ISSN 1429-2335

Bulletin

2(153) 2001

of the Sea Fisheries Institute

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The Bulletin of the Sea Fisheries Institute *is indexed and abstracted in ASFA and FSTA.*

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THIS JOURNAL IS SUPPORTED FINANCIALLY
by
THE STATE COMMITTEE FOR SCIENTIFIC RESEARCH, POLAND

BULLETIN OF THE SEA FISHERIES INSTITUTE
2 (153) 2001

Growth of Vistula sea trout (*Salmo trutta m. trutta* L.) based on adults caught in the Vistula River prior to the construction of the dam in Włocławek

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Abstract. The growth of winter and summer Vistula sea trout was compared using archival material from 1961-1968 before the construction of the dam near Włocławek. The average value of fish body growth during their first year in the sea was back calculated. The second growth measure was the fish size from the same year class (A.B+) during its occurrence in the river both in summer and winter. Growth variability, resulting from sex structure, smolt age and various calendar years, was eliminated by the proper choice of materials. The average body growth in the first year the fish were in the sea was greater in winter sea trout than in summer sea trout, and the differences that were evaluated with t-Student tests were statistically significant. No statistically significant differences were observed for the average lengths and masses of summer and winter sea trout or that the summer sea trout was larger than the winter one. Thus, its longer stay in feeding grounds before its spawning migration compensates for the lower rate of summer sea trout body growth.

Key words: Vistula sea trout, summer stock, winter stock, comparative analysis, fish growth, fish condition

INTRODUCTION

Before the construction of the dam in Włocławek towards the end of the 1960s, anadromous sea trout used the Vistula River as a migration route from its feeding grounds in the Baltic Sea to its spawning grounds in mountain rivers in the south of Poland.

Every year the main spawning migration occurred in two periods. Between June and September summer sea trout which were almost ready to spawn entered the river, and in late fall and winter, a year before the spawning season, winter trout with immature gonads headed towards the spawning grounds (Żarnecki 1963, Borzęcka 1998).

Besides differences in when spawning migrations began and varying degrees of gonad maturity, the clearest differentiating factor between the summer and winter sea trout caught was their size. Dixon (1931) in the 1930s and later Chrzan (1947) and Żarnecki (1952) regarded sea trout which migrated for spawning in winter as very abundant, larger and in better condition than summer trout. However, according to Jokiel and Backiel (1960) it was the summer sea trout that had higher individual mass and body length. The numerous sea trout material, which

was collected in 1961-1968 in the lower Vistula River from fish migrating for spawning facilitated more detailed description of differences in the growth rate of both summer and winter sea trout.

In a previous work regarding Vistula sea trout (Borzęcka 1999), the age structure of both winter and summer sea trout was evaluated during their time in the river before they reached the smolt stage and during their growth in the sea until the beginning of the spawning migration. Also, the frequency of spawning repetition and the variability of the coefficient of smolt recruitment to the sea were characterized for subsequent years.

The aim of the current paper is to carry out comparative analysis of winter and summer sea trout growth in order to broaden the historical picture of the fish which is needed to undertake programs for the restitution of native Vistula sea trout stocks.

MATERIALS AND METHODS

Material collected by the River Fishery Department of the Inland Fisheries Institute in 1961-1968 near Tczew was used for the investigations. The material consisted of scale samples, measurements of fish length (*l. caudalis*) and mass. The fish were dissected and the sex of each specimen was determined based on the gonads. Scales were used for making plastic impressions using Sych's method (1964).

Two measures of fish growth were applied. The first was general and was based on the comparison of the average length and mass of fish at the moment of their entrance to the river. The second was more detailed and referred to the growth rate, i.e. the average growth during the first year the fish was in the sea.

Body growth rate was determined as follows (after Sych 1967b):

$$d_1 = \frac{L}{S}\,(S_{B1} - S_A) \qquad [1]$$

where: L – caught fish length, S – scale radius from *nucleus* to the oral edge,
S_A – part of the radius to the last annual ring laid down in the river zone of scale,
S_{B1} – part of the radius to the first annual ring laid down in the sea zone of scale.

The dependence of body mass on fish length was determined from the following function:

$$W = a \cdot L^b \qquad [2]$$

where: W – caught fish mass; L – caught fish length,
a and b – coefficients determined from empirical data.

The condition described by the Fulton coefficient was also determined:

$$K = \frac{100W}{L^3} \qquad [3]$$

A more precise comparison of the growth of two groups (stocks) of fish required the elimination of nonhomogeneous material. The first issue concerned the sex composition of spawning stocks of Vistula sea trout. Figure 1 presents the annual percentage of both summer

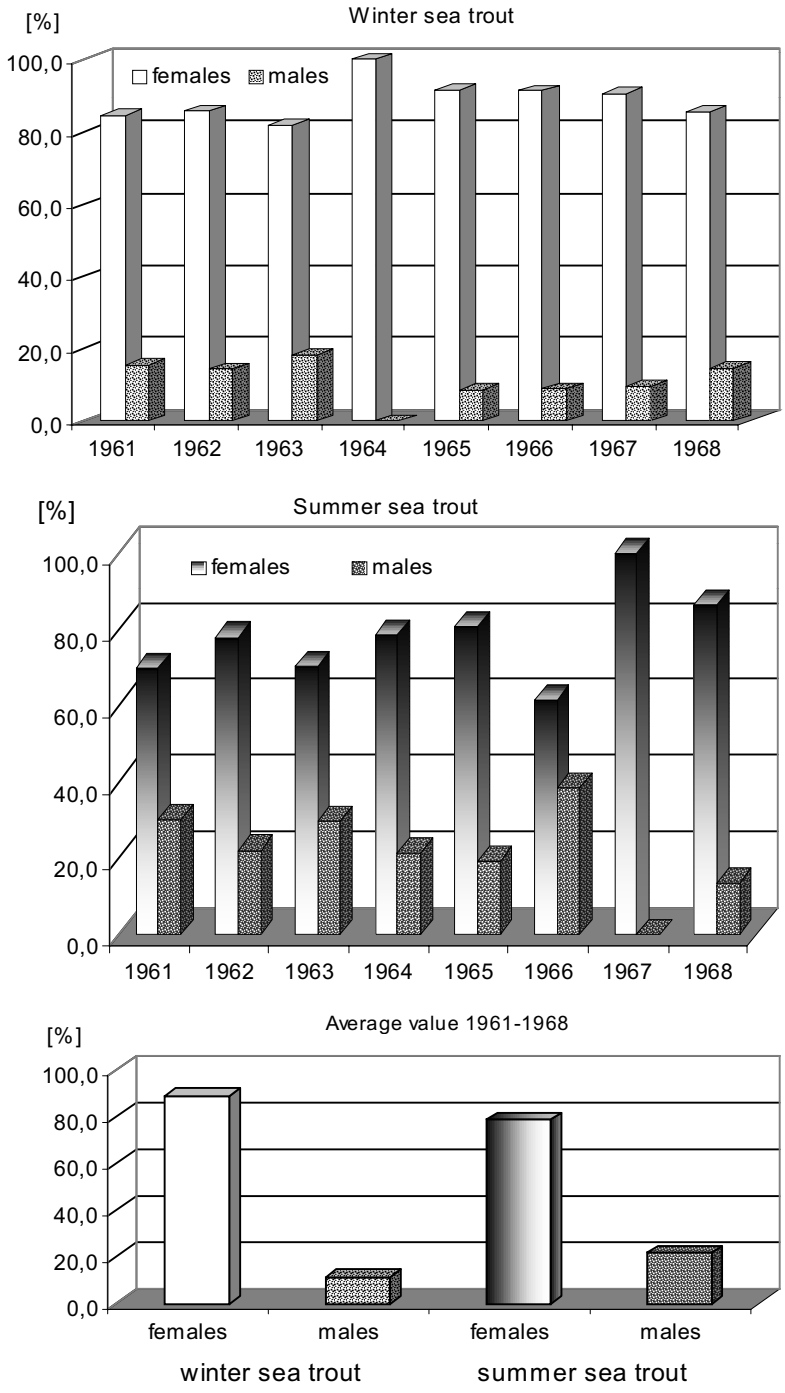

Fig. 1. Contribution of females and males in the winter and summer Vistula sea trout stocks in 1961-1968

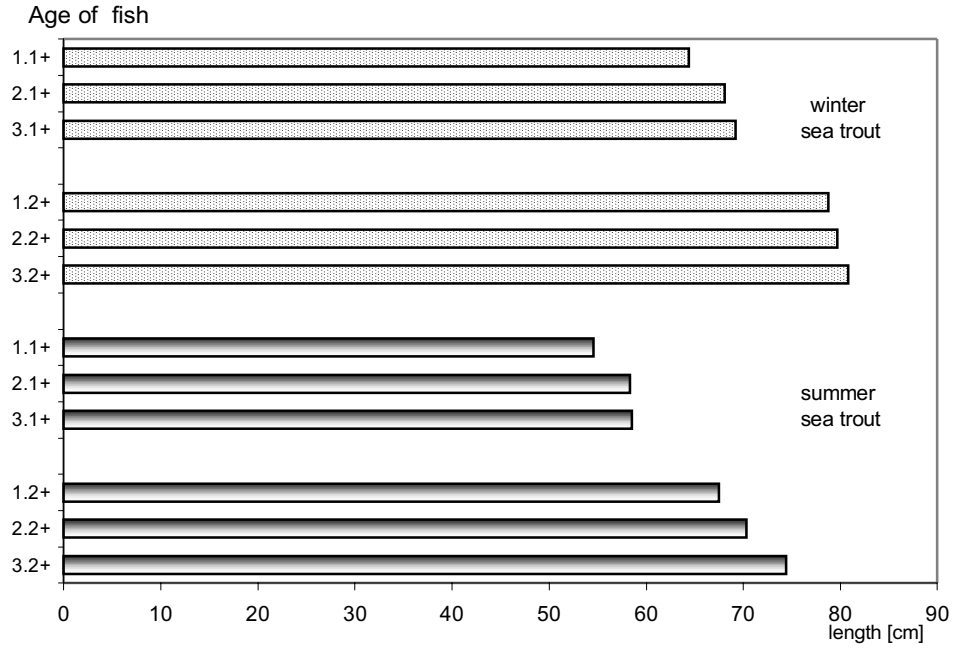

Fig. 2. Average fish length in both Vistula sea trout spawning stocks in relation to smolt age

and winter sea trout females and males and the average values over the period from 1961 to 1968. Females dominated in the material of both seasonal stocks, and the average, long-term percentage of females over the investigated period in the samples of winter and summer sea trout was 88.6%, and 78.5%, respectively. Males specimens constituted from 0% to 18.3% in the winter sea trout material with an average of 11.4% over the investigated period; males were more numerous among summer trout specimens, constituting from 0% to 38.5% of the material, with an average over the investigated period of 21.5% (Fig. 1). The frequencies of males in both stocks, estimated with the statistical test according to Romanowski, differed significantly. Thus, the investigations were limited only to females, which were far more numerous than males.

Fish growth also depends on environmental conditions. Sych (1967a) confirmed that average annual growth, and consequently, the average sea trout sizes, varied significantly in the Vistula River in different calendar years. Therefore, to conduct comparative investigations of the growth rate only females, which were growing in the same years, were selected.

