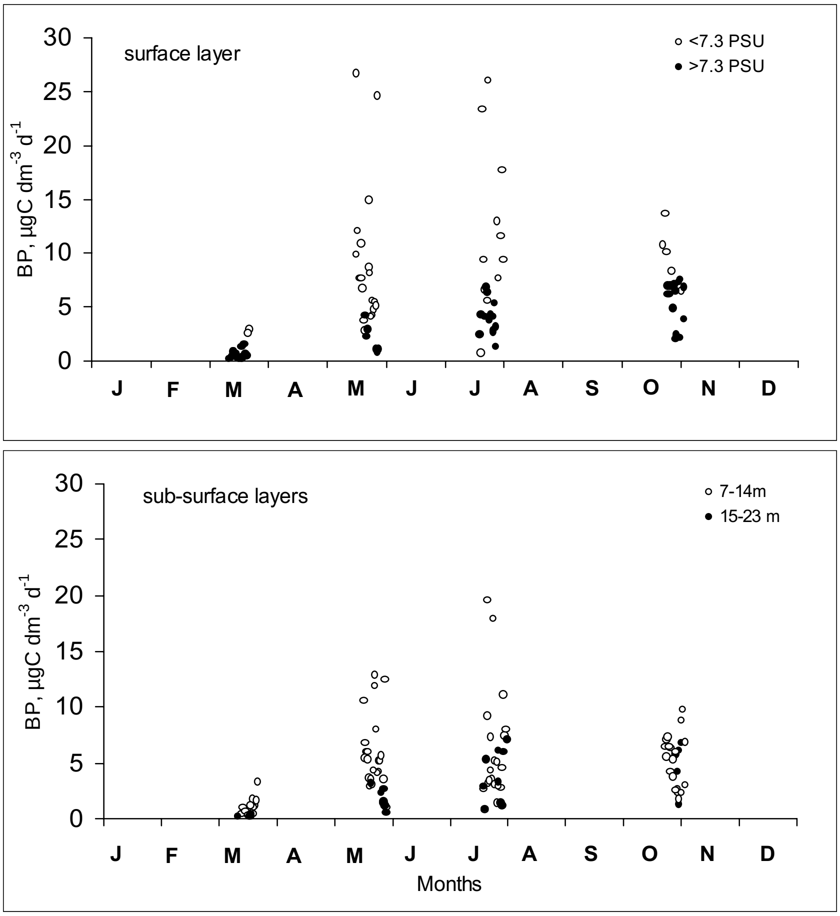

Fig. 5. Bacterial production (BP)

to calculate the total oxygen consumption per sea surface unit. The share of the bottom community in total oxygen consumption amounted to 16% in May 1997, 20% in July 1996 and 33% in October 1997, which was the maximum value.

Bacterial production

Bacterioplankton abundance, biomass and production in the 1996-1997 period is described in detail by Ameryk *et al.* (1999). In the present paper, only the comparison of bacterial production for individual months of the studied period is presented (Fig. 5).

In March 1996, values of bacterial production were very low and ranged from 0.12 to 2.9 µg C · dm^{-3} · d^{-1} in the surface layer. The most intensive bacterial production was observed in May 1997 and July 1996. During these months, the observed data varied very widely. Bacterial production in the surface layer ranged from 0.83 to 26.73 µg C · dm^{-3} · d^{-1} in May, and from 1.18 to 25.9 µg C · dm^{-3} · d^{-1} in July. The average bacterioplankton production in October 1997 was similar to the average production in May 1997 and July 1996, but the value range was smaller (from 1.95 to 13.55 µg C · dm^{-3} · d^{-1}).

Bacterial production strongly depended on the presence of river water. In waters with lower salinity the production was significantly higher, exceeding production in open sea water severalfold. Maximum values of bacterial production were noted at stations near the Świna and Dziwna mouths.

Biochemical oxygen demand

The biochemical oxygen demand of unfiltered water samples incubated for 21 days at 20°C (BOD_{21}-$TOM_{20°C}$) is a measure of oxygen demand in the first phase of the biochemical oxidation of organic matter, the so-called carbon phase (Starmach *et al.* 1976; Dojlido 1995). With the exception of few estuarine stations, the highest BOD_{21}-$TOM_{20°C}$ values were observed in March 1996, when the average oxygen demand in surface layer samples equaled 2.83 ± 0.48 ml $O_2 \cdot dm^{-3}$ (Fig. 6). In the remaining seasons, oxygen demand was lower roughly by a factor of 2 and equaled 1.33 ± 0.58 in May 1997, 1.61 ± 0.72 in July 1996 and 1.62 ± 0.58 ml $O_2 \cdot dm^{-3}$ in October 1997. In estuarine-type waters, with lowered surface salinity, BOD_{21}-$TOM_{20°C}$ was

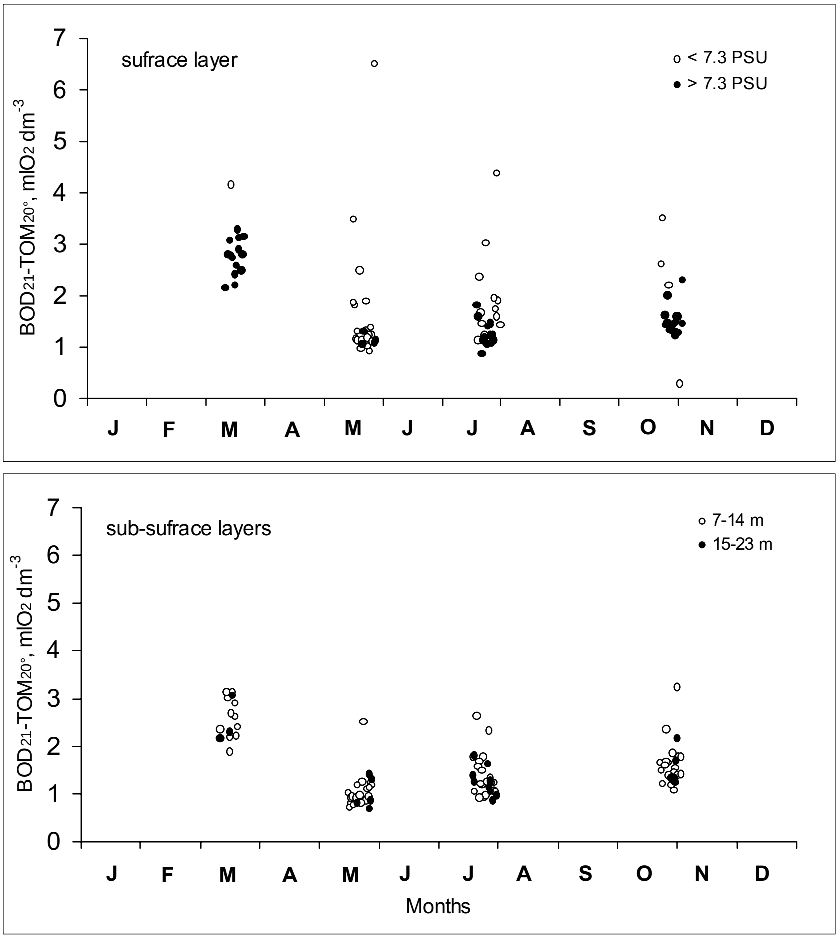

Fig. 6. 21-day biochemical oxygen demand at 20°C (BOD_{21}-$TOM_{20°C}$)

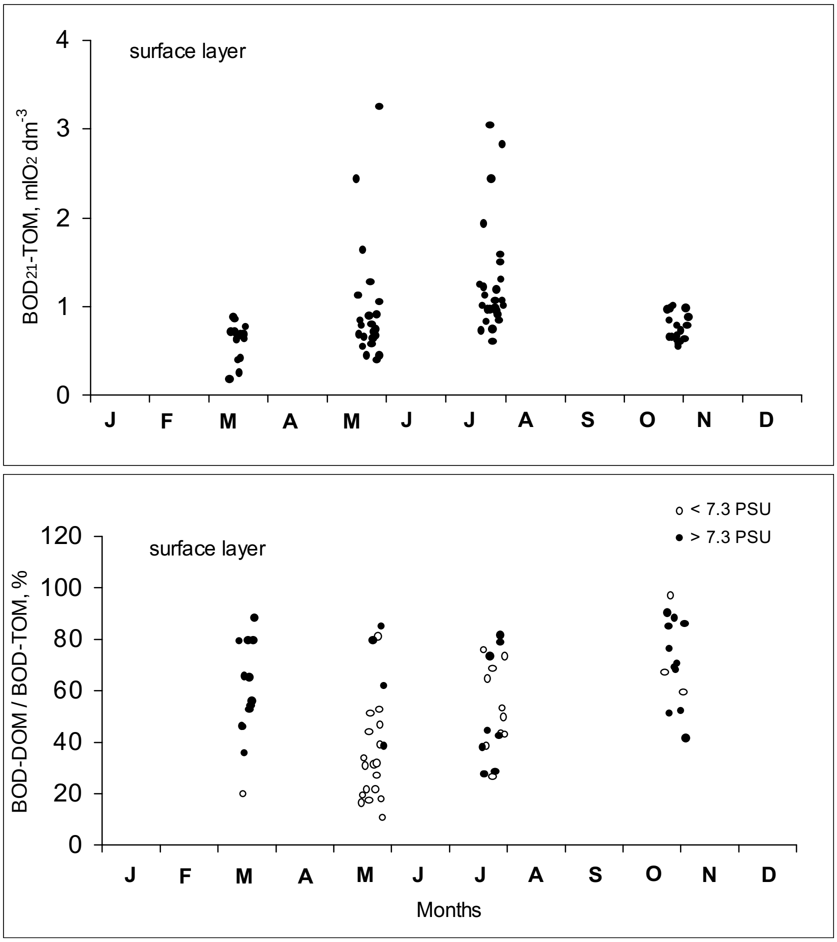

Fig. 7. 21-day biochemical oxygen demand (BOD_{21}-$TOM_{20°C}$) at ambient sea temperature (upper panel) and percentage of DOM in biologically decomposable organic matter at ambient sea temperatures (lower panel)

usually higher than in the open sea waters, especially in the region of the Świna and Dziwna mouths. There was little vertical variability of BOD_{21}-$TOM_{20°C}$ in the pelagial, with the exception of areas of estuarine water occurrence with strong salinity stratification, where surface values were higher than bottom values.

The average BOD_{21}-TOM values determined in natural thermal conditions in surface layer were highest in July 1996 (1.27 ml $O_2 \cdot dm^{-3}$), and the lowest in March 1996 (0.61 ml $O_2 \cdot dm^{-3)}$ (Fig. 7 upper panel), being a very variable portion of BOD_{21}-$TOM_{20°C}$, averaging from 21% in March 1996 (temperature about 2°C) up to 73% in July 1997 (temperatures from 12.5 to 18°C).

The proportions of particulate and dissolved fractions in biologically decomposable organic matter varied broadly. In March 1996 and October 1997, most of the organic matter was made up of dissolved organic matter (DOM). This portion decreased in May 1997 and July 1996. In May 1997, especially in estuarine waters, particulate material prevailed (Fig. 7 lower panel).

DISCUSSION

The comparison of primary production in the Pomeranian Bay and the Gulf of Gdańsk in July 1996 and May 1997 (Fig. 2) seems to indicate lower productivity in the Pomeranian Bay, however, comparison based on wider ranging material do not confirm this. Based on the investigations which were carried out in the southeast Baltic Proper in 1993-1997, Wasmund *et al.* (2000) indicated that primary production was similar in the open waters of the Baltic Proper (Arkona Sea, Bornholm Sea, South Gotland Sea) and in the Pomeranian Bay and the Gulf of Gdańsk, with the exception of river plume areas. Its annual averages ranged from 530 to 578 mg C $\cdot$ m^{-2} $\cdot$ d^{-1} (about 190-210 g C $\cdot$ m^{-2} $\cdot$ y^{-1}). Greater production was observed near river plumes, and the highest average values were noted for those in the Pomeranian Bay (1,156 mg C $\cdot$ m^{-2} $\cdot$ d^{-1}, while the average value for river plumes in the Gulf of Gdańsk was 775 mg C $\cdot$ m^{-2} $\cdot$ d^{-1} and in the Gulf of Riga – 745 mg C $\cdot$ m^{-2} $\cdot$ d$^{-1)}$.

Rates of pelagic community respiration in the Pomeranian Bay were within similar ranges as those reported from the Gulf of Gdańsk, also rates of bottom sediment oxygen consumption were similar (Witek *et al.* 1999). These last values seem to be conservative due to potential underestimation of benthic community respiration resulting from the methodological reasons (lack of stirring between the measurements). Carey (1967) noted that lack of stirring can reduce oxygen uptake to less than 20% of that obtained with the stirring rate similar to the natural condition. The oxygen consumption rate in the sediments during summer in the Pomeranian Bay (Fig. 4) were significantly lower at the majority of stations than those confirmed for the same season at two coastal stations in the Puck Bay (western part of Gulf of Gdańsk) 1,762 and 1,048 ml O_2 $\cdot$ m^{-2} $\cdot$ d^{-1}) by Bolałek *et al.* (1991). However, the coastal results were obtained in much shallower areas (4-8 m).

The importance of allochthonous sources of nutrients for primary production in the Pomeranian Bay

In order to determine how nutrients originating from the Oder River influence primary production in the Pomeranian Bay, the amount of nutrients from the Oder River can be compared with the winter nutrient pool, present in the bay prior to the growth period. According to Institute of Meteorology and Water Management (IMWM) reports, in the 1993-1997 period the yearly load of mineral forms of nitrogen discharged by the Oder River to the Szczecin Lagoon varied from 36.6 to 67.7 thousand tons, and the yearly load of inorganic phosphorus ranged from 1.5 to 2.3 thousand tons (Niemirycz *et al*. 1994, Niemirycz and Margońska 1995, Margońska 1996, Niemirycz and Bogacka 1997, Niemirycz and Bierawska 1998). Material from the Oder undergoes transformation when passing through the Szczecin Lagoon. Some portion of the material, discharged as suspended matter, is deposited on the bottom and is bound to bottom sediments. Dissolved, inorganic forms of nitrogen and phosphorus are utilized by phytoplankton and benthic vegetation of the lagoon; some portion of nitrogen is denitrified. The combined effect of these processes in the Oder estuary has been examined by Grelowski *et al*. (2000). The authors showed that, of the amounts discharged by the Oder to the lagoon, only 40% of inorganic nitrogen and about 68% of inorganic phosphorus reaches the Pomeranian Bay. Averaging loads from the 1993-1996 period and taking into account the results from Grelowski *et al*. (2000), it can be assessed that 21 thousand tons of inorganic nitrogen and 1.2 thousand tons of inorganic phosphorus reaches the Pomeranian Bay annually from the Oder estuary.

Winter concentrations of inorganic nitrogen and phosphorus in the Pomeranian Bay in the 1989-1993 period were determined by Trzosińska and Łysiak-Pastuszak (1996) to be 21.87 mmol N · m^{-3} and 0.99 mmol P · m^{-3}, respectively. However, it appears from the investigations of Nagel *et al.* (1997) and Pastuszak (1999) that the Oder estuary has a strong influence on the nutrient distribution in the Pomeranian Bay even during winter, generating significantly higher concentrations in the southern part of the bay as compared to northern regions. In order to estimate the amounts of N and P available for phytoplankton in the Pomeranian Bay without the Oder contribution, it seems to be more appropriate to consider nutrient concentrations typical for Baltic open waters, especially given the fact that the water exchange time between the Pomeranian Bay and the open Baltic is short (Lass *et al.* 1999). For the 1989-1993 period, winter concentrations of inorganic nitrogen and inorganic phosphorus in the isohaline layer of open Baltic waters amounted to 6.49 mmol N · m^{-3} and 0.59 mmol P · m^{-3}, respectively (Trzosińska and Łysiak-Pastuszak 1996). Assuming the water volume of the Pomeranian Bay equaled 73 km^3 (Majewski 1974), by calculation we obtain 6.6 thousand tons of "marine" inorganic nitrogen and 1.3 thousand tons of "marine" inorganic phosphorus.

In order to complete this picture, the amount of nitrogen originating from the atmosphere should also be estimated. Measurements of atmospheric nitrogen deposition are conducted at the coastal air-monitoring station in Łeba, located about 200 km to the east of the center of the Pomeranian Bay. The atmospheric deposition amounted to about 600 mg N · m^{-2} · y^{-1} for the 1993-1997 period (Woroń 1994, 1995, 1996, 1997, 1988). Adopting this value for the Pomeranian Bay (an area of approximately 6,000 km^2), by calculation we obtain 3.6 thousand tons of nitrogen deposited from the atmosphere. Concentrations of phosphorus in wet deposition over the Baltic Sea are very low (~0.8 µmol · l^{-1}, HELCOM, 1989) and can be disregarded in the total budget calculations.

It can be assumed, therefore, that 67% of inorganic nitrogen in the Pomeranian Bay derives from the Oder River, 12% from the atmosphere and 21% is of marine origin. In the case of phosphorus, marine and land-based shares are approximately even (Fig. 8). The molar N:P ratio in the Pomeranian Bay, calculated on the basis of the above mentioned data, equaled 28:1,

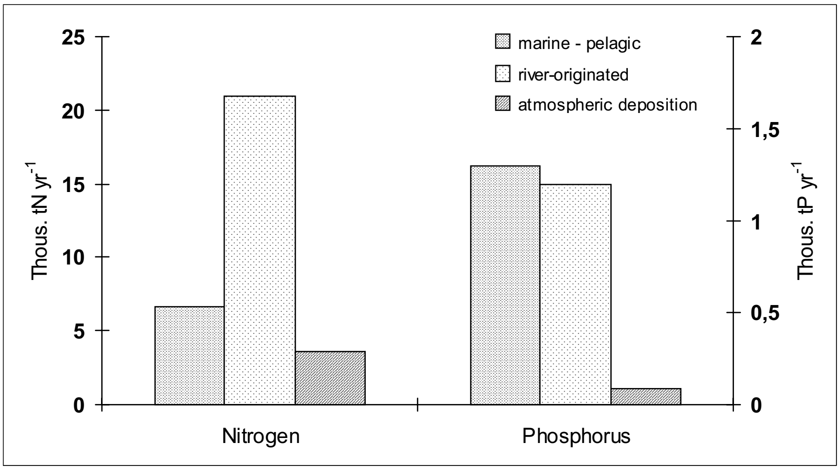

Fig. 8. Sources of nutrients in the Pomeranian Bay. For explanations see text

indicating phosphorus as a factor that potentially limits primary production. In contrast, in the open waters of the Baltic Proper, the primary production limiting factor was nitrogen, which was indicated by a relatively low N:P ratio value, amounting to approximately 10:1 in winter (Trzosińska and Łysiak-Pastuszak 1996). In reality nitrogen and phosphorus limitation was changing in the Pomeranian Bay, both temporary and spatially. Phosphorus relative deficiency was observed in the spring period, especially in the inner Bay, while nitrogen deficits were noted mainly in the summer and autumn periods and in the outer Bay (Pastuszak 1999; Renk 2000).

The importance of allochthonous organic matter as an energy source in the Pomeranian Bay

Besides primary production, allochthonous organic matter seems to be an important source of energy for the Pomeranian Bay community. According to IMWM reports, for the period of 1993-1997, the average organic carbon concentration in the Oder River waters ranged from 11.3 to 12.7 mg C · dm^{-3} with annual mean water flows ranging from 390-747 $m^3 \cdot s^{-1}$ (Niemirycz 1994, Niemirycz and Borkowski 1995, 1996, Heybowicz and Borkowski 1997, Heybowicz *et al*. 1998). The annual organic carbon load, calculated on the basis of the above data, ranged from 146 to 300 thousand tons. This is a higher value than the value of "new" primary production (*sensu* Dugdale and Goering 1967) in the Pomeranian Bay, which can be estimated, on the basis of amounts of phosphorus, the most often limiting factor of the primary production in the bay, to be 100 thousand tons of organic carbon (assuming total, autochtonous and river-originated resources of phosphorus equal to 2.5 thousand tons and a molar C:P ratio in phytoplankton of 106:1, Redfield, 1934). However, only the biodegradable part of the allochthonous matter can be an important energy source for the ecosystem, since the major portion of the organic matter in riverine waters is comprised of refractory materials like lignins and humic compounds, whose mineralization is very difficult in natural conditions (Starmach *et al.* 1976). An indirect measure of the amount of biodegradable organic matter is biochemical oxygen demand. It is measured for a defined period of time, e.g. 5 days, at a standard temperature of 20°C (BOD_5). In the 1993-1997 period, BOD_5 of the organic matter discharged by the Oder River ranged from 73 to 118 thousand tons annually (Rybiński and Makowski 1994, Margońska and Borkowski 1995, Niemirycz 1996, Niemirycz and Bogacka 1997, Niemirycz and Bierawska 1998), which (assuming RQ = 0.9) is equivalent to about 25-40 thousand t C · y^{-1}. It was determined in experiments that BOD_5 makes up about 36-39% of the total biochemical oxygen demand (Witek *et al*. 1999), therefore, the total degradable organic matter load discharged by the Oder can be estimated to be approximately 64-111 thousand t C · y^{-1}. The net effect of processes occurring in the Szczecin Lagoon on the annual BOD load seems to be negligible (Grelowski *et al*. 2000).