The factor which differentiates the sea trout growth is the size of smolt when it reaches the sea. The younger smolts are smaller and the size differences remain throughout life (Chełkowski 1974, Sych, Pałka, Bieniarz 1978, Pałka Bieniarz 1983, Domagała 1986). This relationship has also been revealed in our samples of sea trout (Fig. 2). Therefore, comparisons of the fish growth rate in the sea required material that was homogeneous in terms of age.

Since fish are heterothermic, their growth is largely dependent on ambient temperature. Winter sea trout enter the river after their last yearlong feeding period in the sea. The last sea growth of summer sea trout is finished either at the beginning of summer or in at height. Assuming fish body growth stops in winter in the climatic conditions of Northern Europe, the

group of winter females which entered the river had completed their annual growth at the age of A.1^+ or A.2^+ and were related to the group of summer females aged A.2^+ and A.3^+.

In order to compare the growth of summer and winter sea trout and to take into consideration all of these non-homogeneities, winter females which entered the river at the age of 2.1^+ in 1963 and 1964 were selected along with the summer females at the age of 2.2^+ which began their spawning migrations in 1964 and 1965. These fish had their first growth season in the sea in 1962 and 1963, respectively. Also the average mass and length of older winter sea trout females at the age 2.2^+, which returned to the river in 1964 and 1965, were compared with the averages for the summer sea trout aged 2.3^+ that entered the river in 1965 and 1966; in this case, the fish spent their second year in the sea in 1963 and 1964.

RESULTS

Firstly, differences in the average lengths and masses of winter and summer sea trout females were determined on the basis of the materials that were selected as described above. The t-Student test was used to statistically process the averages. Data in Table 1 indicate that either no significant differences in sizes were confirmed between summer and winter sea trout of

Table 1. Average length and average mass of summer and winter sea trout from the same calendar years of body growth

	Younger fish			
	winter sea trout 2.1+	summer sea trout 2.2+	winter sea trout 2.1+	summer sea trout 2.2+
	1st sea body increment in 1962		1st sea body increment in 1963	
Entering in the river	1963	1964	1964	1965
Sample size	*N* = 48	*N* = 68	*N* = 96	*N* = 79
Average length, cm	67.2 (s.d.2.8)	66.8 (s.d.6.0)	68.1(s.d.4.0)	71.7 (s.d. 5.1)
t value	*t* = 0.39		*t* = 5,4*	
Average mass, kg	3.9 (s.d. 0.7)	4.0 (s.d.1.3)	4.1(s.d. 0.7)	4.7 (s.d.1.1)
t value	*t* = 0.38		t = 4.34*	
Random sub-sample used for back calculations				
Sub-sample size	*N* = 47	*N* = 45	*N* = 50	*N* = 50
Average length, cm	67.0	66.2	67.6	71.7
Average increment d_1, cm	28 (s.d.2.4)	22 (s.d. 5.0)	30.5 (s.d. 3.6)	27.5 (s.d. 4.5)
t value	t = 7.39*		t = 3.71*	
	Older fish			
	winter sea trout 2.2+	summer sea trout 2.3+	winter sea trout 2.2+	summer sea trout 2.3+
	2nd sea body increment in 1963		2nd sea body increment in 1964	
Entering in the river	1964	1965.	1965	1966
Sample size	*N* = 77	*N* = 9	*N* = 22	*N* = 7
Average length, cm	79.5 (s.d. 5.0)	80.9 (s.d. 5.7)	78.4 (s.d. 5.6)	84.9 (s.d. 3.2)
t value	*t* = 0,78		*t* = 2,87*	
Average mass, kg	6.4 (s.d.1.3)	7.1 (s.d.1.7)	6.5 (s.d.1.5)	7.5 (s.d.1.3)
t value	*t* = 1,37		*t* = 1,62	

*Differences significant.

various age groups and calendar years that fish entered the river or that the summer sea trout was considerably larger than the winter sea trout.

The Table 1 also presents data concerning the sizes of first year growth in the sea in 1962 and 1963. It was greater among winter sea trout than among summer sea trout, and the differences calculated with the *t* test were highly significant.

The dependence between fish body mass and length for winter sea trout females aged 2.1^{+}, that attained their first annual growth increment in the sea in 1962 and 1963, is described as follows:

$$W = 0.00004 \cdot L^{2.707} .$$

A similar function was determined for summer sea trout females aged 2.2^{+} from the same years of growth:

$$W = 0.00001 \cdot L^{2.975} .$$

Exponent *b*, which describes the rate of body mass growth as fish length increases was slightly lower for winter sea trout than for summer sea trout (Fig. 3).

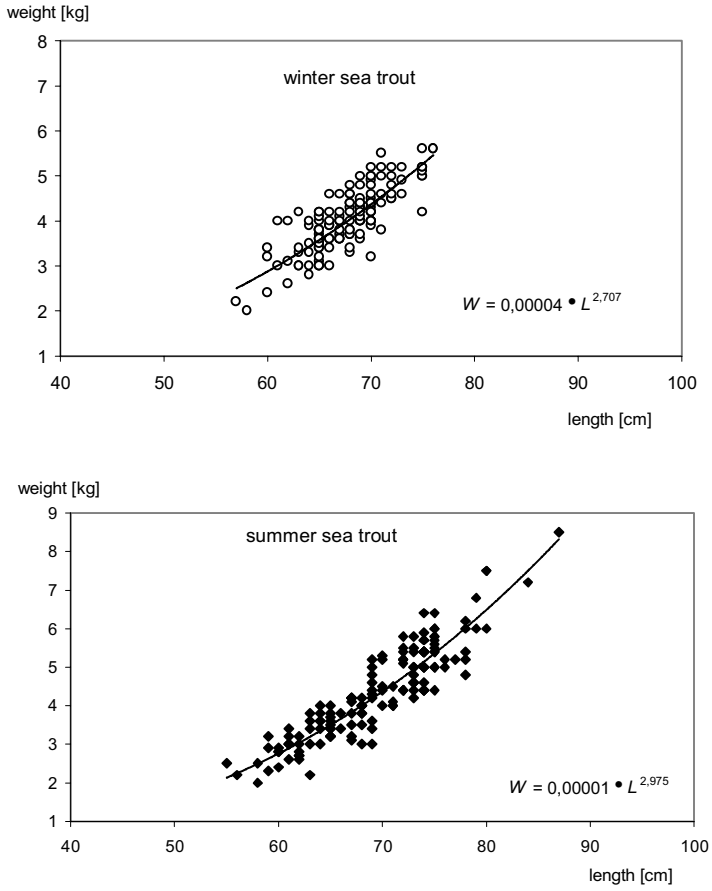

Fig. 3. Function describing the relation between mass and length of summer and winter sea trout in the Vistula River

Next, the derived functions were used with the experimental length data for specimens from both the summer and winter stocks to determine the mass. The differences between the average masses estimated by either one or the other function were significant ($t = 12.2$, $df. = 218$).

The Fulton condition *K* coefficients were similar in both stocks and their average values did not vary significantly. In the case of younger fish, which had accomplished their first growth increment in the sea in 1962 and 1963, the average Fulton coefficients were as follows: for winter females 1.28 ± 0.12 and 1.30 ± 0.15; for summer females 1.30 ± 0.13 and 1.26 ± 0.15. In the case of older fish, the average Fulton coefficients were 1.27 ± 0.14 and 1.32 ± 0.11 for the winter stock and 1.32 ± 0.19 and 1.26 ± 0.12 for the summer stock. The detailed documentation of all results is given in Table 2.

Table 3 presents the average lengths of Vistula sea trout females of a particular age in the sea and the average lengths of the same-aged females originated from other rivers in Poland. The comparison has been favorable both to summer and winter sea trout from the Vistula River. This confirms the exceptional physical qualities of the Vistula sea trout.

DISCUSSION

The rate of fish growth is dependent on a number of factors, both internal, such as sex, genetic predisposition, position in the stock, fish age, and external, like specimen density, food abundance, water temperature, oxygen content in the water, etc. Sea trout, a diadromous fish, is affected by both freshwater and seawater environmental conditions which can vary annually causing changes in fish growth rates. Sych (1967a) proved that average sea trout body growth increments in the Vistula River vary significantly; it follows that average fish sizes in subsequent years vary as well. The data presented in this work reveals the differences between the average mass and length of both winter and summer sea trout which underwent their first two growth increments in the sea in 1962 and 1963 as well as in 1963 and 1964.

It was confirmed that the growth rate of winter sea trout is better than that of summer sea trout. The investigations were carried out using growth measurements after the fish had spent their first season in the sea, since sea trout size is best characterized by the magnitude of body increment in that season (Sych 1967a). The average mass and length of the summer sea trout at the moment they entered the river were higher or the same size as the winter trout. This means that the lower growth rate of summer sea trout in the Vistula River is compensated by their staying in the sea feeding grounds six months longer, which resulted in the spring-summer growth increment just before the migration.

The value of the *b* exponent in the function, which describes the dependence of fish body length and mass in both stocks, was approaching 3, although it was slightly lower in the winter stock. This may indicate the better condition of the summer stock specimens. According to Wawrzyniak's suggestions (1998), the exponent of this function is a good indicator of fish condition. However, the values of the traditional Fulton coefficient were comparable for both stocks of sea trout. It must be kept in mind though, that the high condition coefficient for winter sea trout reflects a concentration of matter and energy in the fatty tissue before the yearlong migration, whereas for summer sea trout both matter and energy have already been moved to a highly developed reproductive system (Piątek 1961).

Table 2. Selected body growth parameters of summer and winter sea trout stocks in 1963-1966 and the average condition coefficients

	Sample size	Entering the river	1st sea body increment	2nd second sea body increment	Average lenght	*t* value	Average mass	*t* value	Magnitude of 1st sea body increment (d_1)	*t* value	Fulton condition coeffitient	*t* value	Function $W = aL^b$	*t* value
Winter sea trout 2.1+	48	1963	1962		67.2 (2.8)	0.39	3.9 (0.7)	0.38	28	7.39*	1.28 (0.12)	0.86	winter sea trout 2.1+	12.2*
Summer sea trout 2.2+	68	1964			66.8 (6.0)		4.0 (1.3)		22		1.30 (0.13)		a = 0.00004, b = 2.707	
Winter sea trout 2.1+	96	1964	1963		68.1 (4.0)	5.4*	4.1 (0.7)	4.34*	30,5	3.71*	1.30 (0.15)	1.75	summer sea trout 2.2+	
Summer sea trout 2.2+	79	1965			71.7 (5.1)		4.7 (1.1)		27,5		1.26 (0.15)		a = 0.00001, b = 2.975	
Winter sea trout 2.2+	77	1964		1963	79.5 (5.0)	0.78	6.4 (1.3)	1.37			1.27 (0.14)	0.93		
Summer sea trout 2.3+	9	1965			80.9 (5.7)		7.1 (1.7)				1.32 (0.19)			
Winter sea trout 2.2+	22	1965		1964	78.4 (5.6)	2.87*	6.5 (1.5)	1.62			1.32 (0.11)	1.18		
Summer sea trout 2.3+	7	1966			84.9 (3.2)		7.5 (1.3)				1.26 (0.12)			

* Differences significant

Table 3. Growth rate of summer and winter sea trout females in the Vistula River in 1960-1968 and sea trout from other Polish rivers

	Average lengths (cm)				
	Vistula River		some other Polish rivers		
Age	winter sea trout	summer sea trout	Rega*	Parsęta*	Reda**
A.1+	67.9	58.3	59.4	55.3	45.1
A.2+	79.8	68.9	66.2	65.1	62.7
A.3+	87.8	81.5	73.2	70.5	63.0
A.4+	93.3	92.8	79.2	82.7	

*(Chełkowski 1969)
**(Dixon 1931)

The comparison of the growth rate of females of the summer and winter stocks in the Vistula River with the females from other Polish rivers indicates the exceptional physical superiority of the Vistula sea trout (Table 3).