There is insufficient data to allow the sound assessment of atmospheric deposition of organic matter to the coastal zone of the sea. Order-of-magnitude estimates can be done using the results of Pęcherzewski (1991), who conducted measurements of organic matter deposition at four stations located along the Hel Peninsula in the 1987-1988 period. As a result of this research, the author assessed the average monthly flux to be 2.4 $g_{d.w.} \cdot m^{-2}$. Adopting this value for the Pomeranian Bay and assuming that carbon comprises 50% of organic matter dry weight, atmospheric deposition to the Pomeranian Bay can be roughly estimated to be about 86 thousand t C · y^{-1}. It is probably difficult for marine organisms to utilize this organic material, which consists mainly of soot and pollens. In the absence of better data, we can estimate that the proportion of the biodegradable fraction in the total organic matter of atmospheric origin is

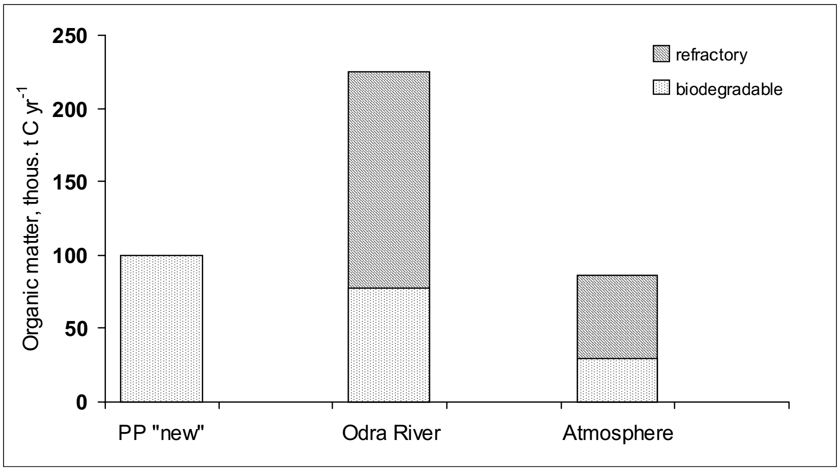

Fig. 9. Sources of organic matter in the Pomeranian Bay. For explanations see text

similar as for riverine organic matter, i.e. it amounts to about 40%. According to this assumption, the organic matter of atmospheric origin which can be degraded biologically amounts to about 30 thousand t C · y^{-1}.

The general budget (Fig. 9, values averaged) shows that half of the biologically decomposable organic matter in the Pomeranian Bay can originate from allochthonous sources.

It is worth noting, however, that biodegradable allochthonous matter requires a long period of time and a high temperature to be fully decomposed. At temperatures found in the Pomeranian Bay during most of the year, especially in spring when the Oder River discharges the major portion of its annual organic matter load, decomposition of biodegradable allochthonous matter is significantly slowed down and even partly inhibited (compare upper panels of Figs. 7 and 8). Thus, as opposed to nutrients, which can be almost entirely utilized by phytoplankton within a few days even at low temperatures and enter the trophic cycle within the Pomeranian Bay before penetrating to the open Baltic, assimilation of allochthonous organic material is more extended in time, and takes place over a much greater area, extending over the boundaries of the Pomeranian Bay.

Carbon flow in the Pomeranian Bay

Although highly productive oceans are regarded, in general, as autotrophic areas (Duarte and Agusti 1998), the balance of production-respiration in estuaries can be negative (Heip *et al.* 1995), or a gradient that ranges from heterotrophy in the upper part of the estuary to autotrophy in its lower part can occur (Kemp *et al.* 1997). Such variability results from the large amount of allochthonous organic matter which is mineralized in estuaries. This being so, determining the trophic status of the Pomeranian Bay which is fed by both inorganic nutrient substances and organic matter appears to be an interesting issue.

Theoretically, determining the trophic status of the Pomeranian Bay based on this research is simple. However, there are many methodological difficulties which complicate the task. One of them is the necessity of converting respiration from oxygen units to carbon units. In this paper it was assumed that the RQ (Respiratory Quotient) = 0.9, although there are no data that confirm that this value is appropriate for the Pomeranian Bay. The other difficulty is properly determining the gross primary production (GPP). In the isotope method, the primary production measured may be underestimated due to the remineralization of ^{14}C that occurs during sample incubation. During long incubation periods, lasting from 12 to 24 h, ^{14}C remineralization may reach 50% (Bender *et al.* 1987, 1999, Fasham *et al.* 1999). It is believed that short incubation periods of about 1 h, yield results close to the GPP (Platt *et al.* 1984). When intermediate incubation periods of 4 h are used, as in this paper, a certain correction coefficient is applied in order to correct the effect of ^{14}C remineralization. Unfortunately, this coefficient is usually not precisely known, so it must be taken from the literature (e.g. 1.06; Ærtenberg Nielsen and Bresta 1984). The other problem involves properly determining community respiration (CR). Measurements of oxygen consumption in the dark do not take into consideration respiration processes, which occur only in the presence of light, such as phytoplankton photorespiration. Although it is believed that photorespiration in phytoplankton can be almost entirely suppressed by the mechanism of CO_2 concentration inside algae cells (Beardall 1989), some researchers reported that in some situations the respiration rate in light may be of an order of magnitude higher than in the dark (Bender *et al.* 1987). Thus, the differences in the methodology may cause the distortion of the picture of the trophic state of the system and lead to false conclusions, especially when the differences between GPP and CR are small and close to the measurement error. Therefore, the comparison of primary production and respiration in the Pomeranian Bay should be regarded with great caution.

Comparison of depth-integrated community respiration (as expressed in carbon units and calculated per sea surface area) with community primary production, reveals that (dark) respiration prevailed over the (^{14}C) primary production at many stations, especially in July 1996 (Fig. 10). In this month, respiration in the pelagic zone was higher than primary production at most stations, with an average pelagic community respiration/primary production ratio equal to 1.23. In May 1997 and October 1997 average respiration in the pelagial was similar to primary production (ratio 1.02 and 0.92, respectively). Most probably, the lowest respiration/primary production ratio in the pelagial was in March 1996. Calculation of pelagic community respiration for March 1996 as $^{1}/_{21}$ fraction of BOD_{21}-TOM determined in natural thermal conditions resulted in depth-integrated respiration values higher than primary production at three stations only. Based on these rough estimations, we found the average pelagic community respiration/primary production ratio in March 1996 to be equal to 0.47.

Of the total pelagic and benthic community oxygen consumption, pelagic community respiration comprised 84% in May, 80% in July and 68% in October, and thus (dark) respiration of the whole community exceeded (^{14}C) primary production by about 20% in May, 54% in July and 34% in October. In March, assumed total respiration values were lower than primary production values (by about 38%). As a rule, total respiration exceeding primary production by the highest factor was observed in the region of the Świna mouth, nevertheless at stations located at the edge of the Pomeranian Bay, deeper than 20 m, respiration substantially surpassing primary production was also observed.

If we assume that ^{14}C primary production represents 80% of the true GPP (median value of the range of 60-100% as reported by Bender *et al.* 1987), only in July would TCR clearly exceed primary production (123% GPP), in May and October it would be on a similar level (96 and 107%, respectively), and in March it would be approximately half of the GPP. If, however, “light” respiration was significantly higher than “dark” respiration, our evaluation of TCR would also be underestimated and the real respiration of the whole biocenosis would exceed primary production throughout the majority of the vegetation season.