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BULLETIN OF THE SEA FISHERIES INSTITUTE
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Larval distribution and abundance of the family Scombridae and Scombrolabracidae in the vicinity of Puerto Rico and the Virgin Islands

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Abstract. Fishes of the family Scombridae are important recreational and commercial species throughout the Western Central Atlantic Ocean. There remain, however, many questions regarding the biology of these fishes that are crucial for the protection of sustainable fisheries. To provide some basic information, this study examines larval distribution and abundance in the vicinity of Puerto Rico and the Virgin Islands, an area of sparse information compared to the Gulf of Mexico and the southeastern United States coast. Seasonal, horizontal and vertical distributions were examined and species-specific patterns were described. *Thunnus atlanticus* and *Katsuwonus pelamis* were abundant during a November/December cruise, while *Thunnus atlanticus*, *Katsuwonus pelamis* and *Euthynnus alletteratus* were abundant during a May cruise. Regional differences were found in the distribution of some species and species specific vertical distributions were identified. *Thunnus atlanticus* was more surface oriented than *Euthynnus alletteratus* and *Katsuwonus pelamis*. These results are discussed relative to prior work in the region.

Key words: larval distributions, vertical distributions, Caribbean Sea, Scombridae, Scombrolabracidae

INTRODUCTION

Early life history studies contribute several types of information to the scientific basis of fisheries management (Lasker 1987). Temporal and spatial distribution of spawning are indicated by the

distribution of fish eggs and larvae, with appropriate consideration of larval transport and mortality (Checkley *et al*. 1999). Stock and population structure are examined with studies of egg and larval distribution and transport (Begg *et al.* 1999), as well as morphological, physiological and chemical analysis of eggs and larvae (Thorrold *et al.* 1998, Burke *et al.* 2000). Fishery-independent estimates of stock abundance are derived from surveys of egg and larval stages (Lasker 1985). Finally, as much of the variability in recruitment is determined during early life history stages (Rothschild 1986), study of the biological and physical processes that affect egg, larval and juvenile survival provides important insights into the basis of variability in fish population abundance (Hare and Cowen 1996, Rice *et al.* 1999) and potentially the ability to predict patterns in recruitment (Megrey *et al.* 1996).

Fishes of the family Scombridae are important commercial and recreational species throughout the world's oceans, yet the degree of early life history information is regionally and species-specific. In the Western Central Atlantic, aspects of scombrid early life history are best understood in the Gulf of Mexico. Larval abundances are used in stock assessments of bluefin tuna (*Thunnus thynnus*), which spawn in the Gulf of Mexico (Scott *et al.* 1993). Seasonal and large-scale horizontal distributions in the Gulf of Mexico have defined general spawning patterns (Houde *et al.* 1977, Grimes *et al.* 1990, Sanvicente-Anorve *et al*. 1998), and smaller-scale distribution and age and growth studies have contributed to the understanding of larval survival and recruitment variability (Richards *et al.* 1989, DeVries *et al.* 1990, Lang *et al.* 1994). On the southeastern United States continental shelf, seasonal and/or large scale distribution of some scombrid species have been documented (Collins and Stender 1987, McGowan and Richards 1989) and small-scale studies of distribution and age and growth have been conducted (DeVries *et al.* 1990, Peters and Schmidt 1997, Powell *et al.* 2000). A regional perspective of scombrid spawning along the southeastern United States, however, is lacking, which precludes the development of fishery-independent estimates of stock abundance based on larval abundances. Similarly, although some process-oriented and larval age and growth studies have been conducted on scombrids along the southeastern US, the cause of variability in larval survival and recruitment remains unresolved. In the Caribbean Sea, early life history information is limited to a large-scale regional distribution study (Richards 1984), and little information is available for the Sargasso Sea or tropical Atlantic east of the Lesser Antilles.

The purpose of this study is to provide additional information on the early life history stages of scombrids in the north central Caribbean Sea: in the vicinity of Puerto Rico and the United States Virgin Islands. Data from two cruises were analyzed. Originally, this work was in response to proposed development of Offshore Thermal Energy Conversion projects proposed for Puerto Rico and the United States Virgin Islands. Basic biological information was needed to evaluate potential impacts of water entrainment at these sites. Although sampling was not designed to examine larval scombrids specifically, owing to the relative lack of information from this region, the data collected during these two cruises contribute to the basic understanding of scombrid biology. Larvae of Scombrolabracidae were included owing to their abundance and potential confusion with scombrid larvae (Richards 1989).

MATERIALS AND METHODS

Ichthyoplankton Collections

May 1984. Ichthyoplankton sampling was conducted 6-11 May 1984 from the NOAA Ship Delaware II at two locations in the northern Caribbean using a 1 m^2 Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS, Wiebe *et al.* 1976) with 333 µm mesh nets (Figure 1). Four MOCNESS tows were made off the southeast corner of Puerto Rico at 10:00,16:40, 20:45 and 23:00, and five MOCNESS tows were made north of St. Croix, Virgin Islands at 12:00, 13:30, 15:15, 19:30 and 2130 (Figure 1). Six depth-discrete samples were collected with each MOCNESS tow: 80-60 m, 60-40 m, 40-30 m, 30-20 m, 20-10 m and 10-0 m. Samples were preserved in 5% buffered formalin and later transferred to 70% ethanol.

November/December 1988. Ichthyoplankton sampling was conducted 25 November – 6 December from the NOAA Ship Delaware II at stations from southwestern Puerto Rico to east of the Virgin Islands (Figure 1). At each station, an oblique bongo tow was made to 200 m and a 10 min neuston tow was made. A 60 cm bongo with 333 µm mesh net and a 1x2 m neuston net with 947 µm mesh net were used. Vertically discrete sampling was conducted at the two locations sampled in May 1984 using a 60 cm BNF-1 with 333 µm mesh nets. The two net rings of the BNF-1 are attached by a specially designed hinge that can be opened and closed with messengers. Vertically discrete samples were collected at 100 m, 60 m, 30 m and 10 m off the southeast corner of Puerto Rico and at 100 m, 50 m, 20 m, and 2 m north of St. Croix, Virgin Islands.

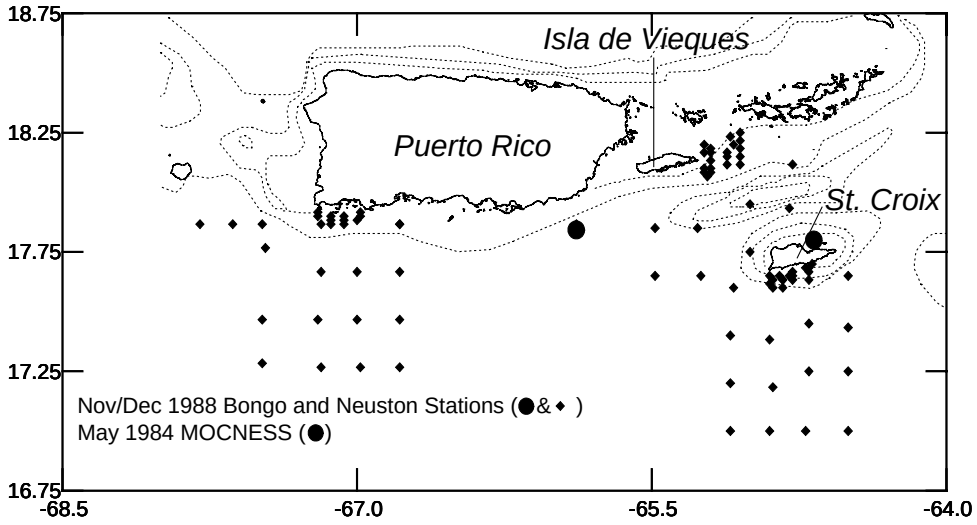

Fig. 1. Map of study area showing stations sampled during May 1984 and November/December 1988.

Species Identification

Larval fish from MOCNESS, bongo and BNF-1 collections were removed, identified, enumerated and measured by staff of the Polish Plankton Sorting and Identification Center. Larval fish from neuston collections were removed, identified, enumerated and measured by employees of the NOAA Beaufort Laboratory. All scombrid and scombrolabracid identifications were verified by two of the authors (JAH and ABP) using published sources, primarily Potthoff (1974), Richards (1989) and Richards *et al*. (1990).

Most *Thunnus* larvae were identified as *T. atlanticus*. All larvae identified to *Thunnus atlanticus* had one to several very small melanophores on the ventral margin. The most common location was ventral to the hypural, but most specimens also had one to three very small melanophores on the posterior half of the ventral margin. In many of the specimens these melanophores were not evident at first, but careful examination revealed pigment. A subset of specimens with this pigment pattern were cleared and stained (n = 41) and all had vertebral counts of 19 + 20, identifying these larvae as *T. atlanticus*. This pigment pattern was then used to identify other larvae as *T. atlanticus*. *Thunnus* larvae with no ventral pigment were not identified below genus.

Data Analysis

Seasonal abundances of scombrid and scombrolabracid larvae were compared between cruises. Only data from the two stations that were sampled during both cruises were analyzed (Figure 1). Total number of larvae of each taxa collected at a station were divided by total water filtered at each station and concentrations expressed in 100 m^{-3}.

Vertical distributions of scombrid and scombrolabracid larvae were examined from the May, 1984 MOCNESS collections. Concentration of larvae within a given depth strata at a given sampling time were expressed in 100 m^{-3}. Weighted mean depth (and standard deviation) of larvae were also calculated using larval concentrations (Brodeur and Rugen 1994). BNF-1 collections were not analyzed in this manner owing to the limited number of larvae collected.

Horizontal distributions of larvae were examined from the broad-scale, November-December 1988 bongo collections. Neuston collections were not analyzed because of a strong day/night bias (see below). Stations were divided into three regions (Figure 1) and non-parametric statistics were used to determine if larval concentrations and larval lengths differed among regions.

RESULTS

Seasonal Abundance

Larval abundance and length distributions indicated that scombrids and scombrolabracids spawned in both spring and winter in the Puerto Rico/St. Croix region (Table 1, Figure 2). *Katsuwonus pelamis* and *Scombrolabrax heterolepis* larvae were collected in both May and November/December, and during both sampling times, most larvae were <5 mm indicating recent spawning. A majority of *Euthynnus alletteratus*, *Thunnus atlanticus* and *Auxis* spp.