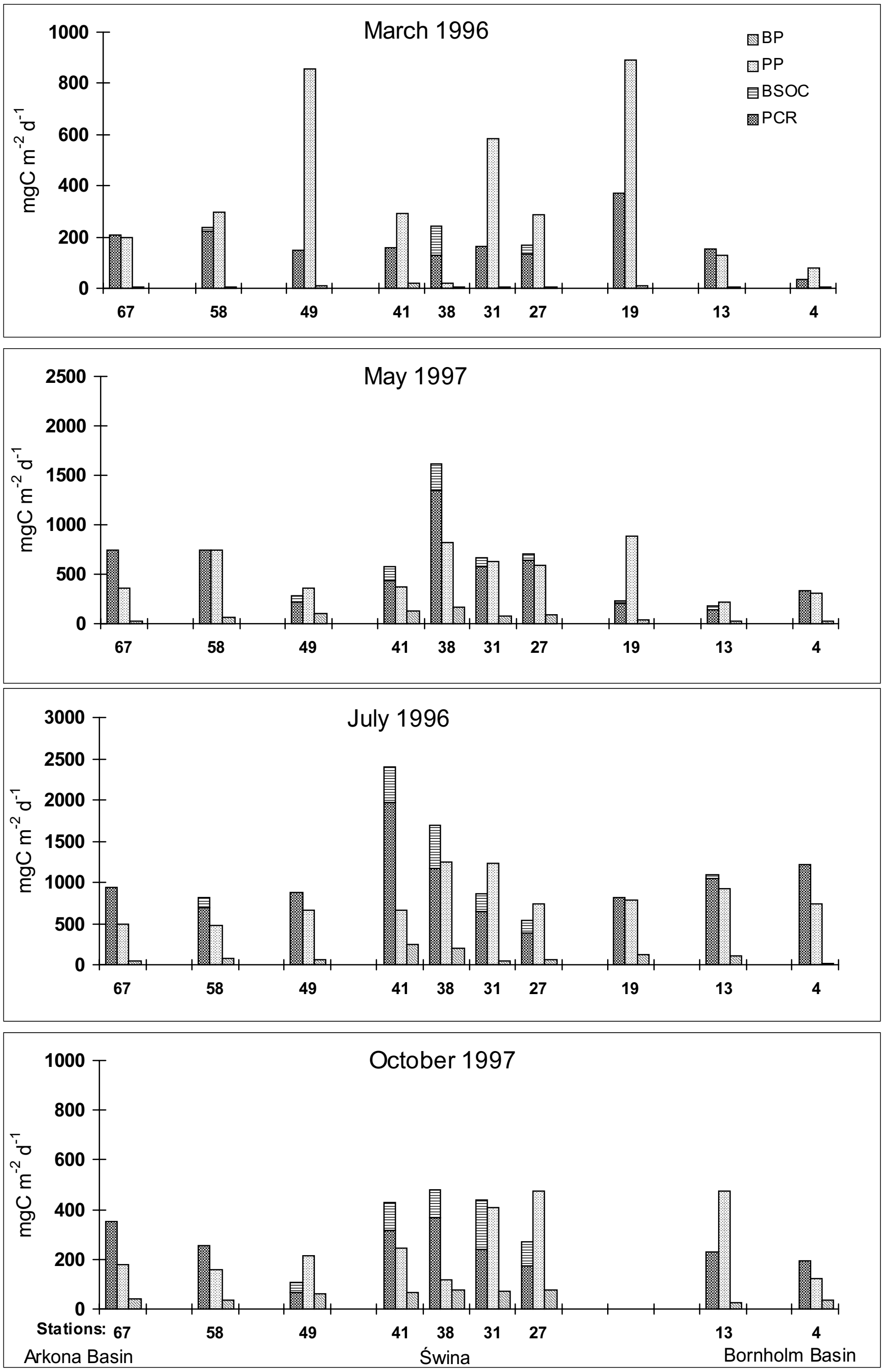

Fig. 10. Comparison of depth-integrated carbon fluxes along V-shaped transect of "complex stations" (compare Fig. 1). PP – primary production (gross), PCR – pelagic community respiration, BSOC – bottom sediment oxygen consumption, BP – bacterioplankton production. Note that BSOC measurements are lacking at several stations

The apparent domination of total respiration over production, which lasts throughout most of the vegetation period, suggests that allochthonous organic material may play an important role as a source of energy in the Pomeranian Bay region. At the beginning of the vegetation period, at low water temperatures, allochthonous organic material was not utilized in a noticeable way, but in the warmer period, with total respiration surpassing primary production by 20 to 50%, external sources of organic matter must have been utilized.

It can be concluded from the community metabolism studies conducted in other coastal regions that on an annual basis those systems which received especially high external loads of organic material were net-heterotrophic (e.g. nearshore Georgia Bight, the recipient region of organic matter exported from macrophyte-dominated marshes – Hopkinson 1985), while those which received large loads of nutrients were net-autotrophic (e.g. highly N-loaded Childs River estuary, Cape Cod – D'Avanzo *et al*., 1996). A tendency of the Pomeranian Bay system, as well as the Gulf of Gdańsk system (Witek *et al.* 1999), towards net-heterotrophy, despite a high nutrient load received from rivers, suggests that in the Baltic Sea organic material delivered from the watershed plays an important role in the community metabolism, at least in coastal regions.

Allochthonous organic matter, especially dissolved organic matter, may be assimilated mainly by bacteria. Allochthonous material utilization depends mostly on its composition, and *inter alia,* on the ratio of the main nutrients: carbon, nitrogen and phosphorus. When the organic matter is rich in nitrogen and phosphorus, utilization of the assimilated carbon for bacterial production is high, and may amount to over 40%, but when the nitrogen and phosphorus content is low compared to the carbon content, production efficiency may decrease and almost all assimilated matter may be simply respired (Hopkinson *et al*. 1989; Kuparinen and Heinänen 1993). The utilization of allochthonous matter for bacterial production in the Pomeranian Bay was probably the highest in the river mouth area and lowered with increasing distance from it. This is indicated by the fact that relatively high bacterial production, exceeding 30% of gross primary production, was found at stations located closest to the Świna mouth, and it decreased with increasing distance towards the open sea (Fig. 11). According to numerous authors (Larsson

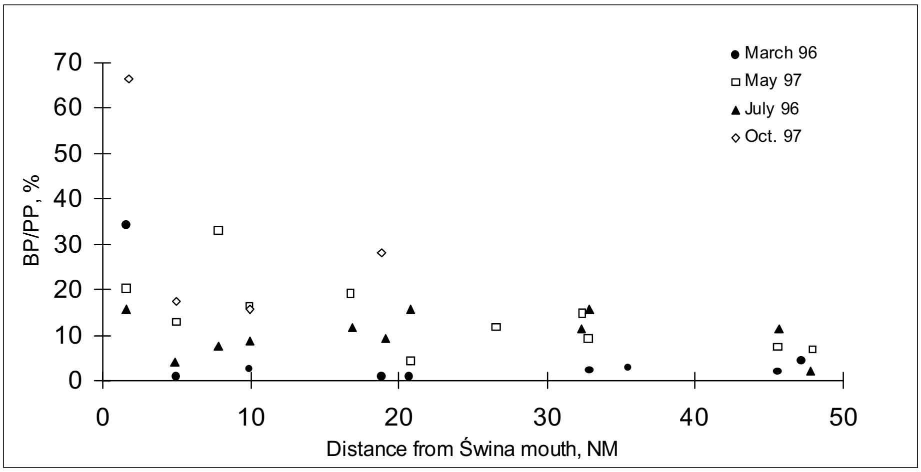

Fig. 11. Depth-integrated daily bacterial production (BP) as a percentage of gross primary production (PP)

and Hagström 1982; Cole *et al*. 1988; Norrman *et al*. 1995), bacterial production in the sea is based mainly on products of phytoplankton photosynthesis and amounts usually to approximately 20-30% of net primary production, which is a fraction of the gross primary production. Bacterial production exceeding this level likely indicates the use of additional sources of high-nutrition-value organic material by bacteria.

Summarizing the influence of allochthonous organic matter on the Pomeranian Bay ecosystem, it can be suggested that this material may cause a marked increase in general community metabolism, however, its utilization for biomass production can be observed mainly in the river-mouth vicinity.

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Seasonal variations of the parameters of photosynthetic light curves in the southern Baltic Sea

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Abstract. This paper presents the photosynthetic light curves for phytoplankton of the southern Baltic Sea. The parameters of these curves depend on temperature. The seasonal variations of the parameters of photosynthetic light curves have been described using the following equations:
The assimilation number $AN = 3.94 - 2.04 \cdot \sin(2\pi x + 0.51) + 0.53 \cdot \sin(4\pi x + 0.33)$
where: x – day, expressed in the form of a decimal fraction of the year. The optimum irradiance for photosynthesis $E_s = 380.7 + 154.8 \sin(2\pi x - 1.89) - 39.3 \sin(4\pi x - 0.53)$. Primary production in the gulf and coastal waters may be limited by phosphate deficiency, while in the open sea waters such limitations result from the deficiency of nitrogen compounds.

Key words: assimilation number, photosynthetic light curve, southern Baltic Sea

INTRODUCTION

Direct, *in situ* measurements of primary production are tedious since they require time consuming incubations (Steemann Nielsen 1958). Therefore, indirect methods are often applied to evaluate primary production (Platt and Sathyendranath 1993). One such method uses the light characteristics of algae photosynthesis from a particular environment and environmental measurements that are essential for such evaluations and which are relatively easy to conduct (Lohrenz 1993). The exact derivation of primary production using the light characteristics of photosynthesis requires the application of proper light characteristics for a given phytoplankton population (Sakshaug *et al.* 1997). A number of publications which review light characteristics of algae photosynthesis both in freshwater (Vollenweider 1965) and in the sea (Aaldering and Jivin 1997) have been published. The light characteristics of photosynthesis in the Baltic Sea expressed on a semi-logarithmic scale have been presented by Woźniak *et al.* (1989), among others, while Renk and Ochocki (1998) have presented them on a linear scale for the open southern Baltic Sea, Renk *et al.* (1999) for the Pomeranian Bay and Renk *et al.* (2000) for the Gulf of Gdańsk. The results which have been published so far have not yet yielded a full description of the seasonal variations of the photosynthetic light curves in the Baltic Sea. The aim of this paper is to present the average parameters of photosynthetic light curves in the southern Baltic Sea which have been obtained from investigations. These parameters may be employed to derive primary production using the results of some simple environmental measurements (Tilzer *et al.* 1993), and for mathematically modeling primary production (Baretta *et al.* 1997).

MATERIALS AND METHODS

This paper presents the parameters of the photosynthetic light curves derived at stations (Table 1) in the southern Baltic Sea in 2000 and at the measuring point on the pier in Gdynia-Orłowo in 1999-2000. In order to calculate the average values of the parameters of the photosynthetic light curves, the results of investigations that had been carried out previously were incorporated: for open Baltic waters – Renk and Ochocki (1998), for the Pomerania Bay – Renk *et al.* (1999) and for the Gulf of Gdańsk – Renk *et al.* (2000).

Table 1. Location of measuring stations

Station	Region	Position		Depth
		N	E	[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
B_{13}	Pomeranian Bay	54° 04`	14° 15`	12
ZN_2	Gdańsk Bay	54° 23`	18° 57.5`	15
	Gdynia-Orłowo			

The photosynthesis rate was measured using the radio-isotope method (Steemann Nielsen 1952) in an incubator. 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. A set of fluorescent lamps (Philips 18W) was used to illuminate the incubator. This setup provided 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, and 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 it at the ambient temperature from which the sample was collected. 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 a Beckman 6000 IC liquid scintillation counter (Aertebjerg-Nielsen and Bresta 1984). The inorganic carbon in the water, which was necessary to determine primary production, was marked by taking water pH measurements before and after acidification with 0.01n HCl at a rate of 1:4 (Anon. 1988).

The chlorophyll 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). Other methodological details were previously described in Renk (1983).

The methodology for deriving photosynthetic light curves is described in Renk and Ochocki (1998). The experimentally derived dependence of the photosynthesis rate versus irradiance was assigned by a light curve proposed by Steele (1962) for the North Sea, which was also used for the Baltic Sea (Renk and Ochocki 1999):

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

where: P_h – photosynthesis rate described as the ratio of primary production over one hour to chlorophyll-a concentration $\left[\frac{\text{mgC}}{\text{mgChl} \cdot \text{h}}\right]$, E – irradiance $\left[\frac{\text{kJ}}{\text{m}^2 \cdot \text{h}}\right]$

AN – assimilation number $\left[\frac{\text{mgC}}{\text{mgChl} \cdot \text{h}}\right]$

E_s – photosynthesis saturation irradiance $\left[\frac{\text{kJ}}{\text{m}^2 \cdot \text{h}}\right]$

The physical sense of the coefficients AN and E_s may be explained through the derivation of the function extreme [1], as follows: E_s is the illumination associated with the greatest photosynthesis rate, so-called saturation irradiance (Yentsch and Lee, 1966), which can be regarded as the optimum illumination for photosynthesis, while AN is the maximum photosynthesis rate, which is called the assimilation number (Parsons and Takahashi, 1973)*.

The impact of nutrient concentration on the rate of the primary production was investigated using the Michaelis-Menten equation, which describes the kinetics of nutrient uptake by phytoplankton (Eppley *et al.* 1968), with the equation constants:

$$AN = AN_o \cdot \frac{x}{k_s + x}$$

where: AN – assimilation number [mg C · mg Chl^{-1} · h^{-1}],

AN_o – assimilation number at very high nutrient concentrations (saturation value of the assimilation number), x – nutrient concentration

k_s – half-saturation Michaelis-Menten constant – nutrient concentration at which assimilation number equals $\frac{AN_o}{2}$.

RESULTS

Figure 1 presents the dependence of the photosynthesis rate on irradiance in the water column up to a depth of 2.5 m in the Gdańsk Deep in March and June. The curves in Fig. 1 were derived using the least squares method and they relate to equation [1]. The results of the derivations of parameters of photosynthetic light curves in the Gulf of Gdańsk (Gdynia-Orłowo region) are presented in Table 2, and those in the open waters of the southern Baltic Sea are presented in Table 3. Figure 1 shows that the maximum photosynthesis rate (the so-called assimilation number) which occurs at optimum irradiance was two times higher in June than in March. It can be stated that the assimilation numbers in the southern Baltic Sea vary seasonally, which is indicated by the dependence of the assimilation number on temperature (Fig. 2). Figure 3 presents the dependence of the optimum irradiance for photosynthesis on temperature. The relatively highly scattered points in the figures may indicate that these parameters also depend on other factors;

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

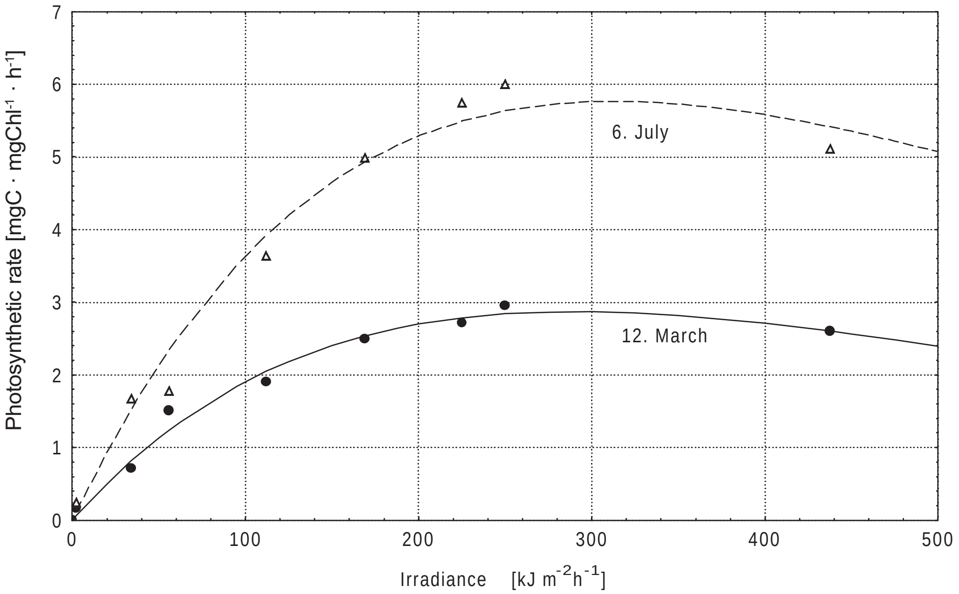

Fig. 1. Relationship between photosynthetic rate and irradiance in the Gdańsk Deep at a depth of 2.5 m in March and June.

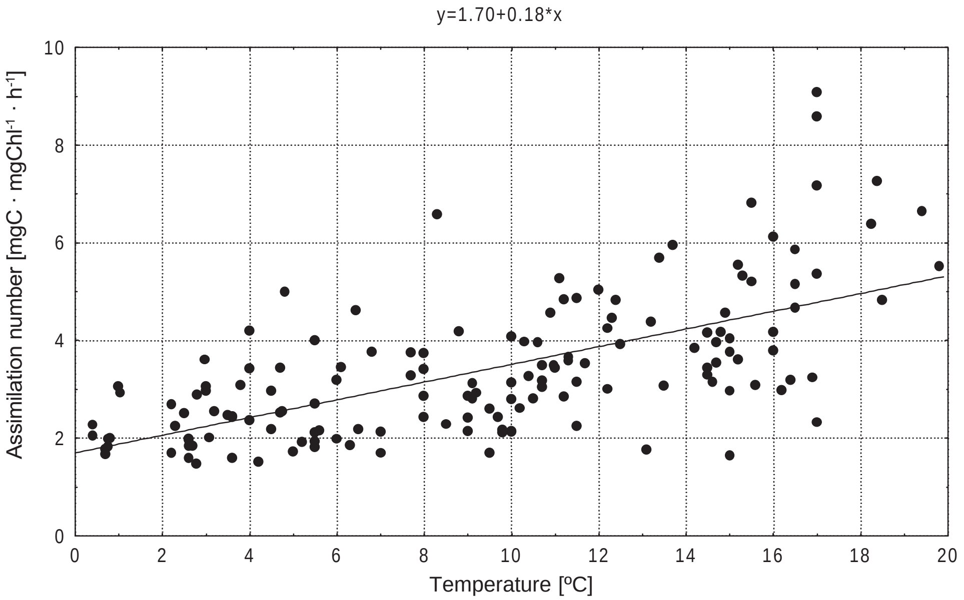

Fig. 2. Relationship between assimilation number and temperature.

the assimilation number may be dependent on nutrient concentration in the environment and optimum irradiance for photosynthesis may depend on the species composition (physiological properties) of phytoplankton populations.

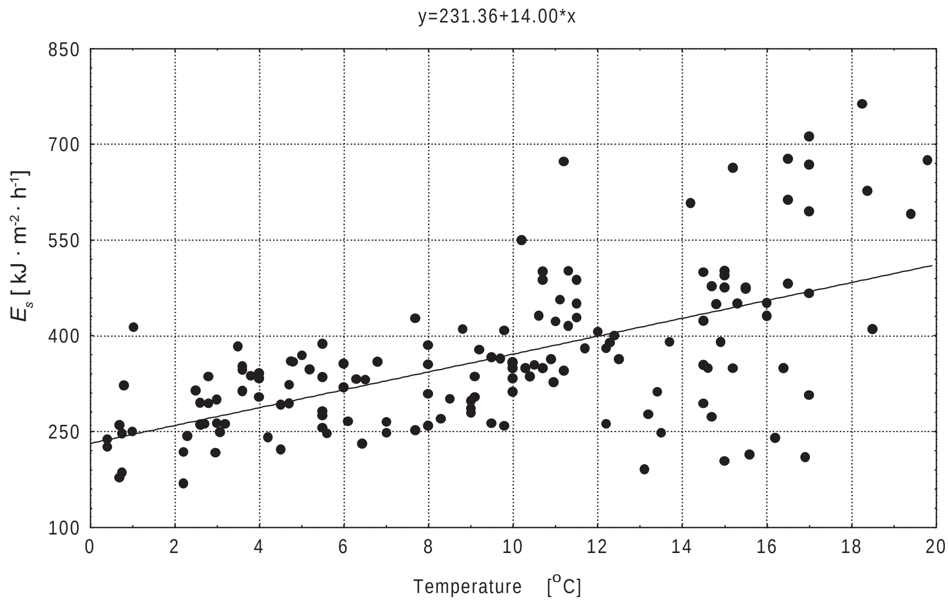

Fig. 3. Relationship between optimal irradiance for photosynthesis E_s and temperature.

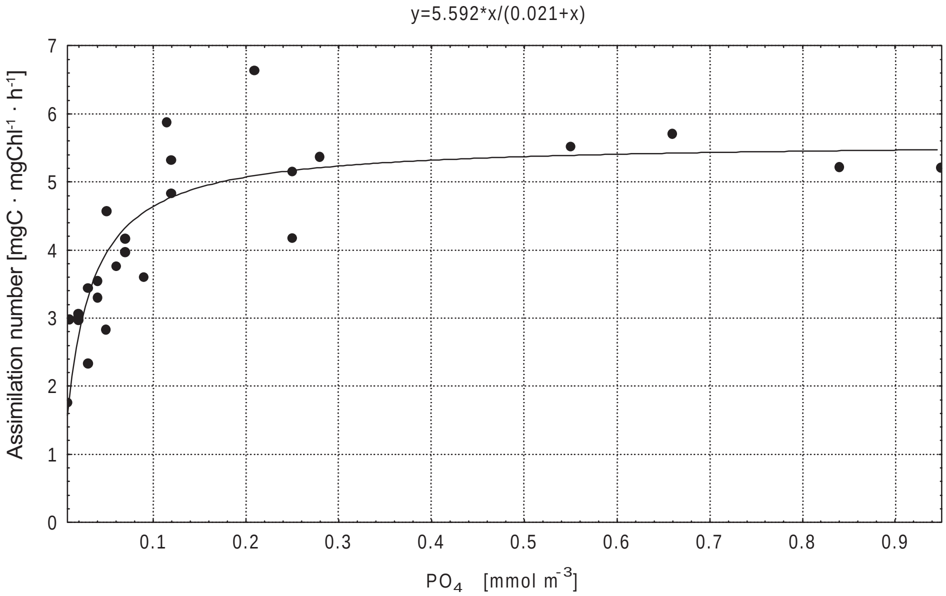

Fig. 4. Relationship between assimilation number and phosphate concentrations in the Gdańsk Bay.