Table 1. Abundance of Scombridae and Scombrolabracidae larvae at the station southeast of Puerto Rico and the station north of St. Croix in November/December of 1988 and in May 1984. Values were calculated using the number of larvae collected and the total volume of water filtered. Concentrations of larvae are presented (number larvae 100 m^{-3})

Species	Nov/Dec 1988		May 1984	
	Southeast of Puerto Rico	North of St. Croix	Southeast of Puerto Rico	North of St. Croix
Katsuwonus pelamis	0.132	0.031	0.044	0.182
Thunnus atlanticus	0.044	0.031	0.576	0.137
Euthynnus alletteratus	0.044	0	0.445	0.190
Scombrolabrax heterolepis	0.088	0	0.052	0.061
Auxis spp.	0	0	0.096	0.114
Scomberomorus cavalla	0	0	0.026	0
Acanthocybium solanderi	0	0	0	0.015
Scombridae	0.219	0.031	0.035	0.008
Thunnus spp.	0	0	0.026	0.008

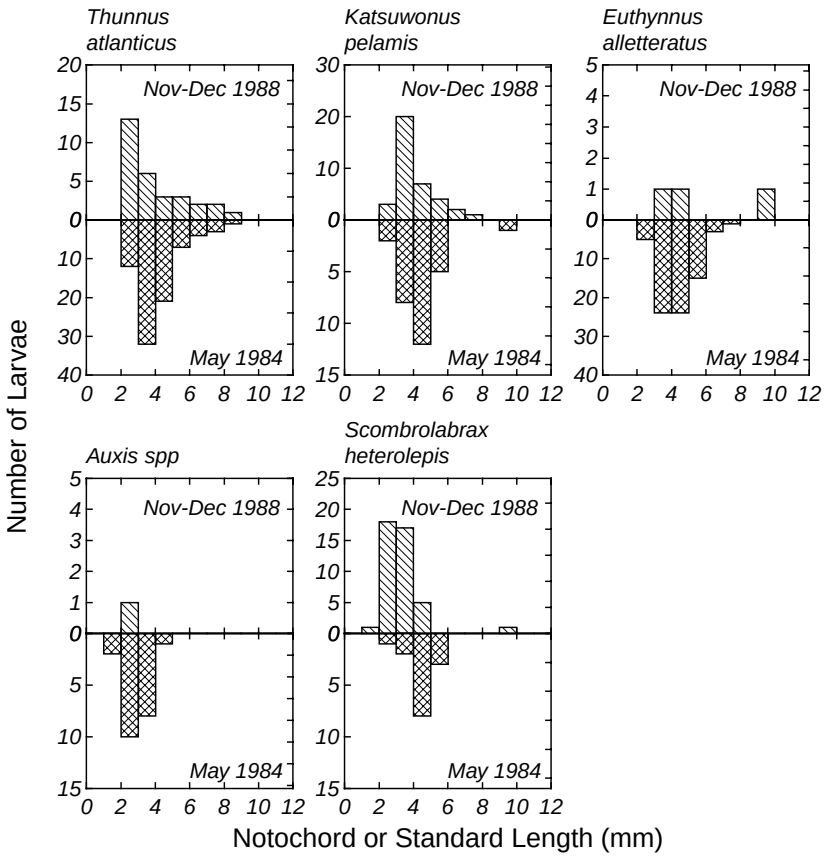

Fig. 2. Comparison of larval lengths from May 1984 MOCNESS collections and November/December 1988 bongo collections.

larvae were also < 5 mm indicating recent spawning, but abundances were greater in May than November/December (Table 1). Few *Scomberomorus cavalla* were collected: three in May 1988 and one in November/December; all were <4 mm. Two, small (2.1 and 2.2 mm) *Scomberomorus maculatus* larvae were collected in November/December. Two, mid sized (4.2 and 6.7 mm) *Acanthocybium solanderi* larvae were collected in May. The concentrations of these less abundant species are somewhat different than presented in Table 1 as the above discussion refers to the collections overall and Table 1 compares only the two stations that were both sampled during May 1984 and November/December 1988.

Vertical Distributions

The presence of several species in neuston collections differed between day and night in November/December 1988 possibly indicating diel vertical movements (Table 2). More *Katsuwonus pelamis* and *Scombrolabrax heterolepis* larvae were collected in night tows, while capture of *Thunnus atlanticus* and *Euthynnus alletteratus* larvae were similar in day and night tows.

Table 2. Number of stations that larvae of Scombridae and Scombrolabracidae were present in neuston collections during day and night in the northern Caribbean during November/December 1988.

Species	Day	Night
Katsuwonus pelamis	4	20
Thunnus atlanticus	16	12
Euthynnus alletteratus	1	2
Scombrolabrax heterolepis	1	16

Concentrations of larvae from vertically discrete sampling in November/December 1988 BNF-1 collections were too low for detailed analysis, but all scombrid larvae were collected near the surface. *Katsuwonus pelamis*, *Thunnus atlanticus* and *Euthynnus alletteratus* larvae were all collected at 10 m southeast of Puerto Rico, at 2 m north of St. Croix and in the neuston net at both locations. *Scombrolabrax heterolepis* were deeper in the water column than the scombrids; all larvae were collected at 30 m.

Concentrations of *Acanthocybium solanderi* and *Scomberomorus cavalla* were also too low from May 1984 MOCNESS collections for detailed analysis, but both these species were found from 20-60 m. The two individuals of *A. solanderi* were collected at 20-30 and 30-40 m at night north of St. Croix. The three individuals of *S. cavalla* were collected at 20-30, 30-40 and 40-60 m southeast of Puerto Rico, two at night and one during the day.

Vertical distributions of more abundant larval scombrids and scombrolabracids in May 1984 MOCNESS collections exhibited complex patterns differing among species, locations and time of day (Figure 3). *Katsuwonus pelamis* larvae were deeper at night compared to day at both locations. *Thunnus atlanticus* larvae were deeper at night southeast of Puerto Rico, but remained in the upper 20 m over time north of St. Croix. North of St. Croix, *Euthynnus alletteratus* larvae were between 10-30 m during the day and 10-40 m during the night. Southeast of Puerto Rico, however, *Euthynnus alletteratus* were higher in the water column at night than during day. Similarly, *Auxis* spp. larvae were higher in the water column during night southeast of Puerto Rico and *Scombrolabrax heterolepis* were higher in the water column at night both southeast of Puerto Rico and north of St. Croix.

Patterns in vertical distribution could be linked to vertical patterns in temperature and salinity. Southeast of Puerto Rico, temperatures and salinities were homogenous in the upper 80 m (22.4°C; 35.2 psu), and there were clear vertical movements of larvae in this upper mixed

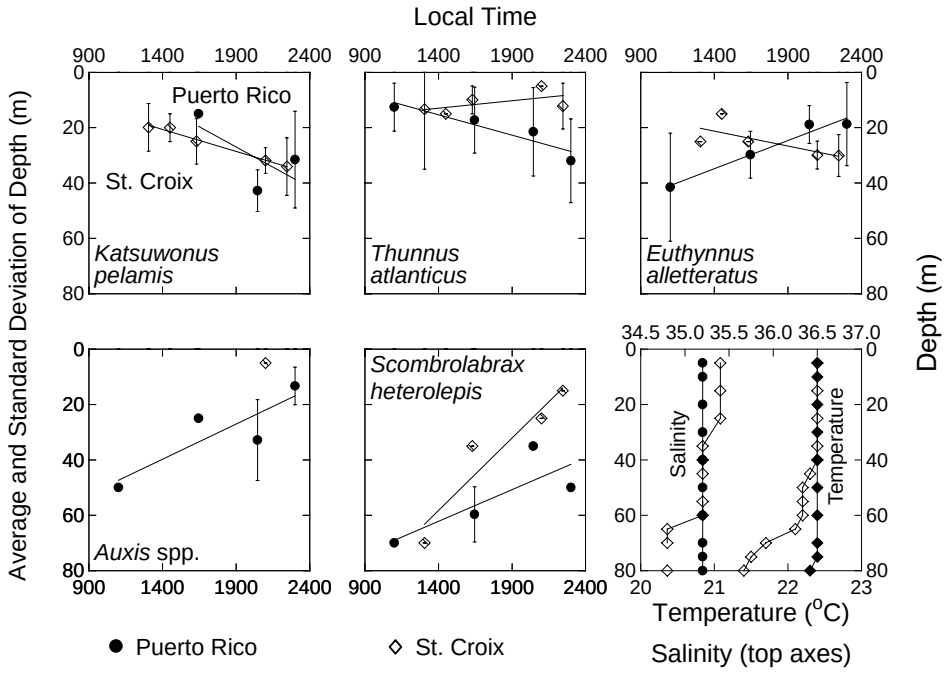

Fig. 3. Average depth (and standard deviation) of larval scombrids caught at different times off of Puerto Rico and St. Croix from May 1984 MOCNESS collections.

layer. North of St. Croix, the upper mixed layer extended to 60 m with a slight decrease in salinity (0.2 psu) at 30 m and a slight decrease in temperature (0.2°C) at 40 m. Again, most of the scombrid larvae occurred in the upper mixed layer, but day/night differences were not as evident in vertical distributions.

Relations between larval length and depth distribution varied among species (Figure 4). Variability in the distribution of *T. atlanticus* larvae increased with length of larvae. Smaller (2.0-3.9 mm) *T. atlanticus* larvae were collected predominantly in the upper 30 m of the water column, while larger larvae (>3.9 mm) were collected as deep at 60-80 m. Similarly, larger *Auxis* larvae were collected deeper in the water column. In contrast, depth of capture and larval length of *Euthynnus alletteratus*, *Katsuwonus pelamis* and *Scombrolabrax heterolepis* were not related to depth of capture.

Horizontal Distribution – November-December 1988

Thunnus atlanticus, Katsuwonus pelamis and *Scombrolabrax heterolepis* larvae were relatively common (Table 1) and widespread (Figure 5-7) in November/December 1988. Concentrations of *K. pelamis* and *S. heterolepis* were not significantly different among regions, but there was a tendency for fewer *K. pelamis* larvae southeast of Puerto Rico (Figure 8). *T. atlanticus* larvae, however, were significantly more abundant south of St Croix compared to south of Puerto Rico and east of Isla de Vieques.

Regional differences in length distributions mirrored differences in larval concentrations (Figure 9). Length distributions of *Katsuwonus pelamis* and *Scombrolabrax heterolepis*

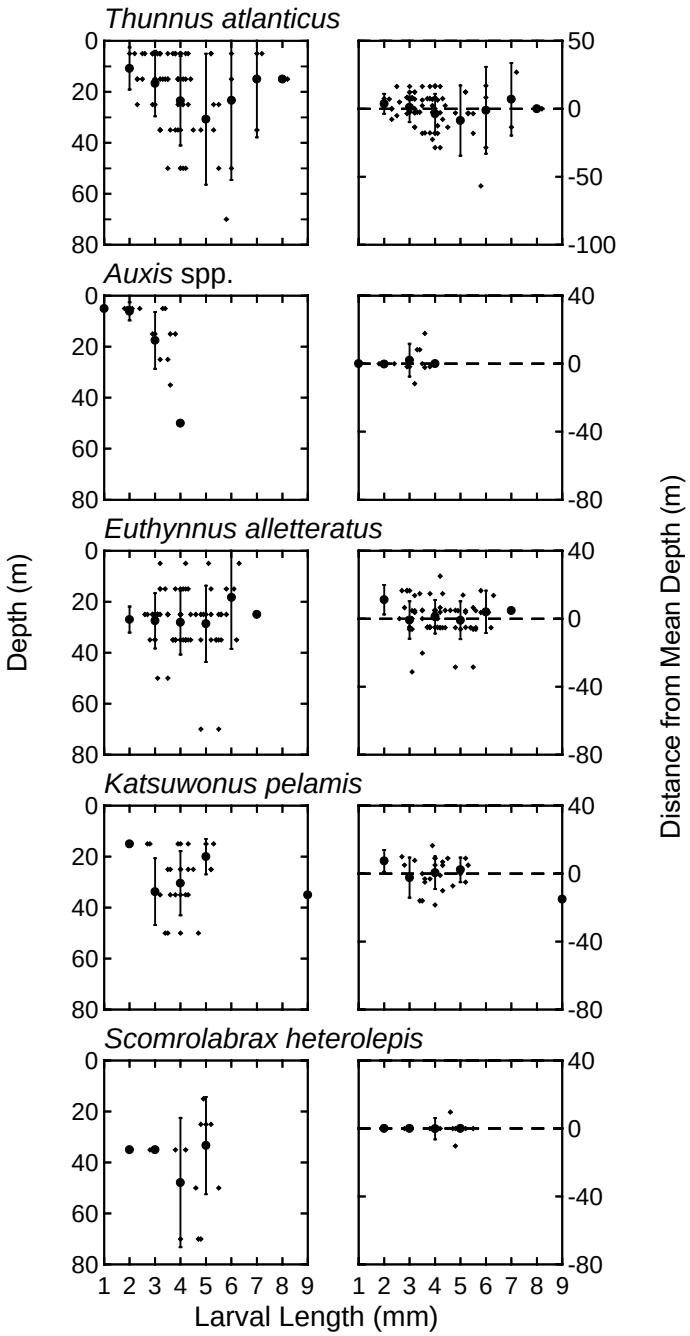

Fig. 4. Relation between larval length and depth of capture and residuals from average depth (see Figure 3) from May 1984 MOCNESS collections. A negative residual indicates larvae deeper than the average depth.