The dependence of the assimilation number on phosphate concentration in the coastal area of the Gulf of Gdańsk (Gdynia-Orłowo region) is illustrated in Fig. 4. The curve in the figure relates to the Michaelis-Menten equation, and the equation coefficients at different tem-

Table 2. Parameters of photosynthetic light curve in the water near Gdynia Orłowo

Date	AN $\left[\frac{\text{mgC}}{\text{mgChl} \cdot \text{h}}\right]$	E_s $\left[\frac{\text{kJ}}{\text{m}^2 \cdot \text{h}}\right]$	r
25. 03. 99	2.63	304.12	0.92
14. 04. 99	1.99	355.73	0.99
17. 05. 99	2.66	408.54	0.99
27. 05. 99	2.25	486.93	0.99
10. 06. 99	5.87	676.62	0.99
24. 06. 99	5.15	612.38	0.99
9. 07. 99	5.52	674.41	1.0
23. 07. 99	6.37	590.42	1.0
5. 08. 99	2.83	504.38	0.99
9. 09. 99	4.83	409.99	0.98
30. 09. 99	2.86	355.47	0.97
28. 10. 99	1.69	365.60	0.98
24. 11. 99	1.51	240.54	0.98
5. 01. 00	1.98	259.94	0.96
10. 02. 00	2.01	248.54	0.96
2. 03. 00	4.19	340.61	0.98
23. 03. 00	3.42	332.69	0.97
30. 03. 00	1.72	369.43	0.97
13. 04. 00	1.81	386.90	0.97
11. 05. 00	1.64	500.90	0.99
27. 06. 00	5.36	667.64	0.97

Table 3. Parameters of the photosynthetic light curve in waters at various stations in the southern Baltic Sea

Date	Station	$AN\left[\frac{\text{mgC}}{\text{mgChl} \cdot \text{h}}\right]$	$E_s\left[\frac{\text{kJ}}{\text{m}^2 \cdot \text{h}}\right]$	r
27. 02. 00	P16	3.05	263.11	0.96
1. 03. 00	ZN2	1.47	293.94	0.98
13. 03. 00	P1	2.96	299.75	0.99
13. 04. 00	P16	3.43	293.74	0.99
14. 04. 00	P5	2.96	291.33	0.99
15. 04. 00	P140	2.42	313.97	0.99
16. 04. 00	P1	4.99	395.03	0.99
17. 04. 00	ZN2	1.92	346.88	1.0
5. 06. 00	ZN2	3.92	362.75	0.94
6. 06. 00	P1	5.68	312.34	0.98
7. 06. 00	P140	4.56	362.96	0.97
8. 06. 00	P16	4.46	389.15	0.99
10. 06. 00	B13	4.86	428.57	0.95

Table 4. Coefficients in the Michaelis-Menten equation for various temperature ranges in the Gulf of Gdańsk

Temp. [^{o}C]	$AN_o\left[\frac{\text{mgC}}{\text{mgChl} \cdot \text{h}}\right]$	$k_s\left[\frac{\text{mmolP}}{\text{m}^3}\right]$
>16	5.59	0.021
10-16	3.69	0.003
6-10	2.62	0.002
<6	2.34	0.010

perature ranges in the Gulf of Gdańsk are presented in Table 4. No correlation in the Gulf of Gdańsk was found between assimilation numbers and concentrations of inorganic nitrogen compounds (nitrates, nitrites, ammonia nitrogen). The dependence between the assimilation number and the silicate concentration in the water was not confirmed.

DISCUSSION

In order to estimate the seasonal variations of the parameters of the photosynthetic light curves, the results of earlier investigations were also employed. These investigations were carried out in the open waters of the southern Baltic Sea (Renk and Ochocki 1998), in the Pomeranian Bay (Renk *et al.* 1999) and the Gulf of Gdańsk (Renk *et al.* 2000). Periodic, seasonal variations of hydrobiological parameters can be described using a trigonometric series (Renk 1989).

Seasonal variations of the assimilation number in the Gdańsk Deep are well correlated ($r = 0.91$) with the curve presented in Fig. 5, which is described by the following formula:

$$AN = 3.94 - 2.04 \cdot \sin(2\pi x + 0.51) + 0.53 \cdot \sin(4\pi x + 0.33)$$

where: x – day expressed in the form of a decimal fraction of the year.

The seasonal variations of the optimum irradiance for photosynthesis E_s in the Gdańsk Deep, presented in Fig. 6 are described by the following function:

$$E_s = 380.73 + 154.77 \sin(2\pi x - 1.89) - 39.27 \sin(4\pi x - 0.53)$$

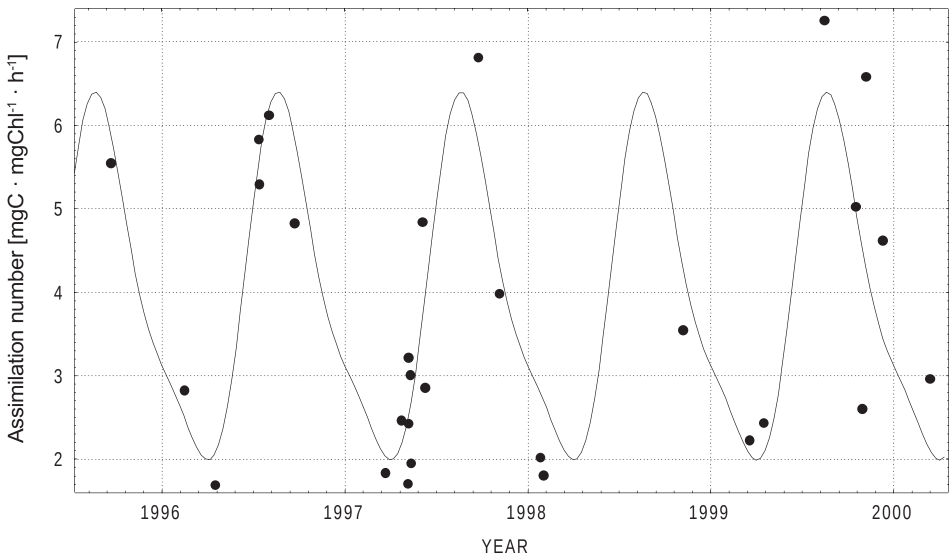

Fig. 5. Seasonal variability of the assimilation number in the Gdańsk Deep.

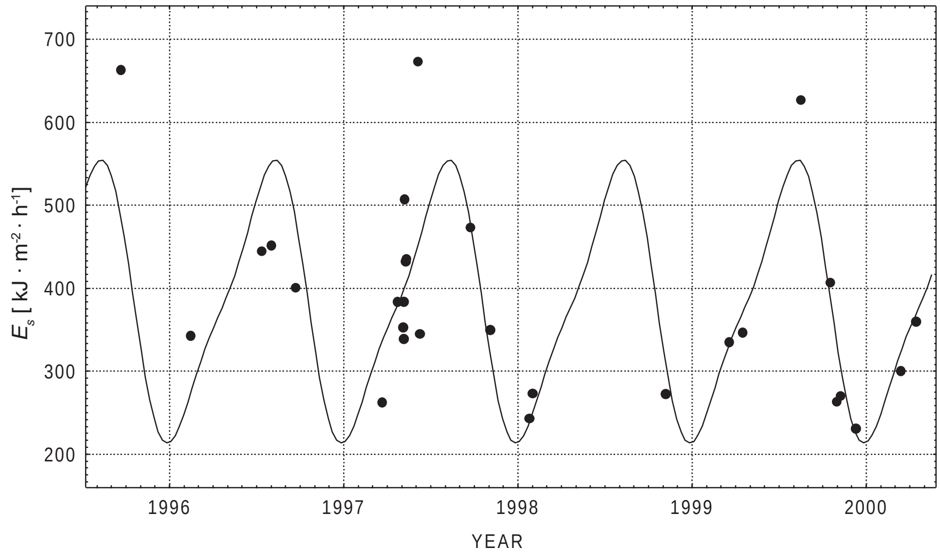

Fig. 6. Seasonal variability of the optimal irradiance for photosynthesis E_s in the Gdańsk Deep.

Similar equations can be used to describe the seasonal variations of the parameters of the photosynthetic light curves in the other parts of the southern Baltic Sea.

The comparison of the parameters of photosynthetic light curves at particular stations in the open waters of the southern Baltic Sea (especially in the Gdańsk Deep, the Bornholm Deep and the southern part of the Gotland Deep) reveals that these parameters vary insignificantly from station to station at the same period of time (Renk and Ochocki 1998). A similar conclusion may be formulated based on the comparison of the parameters of light curves in the Gulf of Gdańsk and the Pomeranian Bay. There are, however, differences between the photosynthetic light curves in open waters and the gulf waters. Using all the results of measurements, including earlier results (Renk and Ochocki 1999), the average values of the parameters of photosynthetic light curves for particular months and in open and gulf waters were collected, and they are presented in Table 5. The table reveals that the assimilation numbers *AN* and the optimum irradiance for photosynthesis E_s also vary seasonally in gulf waters.

The differences of the parameters of light curves which occur between open waters and gulf waters may be connected with differences in temperatures (Eppley 1972), in phytoplankton species composition, and, especially, with nutrient concentrations. In the open waters of the southern Baltic Sea during the vegetative season, the nitrogen to inorganic phosphorus ratio is usually lower than 16, i.e. the value commonly regarded as optimum for biological production (Redfield *et al.* 1963). In summer, concentrations of inorganic nitrogen in the open waters of the southern Baltic Sea are very low (Trzosińska 1992), and, thus, the nitrogen deficiency may limit primary production (Renk and Ochocki 1998).

Limitations of primary production due to inorganic nitrogen deficiency in the central part of the Baltic Sea were also observed by Sen Gupta (1972). The half-saturation constant for nitrogen uptake by phytoplankton, k_s in the Michaelis-Menten equation, which describes the nitrate uptake by phytoplankton in open waters of the southern Baltic Sea was estimated

Table 5. Average parameters of photosynthetic light curves in particular months

Month	Southern Baltic (open waters)			Gulf waters			Vistula Lagoon		
	AN $\left[\frac{\text{mgC}}{\text{mgChl} \cdot \text{h}}\right]$	E_s $\left[\frac{\text{kJ}}{\text{m}^2 \cdot \text{h}}\right]$	n	AN $\left[\frac{\text{mgC}}{\text{mgChl} \cdot \text{h}}\right]$	E_s $\left[\frac{\text{kJ}}{\text{m}^2 \cdot \text{h}}\right]$	n	AN $\left[\frac{\text{mgC}}{\text{mgChl} \cdot \text{h}}\right]$	E_s $\left[\frac{\text{kJ}}{\text{m}^2 \cdot \text{h}}\right]$	n
January	2.00	239.0	2	1.93	258.7	1	–	–	–
February	2.32	279.4	4	2.66	279.6	6	1.96	196.3	4
March	2.55	295.8	7	2.42	281.7	15	2.67	273.1	3
April	2.94	344.7	12	2.36	339.6	10	2.27	316.7	6
May	2.63	357.6	8	2.52	377.1	29	5.40	395.1	6
June	3.91	360.9	8	4.48	471.6	9	4.76	390.6	6
July	5.56	391.3	4	4.15	374.6	29	4.84	545.5	6
August	5.76	502.6	7	5.20	449.5	9	5.11	447.8	6
September	4.44	418.6	7	4.41	476.0	2	3.79	449.5	6
October	3.64	413.5	7	3.24	409.1	16	2.63	220.6	5
November	3.57	342.3	9	2.76	277.3	6	2.02	193.9	4
December	3.56	243.4	4	2.44	251.8	2	–	–	–

at 0.012 to 0.19 mmol · m^{-3} (Renk and Ochocki 1998). According to other authors (Nehring *et al.* 1987), inorganic nitrogen concentrations in the open waters of the southern Baltic Sea in summer also fall to that level or below.

Nutrient concentrations are higher in gulf waters than in open sea waters (Trzosińska 1990). Also, with the smaller distance to river mouths the N:P ratio increases in the Gulf of Gdańsk (Renk *et al.* 1976), as well as in the Pomeranian Bay (Humborg 2000). Near the river mouths the N:P ratio is much higher than the optimum for phytoplankton growth (Pastuszak *et al.* 1996). Thus, limitations of biological production occur sporadically in gulf waters and, if they do occur, they are the result of phosphate deficiency. This is illustrated by the curve in Fig. 4 which describes the dependence of the assimilation number on the phosphate concentration in waters near Gdynia-Orłowo. Similar dependencies of the assimilation numbers on phosphate concentrations were also obtained in the Pomeranian Bay (Renk *et al.* 1999).

Primary production limitations can occur in the open waters of the southern Baltic Sea due to the deficiency of nitrogen compounds (Renk and Ochocki 1998), while in the Pomeranian Bay and the Gulf of Gdańsk, phosphates have a greater impact on the photosynthesis rate than do nitrogen compounds (Renk *et al.* 1999).

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Bacterial microflora in the contents of Baltic herring (*Clupea harengus*) intestinal tracts during spawning in the polluted Vistula Lagoon

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Abstract. Quantitative investigations revealed that bacteria incubated on a common agar medium at temperatures of 20°C (TVC 20°C) and 37°C (TVC 37°C) occurred in the ranges of 3,800 to 18,300 and from 900 to 6,700 cfu in 1 ml of Vistula Lagoon water, respectively. The same bacteria groups identified in herring intestinal tract contents varied from 4,210 to 37,700 (TVC 20°C) and 950 to 28,840 (TVC 37°C) cfu/g.

Qualitative investigations revealed a similar composition of bacteria in water and intestinal tract contents. The following bacteria were confirmed in both environments: *Vibrio, Pseudomonas, Aeromonas, Enterobacter, Escherichia, Streptococcus* and *Staphylococcus*. *Bacillus* and *Micrococcus* occurred only in the water.

Key words: Baltic Sea, Vistula Lagoon, bacteria, water, herring, intestinal tract

INTRODUCTION

In recent years, significant interest has been paid to investigations of the dependencies between microorganism occurrence in various basins and the fish inhabiting them. These investigations have shown that bacterial microflora in fish is not stable and depends on many factors which have an impact on its qualitative and quantitative variations. An important role is played by environmental conditions (Trust and Sparrow 1974, Estave and Garay 1991, Niewolak and Tucholski 1995, Zmysłowska *et al.* 2000a, b), as well as by the fish developmental stage, fish species and condition (Sugita *et al.* 1988a, b), the type of food and the physiological conditions of the fish (Sugita *et al.* 1985). Geldreich and Clarke (1966) state that the fish microflora reflects the bacteriological state of the water; thus, it may be a potential water pollution indicator. Among the Baltic fish which feed on plankton (herring and sprats), there is a similar number of bacteria present in the contents of their intestinal tracts throughout the year (from 10^2 to 10^7 cells in 1 g). Certain numbers of bacteria are relatively stable and higher for given fish species during the feeding period, while during the starvation period, e.g. spawning migrations, they are lower (Zaleski 1985).

The Vistula Lagoon is located in the southern part of the Baltic Sea (between 19°13'E, 20°25'E, 54°15'N and 54°44'N). The lagoon is shallow (average depth 2.4 m) and narrow (average width 8.9 km). Both of these factors influence the basin's thermal and salinity conditions. The total drainage area is 23 thousand km^2. The salinity varies from 0.82‰ to 4.5‰ annually. The shallow and well-mixed Vistula Lagoon is well oxygenated, despite strong eutrophication. The highest amount of oxygen is found in spring and the amount decreases in summer.

There are three basic biological groups of herring in the Baltic which are divided with respect to spawning: coastal fall herring, coastal spring herring and open sea spring herring. The spawning grounds of the coastal spring herring are near river mouths and in the Vistula Lagoon, specifically near Nowa Pasłęka and along the Vistula Spit up to the Vistula River mouth. Baltic herring stop feeding at a certain point prior to spawning. After laying their eggs and returning to the open Baltic, they begin to feed. No information regarding microbiological investigations of Baltic herring which migrate to the Vistula Lagoon for spawning in spring were found in the literature. This lack of information also contributed to the importance of undertaking the current investigations. This work focused on investigations of the quantitative and qualitative composition of bacterial microflora in the intestinal tract contents of Baltic herring during spring spawning in the Vistula Lagoon. The studies were carried out with consideration for the thermal conditions and degree of organic pollution which prevailed in the aquatic environment at the study sites.

MATERIALS AND METHODS

The investigation material was composed of water from the Vistula Lagoon and the contents of Baltic herring intestinal tracts during spawning (March-April).

Water samples

For bacteria analyses water was sampled at three stations in the Vistula Lagoon – D, F, H (Fig. 1). The stations were located along the central part of the Vistula Lagoon, in places perpendicular to urban areas on the shore, which makes them the most representative sites in the basin in terms of pollution. In this work, the water pollution index was derived from the ratio of the number of TVC 20°C / TVC 37°C bacteria. According to Mucha and Deubner (1972), if the number ratio of heterophylic bacteria which grow at temperatures of 20°C and 37°C is lower than 10, then the waters are strongly polluted, while if it varies from 10 to 1,000 then waters are only slightly polluted. The samples were collected twice in March and twice in April 1989 from depths of 0.5 m using a Ruttner apparatus. Good water mixing in the Vistula Lagoon during spring circulation results in the relatively uniform distribution of micro-organisms in the water. Due to the stormy weather on 7 April 1989, samples for microbiological investigations were collected only at station D.

Water samples were diluted with a saline solution (0.85% NaCl) and then the medium was inoculated. After incubation, the colonies grown were counted and then recalculated into units comprising colonies in 1 ml of water (cfu/ml).

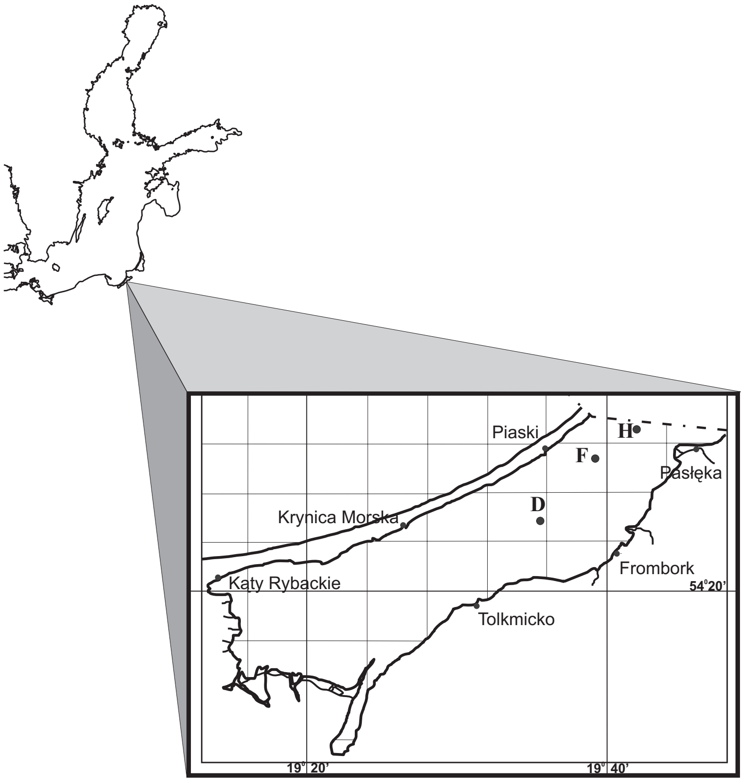

Fig. 1. Map of the Vistula River Lagoon; D, F, H – sampling localities.

Fish samples

Samples of the contents of five herring intestinal tracts were collected from fish caught at the same three stations (D, F, H) and at the same time as the water samples. The samples of intestinal tract contents of five fish were weighed, diluted ten-fold with saline solution (0.85% NaCl) and homogenized. This suspension was then treated in the same manner as the water samples. The results were recalculated into cfu/g of the contents of the intestinal tract.

The following parameters were determined for both types of samples: the total number of bacteria on a common agar medium after 72 h of incubation at a temperature of 20°C (TVC 20°C) and the total number of bacteria on a common agar medium after 24 h incubation at a temperature of 37°C (TVC 37°C).