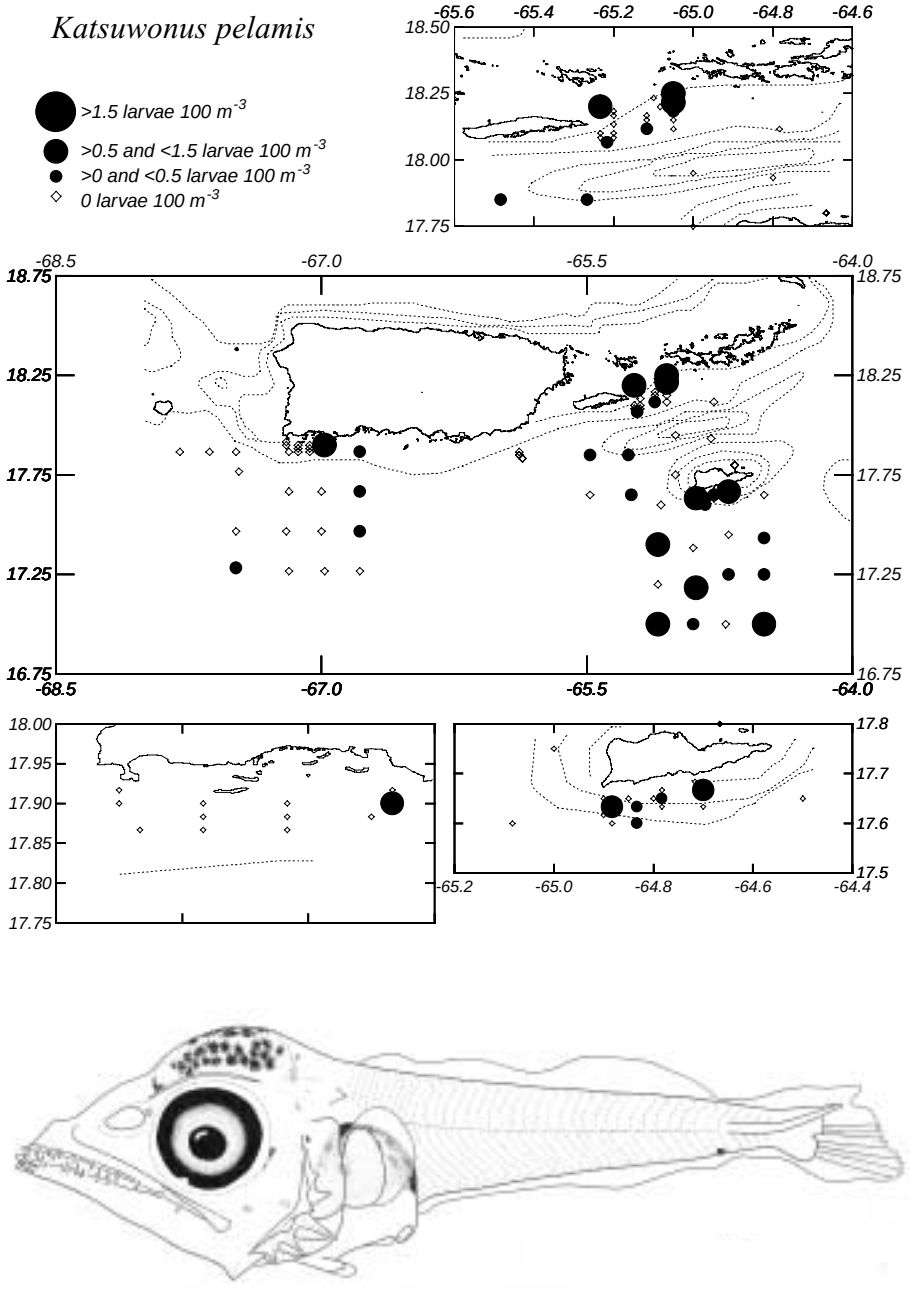

Fig. 5. Horizontal distribution of *Katsuwonus pelamis* from November/December 1988 bongo collections. Illustration from Collette *et al.* (1984).

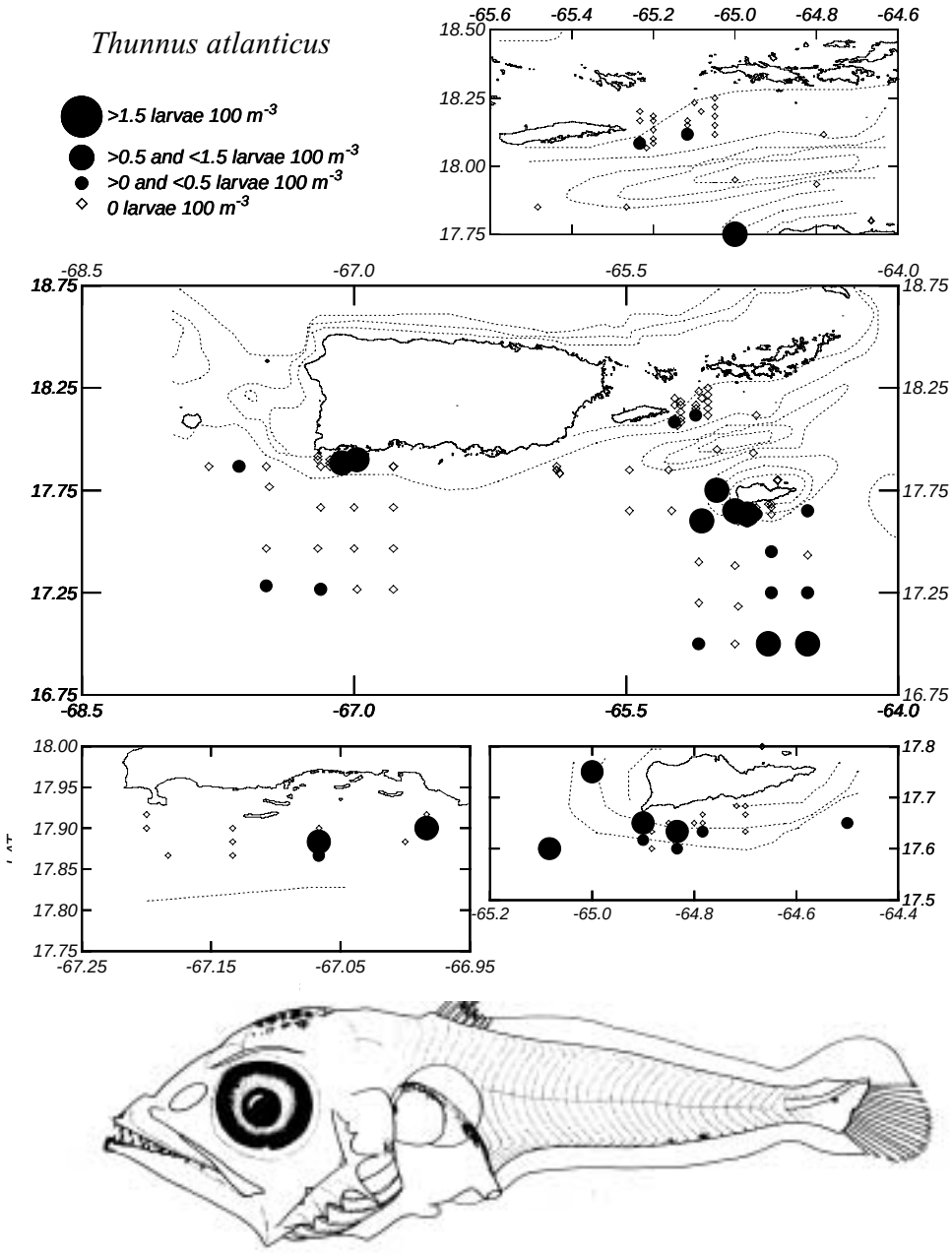

Fig. 6. Horizontal distribution of *Thunnus atlanticus* from November/December 1988 bongo collections. Illustration from Richards (1989).

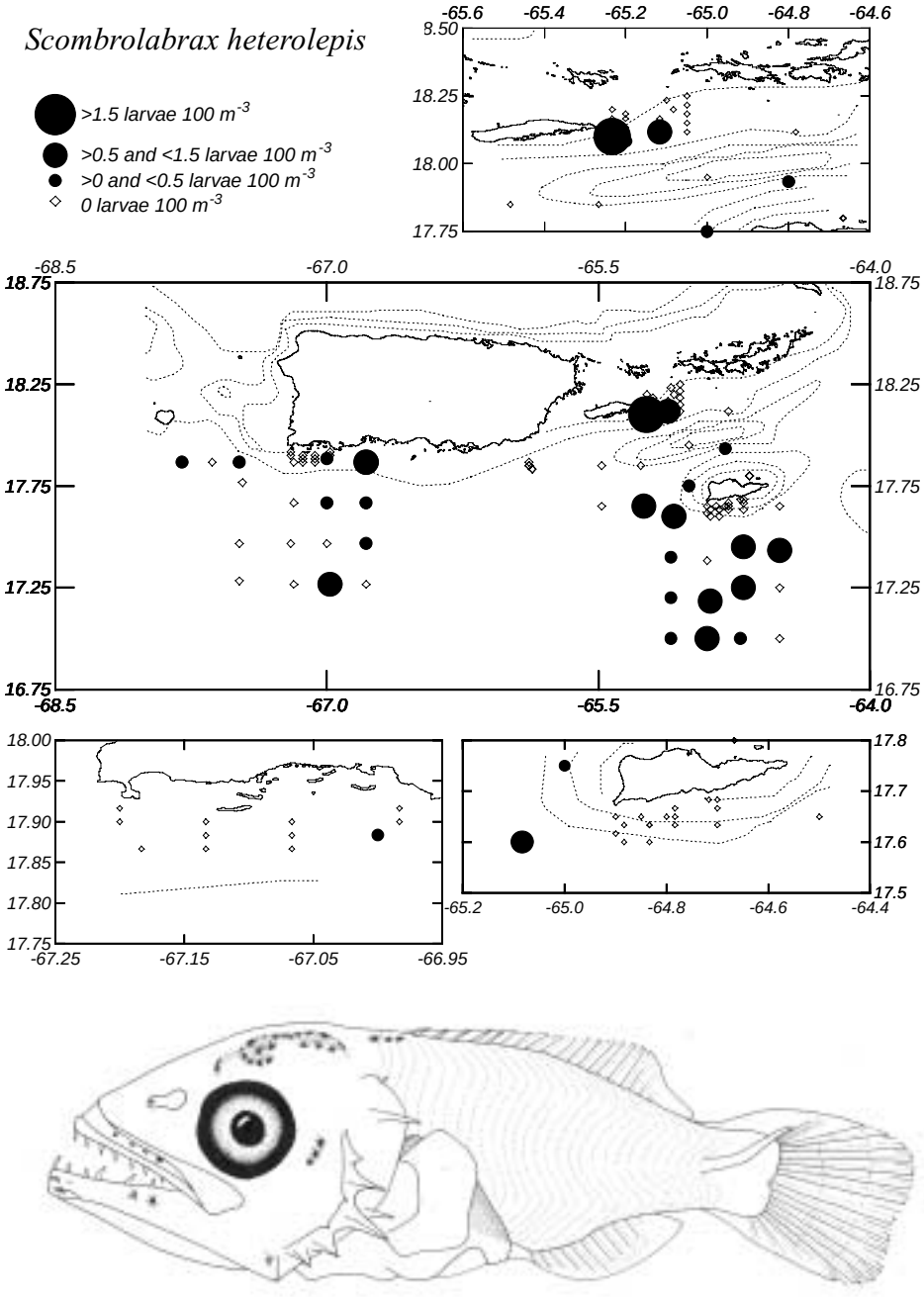

Fig. 7. Horizontal distribution of *Scombrolabrax heterolepis* from November/December 1988 bongo collections. Illustration from Collette *et al.* (1984).

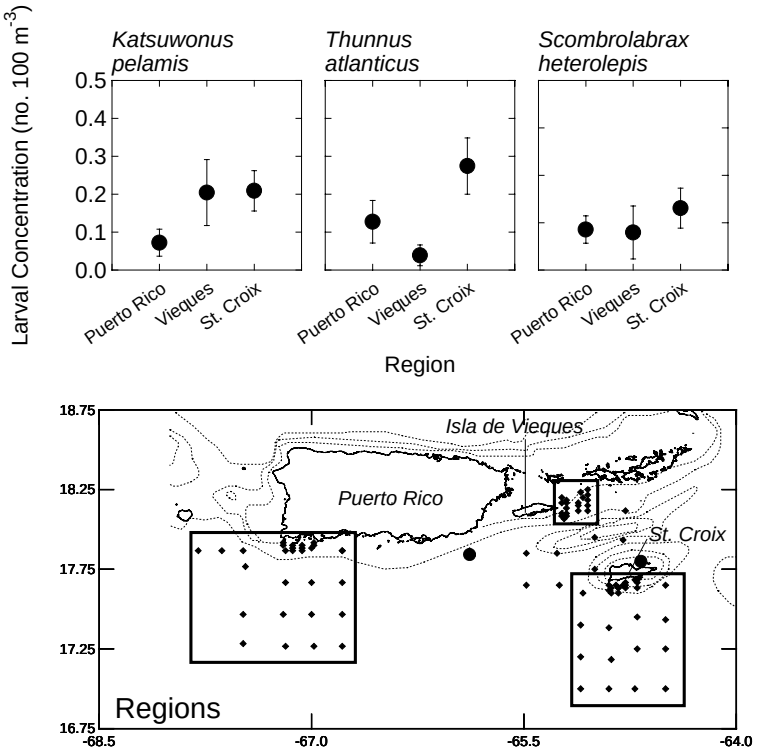

Fig. 8. Comparison of larval concentrations between regions (shown in map) from November/December 1988 bongo collections.

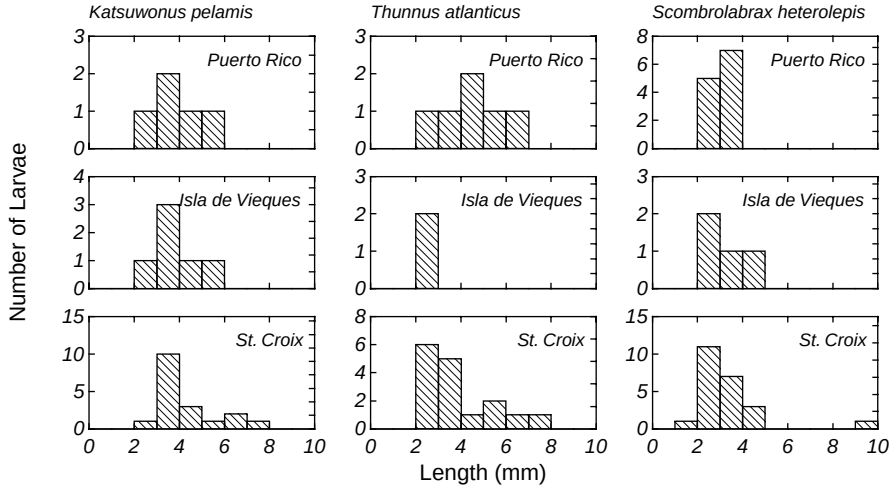

Fig. 9. Comparison of larval lengths between regions (shown in Figure 8) from November/December 1988 bongo collections.

were not significantly different among regions. However, length distributions of *Thunnus atlanticus* were significantly different among regions; the few fish collected south of Puerto Rico were larger than those collected east of Isla de Vieques and south of St. Croix. Small individuals of all three species were collected in all regions suggesting widespread spawning.

Auxis spp. and *Scombromorous cavalla* larvae were collected only east of Isla de Vieques, while *S. maculatus* larvae were collected inside the 1000 m isobath southeast of Puerto Rico.

DISCUSSION

Combining the results of this study with those of Richards (1984) provides a preliminary evaluation of seasonal patterns in scombrid spawning in the northern Caribbean (Table 3). For example, *Katsuwonus pelamis* larvae were collected during all time periods indicating year round spawning in the northern Caribbean. Erdman (1976) found *K. pelamis* in or near spawning condition in every month of the year in the northern Caribbean demonstrating year round spawning. More larvae were collected in July and August than during other time periods suggesting a modest peak in spawning during summer. *Thunnus atlanticus* larvae were also collected during all time periods, but larval abundances suggest that spawning seasonality is more pronounced than in *K. pelamis*, with peak spawning in the spring and summer. Larval abundances of *Scombrolabrax heterolepis* were more consistent over time, with fewest larvae collected during November/December. Overall, larval abundances indicate that several species of Scombridae spawn in the northern Caribbean throughout the year with peak spawning in spring and summer.

Scombridae larvae inhabit the upper portion of the water column, yet larvae of different species exhibited different vertical distributions. *Thunnus atlanticus* larvae were found shallower than other scombrid larvae (Figure 3). At the Puerto Rico station, where temperature and salinity were homogenous to 80 m, the mean depth of *T. atlanticus* larvae increased from 10 m to 35 m from day to night. At the St. Croix station, where a slight halocline was present at 30 m and a thermocline started at 40 m, there was no increase in mean depth from day to night. *Euthynnus alletteratus* exhibited a similar pattern in vertical distribution as *Thunnus atlanticus*. Davis et al. (1990) found two congeners, *T. maccoyii* and *T. alalunga*, close to the surface off western Australia. Both species moved deeper during the night when no pycnocline was present, but a pycnocline in the upper 35 m coincided with restricted larval vertical distributions. Movement deeper at night may be part of an active diel migration or caused by greater variance in vertical distribution resulting in a greater mean depth. Similarly, restriction above a pycnocline may result from active behavior or from passive distributions related to larval density relative to the density of seawater (Sclafani et al. 1993, Boehlert and Mundy 1994).

Diel vertical distributions of *Katsuwonus pelamis* larvae were opposite of those described in previous studies. *K. pelamis* larvae were found deeper than *Thunnus* larvae similar to the results of other studies (Davis *et al*. 1990, Leis *et al.* 1991, Boehlert and Mundy 1994). However, in this study, *K. pelamis* larvae were deeper at night than during the day, yet previous studies suggest a shallower distribution during the night (Davis *et al.* 1990, Boehlert and Mundy 1994). The neuston collections made in November/December also suggest a shallower distribution during the night. The reason for this discrepancy is unclear but ontogenetic changes in vertical distribution is one possible explanation (Figure 4).

Table 3. Rank abundance of Scombridae and Scombrolabracidae larvae in the northern Caribbean during four seasons. July/August and February/March data from Richards (1984). November/December and May data from this study. Rank abundances are compared rather than absolute abundances owing to differences in gear types.

Rank Abundance	Season			
	Jul/Aug	Nov/Dec	Feb/Mar	May
Common	*Katsuwonus pelamis* *Thunnus atlanticus*			*Euthynnus alletteratus* *Thunnus atlanticus*
Uncommon	*Auxis* spp. *Scombrolabrax heterolepis*	*Katsuwonus pelamis* *Thunnus atlanticus*	*Katsuwonus pelamis* *Auxis* spp. *Scombrolabrax heterolepis*	*Katsuwonus pelamis* *Auxis* spp. *Scombrolabrax heterolepis*
Rare	*Euthynnus alletteratus* *Acanthocybium solanderi* *Scomber japonicus*	*Euthynnus alletteratus* *Scombrolabrax heterolepis*	*Thunnus atlanticus* *Sarda sarda* *Euthynnus alletteratus* *Thunnus alangua*	*Scomberomorus cavalla* *Acanthocybium solanderi*
None-Very Rare	*Sarda sarda* *Thunnus alangua* *Scomberomorus cavalla* *Scomberomorus maculatus*	*Auxis* spp. *Acanthocybium solanderi* *Scomber japonicus* *Sarda sarda* *Thunnus alangua* *Scomberomorus cavalla* *Scomberomorus maculatus*	*Acanthocybium solanderi* *Scomber japonicus* *Scomberomorus cavalla* *Scomberomorus maculatus*	*Sarda sarda* *Thunnus alangua* *Scomber japonicus* *Scomberomorus maculatus*
Rare				
Source	Richards (1984)	this study	Richards (1984)	this study

No striking horizontal differences were found in larval Scombridae distribution in the northern Caribbean. Some regional differences were found for specific species (Figure 8), but the relatively common species (*Katsuwonus pelamis*, *Thunnus atlanticus*, and *Scombrolabrax heterolepis*) were not exclusive to particular areas. Either spawning is widespread or physical processes disperse larvae over a wide area from spatially discrete spawning sites. There is little information as to the spatial extent of scombrid spawning in the northern Caribbean. General currents in the area have been described, but to quantify larval transport, a more detailed view of currents and larval vertical distributions are required (Cowen and Castro 1994, Hare *et al.* 1999; Cowen *et al*. 2000).

Broad-scale surveys have limited utility for the evaluation of larval scombrid abundance. Several studies have found that larval scombrids are concentrated around oceanographic features (McGowan and Richards 1989, Richards *et al.* 1989, Lang *et al.* 1994). Similarly, larval scombrids have been found at high abundances close to coral reefs (Leis *et al.* 1991). Several of these studies have found high densities of larvae associated with specific oceanographic habitats. In this study and Richards (1984), concentrations of scombrid larvae were relatively low. This could result from actual low concentrations of scombrid larvae in the northern Caribbean or from the fixed-station surveys missing dynamic oceanographic features that serve as larval scombrid habitat.

FUTURE QUESTIONS

Although this study was not designed specifically to sample larval scombrids, the results have contributed to our knowledge of scombrid biology in the northern Caribbean. From these results, specific questions can be identified that require further investigation to realize the potential utility of larval fish studies in the support of managing scombrid resources in the vicinity of Puerto Rico and the Virgin Islands (Lasker 1987).