Morphologically different bacteria colonies, grown on the common agar medium at temperatures of 20°C and 37°C, were identified. The shape of the cells, their motion ability, Gram staining and spore production were carried out microscopically, and catalase and oxidase enzyme tests were carried out. The following bioMérieux biochemical tests were used for further investigations: Api 20 NE (colonies grown at 20°C); Api 2E and Api Staph. (colonies grown at 37°C).

A total of 120 strains were isolated and classified to genus from the Vistula Lagoon water samples and 100 for the Baltic herring intestinal tract contents samples.

RESULTS

The results obtained show that among the three investigation stations in the Vistula Lagoon no significant quantitative diversity among the bacteria groups which were grown on a common agar medium at temperatures of 20ºC (TVC 20°C) and 37°C (TVC 37°C) were observed. The smallest bacteria numbers were confirmed in the first investigation period, in early March, while the highest were observed in the samples collected on 14 April. This must have been in response to the rise in temperature (Table 1) over time. Between 8 March and 14 April the total number of bacteria at TVC 20°C grew from 3,800 to 18,300 and at TVC 37°C from 650 to 6,700 cfu in 1 ml of water. The highest bacteria numbers were usually present at station D, and the lowest were at station F (Table 2).

The results revealed that the values of this pollution index, according to Mucha and Deubner (1972), in the Vistula Lagoon were lower than 10. They ranged from 2.23 to 6.92 which indicates that the basin is highly polluted (Table 3).

The total numbers of bacteria TVC 20°C and TVC 37°C in the contents of herring intestinal tracts varied from 3,060 to 37,720 and from 950 to 28,350 cfu/g, respectively. The lowest bacteria numbers, as was the case with the water samples, were found in samples from 8 March; after this they increased and reached their maximum on 14 April (Tab. 4).

At the three water stations in the Vistula Lagoon, a total of 120 bacterial strains were isolated and classified to genus as follows: *Vibrio*, *Pseudomonas*, *Bacillus*, *Aeromonas*, *Streptococcus*, *Micrococcus*, *Enterobacter*, *Escherichia*, *Staphylococcus* (Table 5). A total of 100 bacterial strains were isolated from herring intestinal tract contents samples, which, with the exception of *Bacillus* and *Micrococcus*, belonged to the same genera as those found in the water (Table 6).

Table 1. Water temperature in the Vistula Lagoon [°C]

Date	Station		
	D	F	H
8 March 1989	6.5	5.8	5.5
20 March 1989	7.2	7.0	6.7
7 April 1989	8.8	8.5	8.2
14 April 1989	11.4	10.9	10.6

Table 2. Total number of bacteria TVC 20°C and TVC 37°C (cfu/ml) in the Vistula Lagoon water

Date	Station					
	D		F		H	
	TVC 20°C	TVC 37°C	TVC 20°C	TVC 37°C	TVC 20°	TVC 37°C
8 March 1989	4,200	900	3,800	1,280	4,500	6,500
20 March 1989	10,000	1,780	7,800	1,780	9,500	2,100
7 April 1989	10,700	4,800	–	–	–	–
14 April 1989	18,300	6,700	18,300	6,700	12,800	5,400

– no sample

Table 3. Water pollution index for the Vistula Lagoon
based on the ratio of the number of TVC 20°C / TVC 37°C bacteria

Date	Station		
	D	F	H
8 March 1989	4.67	2.97	6.92
20 March 1989	5.62	4.31	4.52
7 April 1989	2.23	–	–
14 April 1989	2.73	2.69	2.37

– no sample

Table 4. Total number of bacteria at TVC 20°C and TVC 37°C in (cfu/g) in Baltic herring
intestinal tract contents

Date	Station					
	D		F		H	
	TVC 20°C	TVC 37°C	TVC 20°C	TVC 37°C	TVC 20°C	TVC 37°C
8 March 1989	5,060	3,060	6,640	3,600	4,210	8,730
20 March 1989	12,020	950	18,170	1,400	14,970	1,340
7 April 1989	19,940	24,210	–	–	–	–
14 April 1989	37,720	28,840	28,350	10,150	25,630	17,000

– no sample

Table 5. Species composition of bacterial microflora in Vistula Lagoon water samples

Bacteria genus	Station						Total	
	D		F		H			
	n	[%]	*n*	[%]	*n*	[%]	*n*	[%]
Vibrio *	13	32.50	15	37.50	14	35.00	42	35.00
Pseudomonas *	11	27.50	10	25.00	12	30.00	33	27.50
Bacillus *	4	10.00	3	7.50	3	7.50	10	8.33
Aeromonas *	3	7.50	4	10.00	2	5.00	9	7.50
Streptococcus **	2	5.00	2	5.00	3	7.50	7	5.83
Micrococcus *	2	5.00	3	7.50	1	2.50	6	5.00
Enterobacter **	2	5.00	2	5.00	2	5.00	6	5.00
Escherichia **	2	5.00	1	2.50	2	5.00	5	4.17
Staphylococcus **	1	2.50	0	0.00	1	2.50	2	1.67
Total	40	100.00	40	100.00	40	100.00	120	100.00

n – number of isolated strains
*in an agar medium at 20°C
**in an agar medium at 37°C

At all three stations, the highest percentage of bacteria were strains of the V*ibrio* genus, which constituted from 32.5% to 37.5% in the Vistula Lagoon water samples and from 53.33% to 66.67% of the intestinal tract contents samples. The lowest percentage contribution was from strains of the genus *Staphylococcus* ranging from 0% to 2.50% in water samples and from 0.0% to 3.33% in intestinal tract samples, respectively (Table 5 and 6).

Table 6. Species composition of bacterial microflora in intestinal tract contents of the Baltic herring in the Vistula Lagoon

Bacteria genus	Station							
	D		F		H		Total	
	n	[%]	*n*	[%]	*n*	[%]	*n*	[%]
Vibrio *	24	60.00	20	66.67	16	53.33	60	60.00
Pseudomonas *	6	15.00	4	13.33	3	10.00	13	13.00
Aeromonas *	4	10.00	3	10.00	3	10.00	10	10.00
Enterobacter **	2	5.00	2	5.67	2	6.67	6	6.00
Streptococcus **	3	7.50	1	3.53	3	10.00	5	5.00
Escherichia **	0	0.00	0	0.00	2	6.67	2	2.00
Staphylococcus **	1	2.50	0	0.00	1	3.33	2	2.00
Total	40	100.00	30	100.00	30	100.00	100	100.00

n – number of isolated strains
* in an agar medium at 20°C
** in an agar medium at 37°C

DISCUSSION

The results revealed the quantitative diversity of heterotrophic bacteria (TVC 20°C and TVC 37°C) between the two environments, the sampling periods and at the three stations.

Higher amounts of bacteria were always found in the intestinal tract contents of Baltic herring than in the Vistula Lagoon water samples; this complies with results obtained by other researchers (Esteve and Garay 1991, Zmysłowska *et al.* 2000a, b, c).

Temperature has a significant impact on the occurrence and development of bacteria in water basins (Zmysłowska *et al.* 2000b, c). The bacteria of both investigated groups (TVC 20°C and TVC 37°C) occurred at the lowest levels in early March; their numbers increased until they reached the maximum in the middle of April. This was connected with temperature which increased during this period from 5.6°C to 11.4°C. Equally low numbers of bacteria were found in herring intestinal tract contents at the beginning of spawning (8 March), while the highest were found on 15 April. These dependencies have been confirmed statistically by applying the linear regression model at different levels of significance.

The quantitative diversity of TVC 37°C bacteria at particular stations in respective investigation periods should be connected to the organic matter input from the drainage area. This is confirmed by the values of the organic pollution index of the Vistula Lagoon water which, in all water samples investigated, was lower than 10.0, and it was the lowest on 14 April (from 2.37 to 2.73). The highest abundance of bacteria (TVC 20°C and TVC 37°C) in the water and Baltic herring intestinal tract contents samples was also confirmed during this period

In addition to quantitative relationships between the bacterial microflora of fish and water, there are also qualitative relationships. Lésel (1979a) states that not all bacteria taxonomic groups which occur in water are also present in the intestinal tracts of fish. This does not confer with this author's own results, in which the presence of the bacteria *Bacillus* and *Micrococcus* genera were not confirmed in the herring intestinal tracts, although they appeared in the Vistula Lagoon water. This was probably due to the different environmental conditions between Vistula Lagoon water and the intestinal tracts of Baltic herring. It can be presumed that the microflora of the intestinal tracts was dependent on that which occurred in the Baltic Sea at the time the fish were feeding there. The author's own results as well as the results obtained by other authors (Trust and Sparrow 1974, Lésel 1979b, Estawe and Garay 1991, Zmysłowska *et al.* 2000a, c) confirm that Gram-negative rod-bacterium were the dominating microflora of both the water and the fish.

The author's own investigations revealed that, among the bacterial strains that were isolated, those of the genus *Vibrio* were most common both in the Vistula Lagoon water samples (from 32.50% to 37.50%) and those from herring intestinal tract contents (from 53.33 % to 66.67%). The lowest percentages were recorded for the *Staphylococcus* genus at 1.67% and 2.00%, respectively. In addition, the following bacteria genera were found in the intestinal tract contents: *Pseudomonas*, *Aeromonas*, *Enterobacter*, *Streptococcus*, *Escherichia.* This result complies with those obtained by Austin and Allen-Austin (1985) who report that the dominating bacterial microflora among sea fish are constituted by species of the genera *Vibrio, Aeromonas* and *Pseudomonas.* Aiso *et al.* (1968), confirmed that the bacterial microflora of the mackerel (*Trachunis japonicus)* intestine consists almost entirely of the genus *Vibrio*. A similar phenomenon was observed in Baltic cod, herring and sprats caught in August and January when the *Vibrio* genus constituted 100% of the bacterial population in the digestive tracts (Zaleski 1985).

In summation, it must be emphasized that quantitative differences in the studied bacteria were dependent on the prevailing environmental conditions. Increases in water temperature caused rises in their numbers both in the water and the intestinal tract contents of Baltic herring. An additional factor which contributed to the development of microflora bacteria was the organic pollution of the waters of the Vistula Lagoon (organic pollution index < 10.0). Rises in this index caused a several-fold increase in the numbers of the studied bacteria which are indicators of the degree of pollution.

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