- Frontal features should be sampled simultaneously with non-frontal features to identify and describe scombrid spawning and larval habitat in the northern Caribbean. Based on these results, spawning biomass or larval abundances could then be quantified by stratifying sampling by larval habitat rather than by fixed-station sampling or randomly stratifying sampling spatially.
- Similar to evaluating oceanographic features as scombrid spawning and larval habitat, smaller-scale sampling in the vicinity of reefs is required to evaluate the potential for high concentrations of scombrid larvae in these areas.
- Patterns in vertical distribution need to be more clearly resolved, particularly the influence of water column structure and day/night cycles.
- A better understanding of larval vertical distributions should be coupled with more detailed views of the region's currents to predict patterns in larval scombrid dispersal. Such work will lead to a better understanding of connectedness between regions on meso- (e.g. Puerto Rico and Virgin Islands) and large-scales (e.g. Caribbean and Gulf of Mexico) and of recruitment dynamics on a population-scale.

Acknowledgements. *We first want to thank the staff of the Polish Sorting and Identification Center. Without their hardwork and dedication, this contribution would not have been possible. We also thank Gretchen Bath, William Crosby, and Nannie Gaskill for their assistance in various aspects of this work. Bill Richards and Bob Cowen made valuable comments on an early draft of this manuscript. Finally we appreciate the contribution of those who worked at sea to collect these samples. This study was originally funded by the NOAA National Ocean Service, Office of Ocean and Coastal Resource Management through an agreement with the National Marine Fisheries Service.*

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BULLETIN OF THE SEA FISHERIES INSTITUTE
2 (153) 2001

Main phytoplankton assemblages in the Gulf of Gdańsk and the Pomeranian Bay from 1994 to 1997

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Abstract. The comparison of the phytoplankton composition of 156 samples collected during 11 cruises in the Gulf of Gdańsk and the Pomeranian Bay based on clustering analyses led to the identification of ten algae assemblages at a similarity lower than 50%. The most distinct phytoplankton assemblages were found in samples collected at stations located directly near the Vistula River mouth and a local, single-species assemblage formed by dinoflagellate *Peridiniella catenata* in the Gulf of Gdańsk. Other assemblages were relevant to subsequent seasons of the vegetative cycle: winter-spring, summer and autumn.

The relationship of the phytoplankton assemblage with environmental conditions (low salinity, high nutrient concentrations) was the most evident near the Vistula River mouth. In other areas, phytoplankton composition changed seasonally and was mainly correlated with temperature, and/or day length. The differences in phytoplankton composition between the Gulf of Gdańsk and the Pomeranian Bay were relatively small at a similarity higher than 50%.

Key words: phytoplankton, Baltic Sea, estuary, assemblages, diversity

INTRODUCTION

The Gulf of Gdańsk and the Pomeranian Bay are both of significant importance in the functioning of the Baltic ecosystem. The Vistula River mouth is located in the Gulf of Gdańsk, and is second only to the Newa River in the volume of freshwater it contributes to the Baltic Sea (approximately 34 km^3/year). The largest river mouth in the western region of the Baltic Sea is that of the Oder, which contributes approximately 18 km^3 of freshwater annually. The nutrient load carried by these two rivers comprises a significant portion of the total nutrient input to the Baltic Sea. For example, the 1995 loads of total nitrogen and total phosphorus from both the Vistula and Oder Rivers was 25% and 33%, respectively, of the total input of these elements to the Baltic Sea from all land sources (excluding atmospheric input; HELCOM 1998).

Although the areas of the two basins are similar (Gulf of Gdańsk – about 5,000 km^2, Pomeranian Bay – about 6,000 km^2), their topography and functioning differ. The Gulf of Gdańsk is a relatively deep basin with a maximum depth of 117 m. It is permanently stratified (halocline at depths of about 70-90 m) and organic matter accumulates in its sediments and

long periods of oxygen depletion occur in its deeper areas (Majewski 1990). The Pomeranian Bay is a shallow basin (its outer, northern border is located along the 20 m isobath) that is well mixed by wavy motion (Majewski 1974). The level of organic matter accumulation in its sediments is not very significant, and its role is rather that of a transporter of allochthonous matter from the near-mouth area to deeper adjacent basins (Jost and Pollehne 1998). Additionally, the type of river estuary that feeds the two basins differs. The estuary of the Oder River is a lagoon type; allochthonous matter that is transferred with the river water is initially transformed in the Szczecin Lagoon before it reaches the Pomeranian Bay (Grelowski *et al.* 2000). The Vistula River flows directly into the Gulf of Gdańsk.

The phytoplankton composition in the Gulf of Gdańsk has been the subject of many investigations (Rumek 1950, Ringer 1973, 1975, Pliński *et al.* 1982; Pliński and Picińska 1986, Bralewska 1992, Witek *et al.* 1993, Wrzołek 1993, Pliński 1995, Wrzołek 1996, Niemkiewicz and Wrzołek 1998). The phytoplankton composition in the Pomeranian Bay is far less well-known in comparison with that of the Gulf of Gdańsk (Zembrzuska 1973, Wiktor and Kruk-Dowgiałło 1992, Ochocki *et al.* 1995a, Łysiak-Pastuszak *et al.* 1998, Gromisz *et al.* 1998, Gromisz *et al.* 1999). In most of these works, the diversity of phytoplankton composition was investigated in relation to the season or measuring station location. Significant seasonal variations of phytoplankton have been well-documented as well as certain spatial diversity connected with the distance to river mouths or the open sea. However, only in one of these works were objective statistical methods used to analyze the diversity of phytoplankton composition (Gromisz *et al.* 1999).

Ecological research was conducted by the Sea Fisheries Institute in the Gulf of Gdańsk and the Pomeranian Bay from 1994 to 1997. During the numerous cruises that were undertaken in different seasons, measurements of various environmental factors were taken and the composition and biomass of phytoplankton were measured using the same methodology in both regions. This paper presents the results of these investigations focusing on the application of statistical methods to identify the main phytoplankton assemblages in both basins and to evaluate the significance of regional differences. An additional aim of this work is to indicate which environmental factors have the greatest impact on phytoplankton taxonomic diversity.

MATERIALS AND METHODS

Samples used for taxonomic composition evaluations and determining phytoplankton biovolume were collected during seven cruises of R\V BALTICA in the Gulf of Gdańsk from 1994 to 1997 and four cruises in the Pomeranian Bay from 1996 and 1997. Cruises in the Gulf of Gdańsk were undertaken as follows: in 1994 – April (7 stations), July (15 stations) and November (7 stations); in 1995 – August (6 stations); in 1996 – February (15 stations), July (6 stations), and in 1997 – May (15 stations). Figure 1 presents the location of all the measuring stations in the Gulf of Gdańsk. Cruises in the Pomeranian Bay were carried out as follows: in 1996 – March (18 stations), July (24 stations); in 1997 – May (24 stations), October (19 stations). Figure 2 presents the location of all the measuring stations in the Pomeranian Bay.

Samples used for evaluating phytoplankton composition in the Gulf of Gdańsk were collected only in the surface sea layer, while in the Pomeranian Bay the samples were collected from both surface waters and those at a depth of about 10 m. These samples were integrated in the laboratory by mixing two equal volumes of water from each level. The samples were pre-

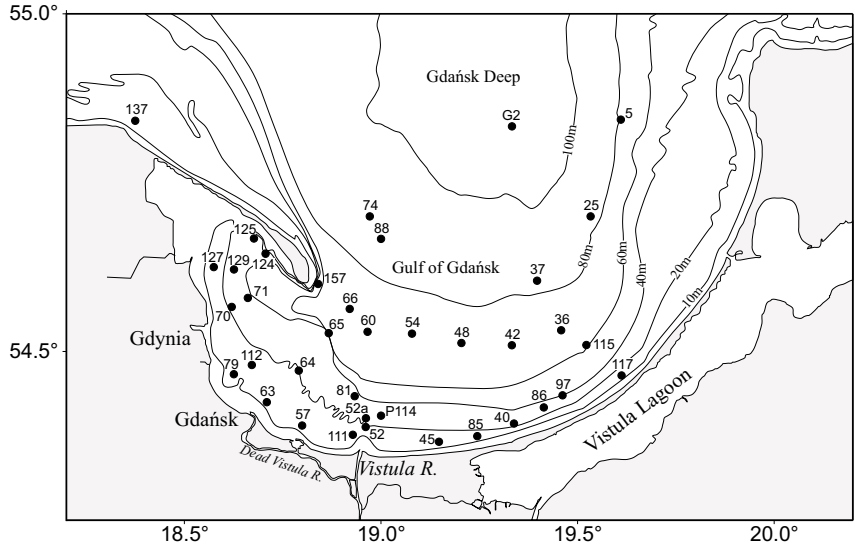

Fig. 1. Location of sampling stations in the Gulf of Gdańsk

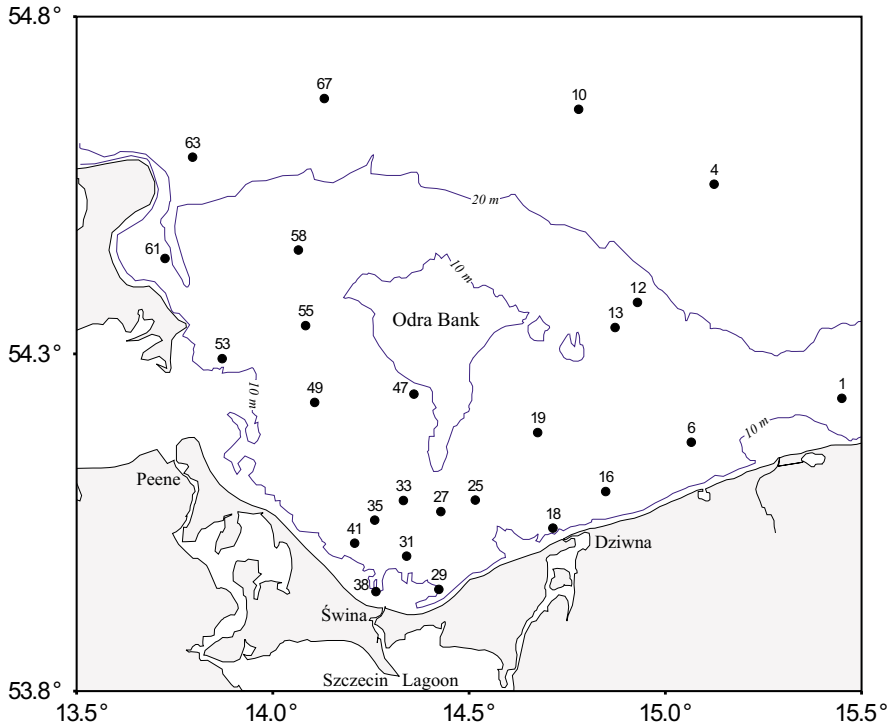

Fig. 2. Location of sampling stations in the Pomeranian Bay

served with Lugol's solution (Edler 1979) and then analyzed using an inverted microscope (Utermöhl 1958). This work does not consider the composition and biovolume of heterotrophic dinoflagellates. Autotrophic dinoflagellates were distinguished from the heterotrophic ones using chlorophyll autofluorescence excited with blue light. Thus, a separate water portion was preserved with alkaline Lugol's solution, a 3% $Na_2S_2O_3$ solution and alkaline formaldehyde and then frozen (Sherr and Sherr 1993). After slowly defrosting the sample in the laboratory, cell autofluorescence was observed under an Olympus IMT-2 inverted microscope with an IMT 2 RFL epifluorescent attachment.

The abundance was estimated for each species or higher systematic unit (whenever species identification was impossible), and with the aid of the geometric method the average cell volume was also assessed. Using these data, the biovolume of each taxon was determined for each sample. The value of the *PIE* (probability of interspecific encounters) diversity index was also estimated for each station. In the original version, this index describes the probability of two randomly seen individuals belonging to different species (Lampert and Sommer 1996), and it is calculated using the abundance of each taxa. In this work, abundance was replaced by biovolume and species diversity was calculated as follows:

$$PIE = B/(B + 1)(1 - \Sigma p_i^2),$$

where: B – total phytoplankton biovolume;
p_i – contribution of species i in total phytoplankton biovolume.

The similarity of taxonomic composition in samples was evaluated by analyzing assemblages using the PRIMER program. The analysis was based on each taxon's percentage of the phytoplankton biovolume and was carried out in accordance with the Bray-Curtis similarity coefficient, which is defined as follows:

$$S_{jk} = 100\left[1 - \frac{\sum_{i=1}^{p} \left| y_{ij} - y_{ik} \right|}{\sum_{i=1}^{p} \left(y_{ij} + y_{ik} \right)}\right]$$

where: y_{ij} – percentage of the biovolume of species i in sample j;
y_{ik} – percentage of the biovolume of species i in sample k.

In order to increase the significance of rare species in the phytoplankton biovolume, logarithmic data transformation (log(1+y)) was done before calculating the similarity. In order to present the results of clustering analysis in graphic form, hierarchical agglomerative clustering was used, in which the similarity matrix was sorted according to group-average linkage strategy. The result of the hierarchical clusterings are presented in the form of dendrograms, with the x axis representing the full set of samples and the y axis defining the similarity level at which two samples or group are considered to have fused (Clarke and Warwick 1994).

This work also used hydrological data which were collected using a CTD Niels Brown probe, data on chlorophyll concentrations (Ochocki *et al.* 1995b, Ochocki *et al.* 1999, Renk *et al.* 2000) and hydrochemical data. Chemical analyses were carried out using the standard-

ized methods of the Baltic Monitoring Program (Anon. 1988, Anon. 1983, Grasshoff *et al.* 1983). Results are presented in box-and-whisker plots that were made using the STATISTICA program. Each box includes the middle 50% of the data (quartile 2 and 3) and the median is marked. The lines below and above the box, whiskers, present the range of the nonoutliers. The outliers, located above and below the box, present the data values 1.5 times greater than the interquartile range (Anon. 1997).

RESULTS

Cluster analysis

In order to emphasize the most important features of phytoplankton diversity in the Gulf of Gdańsk and the Pomeranian Bay, clustering analysis was carried out on all the phytoplankton samples from all the cruises in both basins. Ten groups of samples were identified at a similarity level of 50% (Fig. 3). This means that the phytoplankton similarity among samples from different groups was lower than 50%, while within each group, the phytoplankton similarity among samples was greater than 50%. The groups in Figure 3 have been numbered, from the most distinct, with the lowest degree of similarity, to the least distinct, with the greatest degree of similarity. Table 1 presents the location, cruise dates and the number of samples that belong to each group, and the range of chlorophyll-a concentration at the stations. The other columns present the dominant species or the higher phytoplankton systematic units (which constitute about 75% of the sample biovolume) and their percentage of the biovolume, as well as the

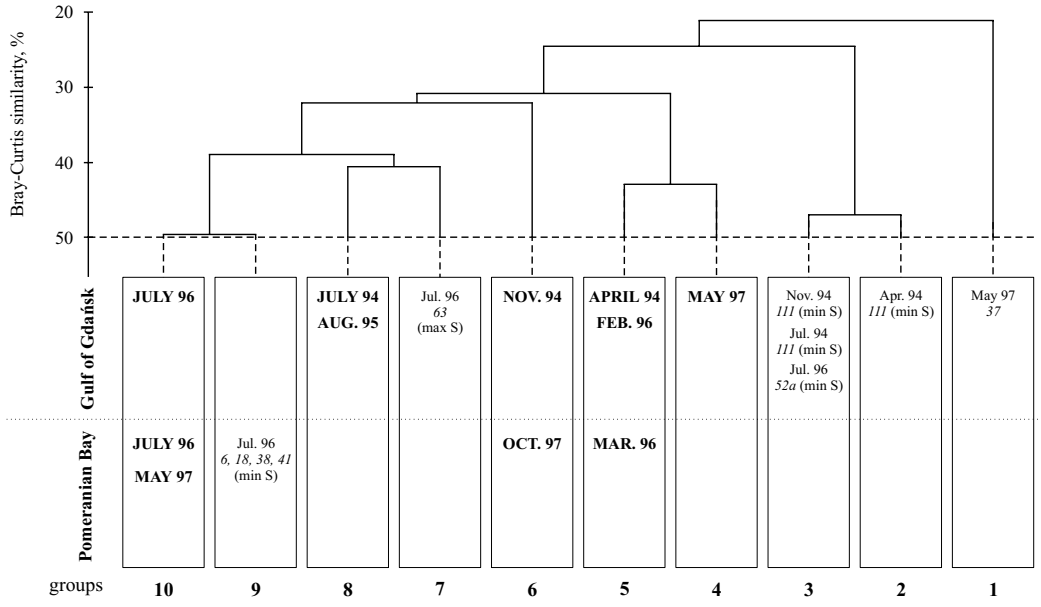

Fig. 3. Sample groups from particular cruises identified based on cluster analysis. Cruises in bold are those in which the majority of stations were in a given group; italics identify single stations. Values of extreme salinity conditions are in brackets.

Table 1. Taxa which comprised the largest percentage of the phytoplankton biovolume and the highest frequency in groups identified based on cluster analysis, as well as characteristics of the region and season when they occur. (The major taxa are in bold; together they constitute 75% of sample biovolume).
GG – Gulf of Gdańsk. PB – Pomeranian Bay

Group Assemblage	Location	Season	Number of samples	Chlorophyll a range[a] [mg m^{-3}]	Dominant taxa	Percentage of the biovolume average [%]	Percentage of the biovolume range [%]	Frequency [%]
1 single-species	**GG**	**May 97**	1	7.24	***Peridiniella catenata***	94.7		
					Aphanizomenon sp.	2.2		
2 river mouth	**GG Vistula**	**Apr 94**	1	31.21	**Centrales 5-20 µm**	78.1		
					Asterionella formosa	4		
					Aulacoseira granulata	2.7		
3 river mouth	**GG Vistula**	**Jul 94**	1	57.6	**Centrales 5-20 µm**	58.1	44.2-77.9	100
		Nov 94	1	39.62	**coccal green algae 1.5-5 µm**	4.8	1.2-10.3	100
		Jul 96	1	19.66	***Aulacoseira granulata***	3.4	0.3-8.4	100
					***Scenedesmus* spp.**	3.1	1.7-4.3	100
					Pennales (e.g. *A. formos, Nitzschia* sp.)	2.6	0.5-5.9	100
					Skeletonema costatum	2.2	0.2-4.6	100
					Pediastrum boryanum* + *P.duplex	1.9	0.3-4.3	100
					Cryptophyceae	1.4	0.1-2.8	100
					Aphanizomenon sp.	0.8	0.3-1.1	100
					Crucigenia spp.	0.7	0.1-1.2	100
					other non def.	1.6	0.7-3.3	100
4 late spring "dinoflagellates-ciliates"	**GG**	**May 97**	14	0.99-9.37	***Peridiniella catenata***	34.7	0.5-79.8	100
					Mesodinium rubrum	27.5	6.8-62.6	100
					Cryptophyceae	5.8	2.7-14.9	100
					***Pyramimonas* spp.**	5.4	1.1-11.9	100
					Heterocapsa rotundata	2.9	0.8-10.0	100
					other non def.	3.8	0.7-78.0	100
5 winter early spring "diatoms"	**GG**	**Apr 94**	6	1.37-32.73	**Centrales 5-20 µm**	43.5	4.2-92.3	100
		Feb 96	15	0.43-1.73	***Mesodinium rubrum***	17.8	0.9-57.2	100
	PB	**Mar 96**	18	0.9-17.0	***Peridiniella catenata***	12.5	0-57.4	85
					Cryptophyceae	8.1	0.2-24.0	100
					Skeletonema costatum	3.6	0-13.6	97
					Chaetoceros spp.	2.1	0.2-28.5	100
					other non def.	4.0	0-9.9	97

6	**GG**	**Nov 94**	6	4.02-8.89	***Coscinodiscus granii***	73.2	8.5-96.4	100
autumn	**PB**	**Oct 97**	19	1.7-6.7	**Cryptophyceae**	10.2	0.6-24.1	100
"diatoms"					*Actinocyclus octonarius*	7.3	0-78.8	68
					Mesodinium rubrum	1.2	0.1-3.7	100
					other non def.	2.8	0.9-6.8	100
7	**GG**	**Jul 96**	1	4.09	***Heterocapsa triquetra***	79.5		
single-species					*Aphanizomenon* sp.	6.9		
					Dinophysis norvegica	4.2		
					Aphanothecoideae	2.2		
					other non def.	1.9		
8	**GG**	**Jul 94**	14	2.67-11.27	**Aphanothecoideae**	14.9	16-43.7	100
summer		**Aug 95**	6	2.36-5.94	***Aphanizomenon* sp.**	11.2	1.2-28.7	100
warm water					***Nodularia spumigena***	10.3	0.1-55.8	100
"blue-green					***Oocystis* spp.**	9.8	0.1-63.0	100
algae"					***Heterocapsa triquetra***	7.1	0-29.7	95
					Gomphosphaerioideae	6.5	0.1-29.2	100
					Centrales 5-20 µm	4.9	0.1-18.8	100
					Cryptophyceae	4.6	0.9-17.6	100
					Anabaena sp.	3.9	0.1-37.1	100
					Oscilatorialles	3.7	0-13.4	95
					other non def.	13.1	3.2-24.5	100
9	**PB**	**Jul 96**	4	2.6-12.0	**Cryptophyceae**	19.0	11.3-33.2	100
river mouth	**Świna**				***Coscinodiscus granii***	18.8	8.7-43.2	100
	Dziwna				***Cylindrotheca closterium***	15.9	0.9-43.5	100
					Centrales 5-20 µm	12.5	8.5-17.4	100
					Heterocapsa rotundata	4.6	1.7-9.9	100
					Pyramimonas spp.	3.1	1.9-4.6	100
					Skeletonema subsalsum	3.1	0-6.1	75
					other non def.	10.9	5.8-14.8	100
10	**GG**	**Jul 96**	4	2.2-4.6	**Cryptophyceae**	36.3	6.4-73.6	100
summer	**PB**	**Jul 96**	20	1.0-3.2	***Pyramimonas* spp.**	8.2	1.3-47.8	100
cold water		**May 97**	24	0.9-4.7	***Heterocapsa rotundata***	7.3	0.2-19.0	100
"flagellates"					***Aphanizomenon* sp.**	7.0	0-40.0	83
					Mesodinium rubrum	2.4	0.1-21.7	100
					other non def.	20.0	5.9-50.8	100

a) after Ochocki *et al.* 1995b. Ochocki *et al.* 1999. Renk *et al.* 2000

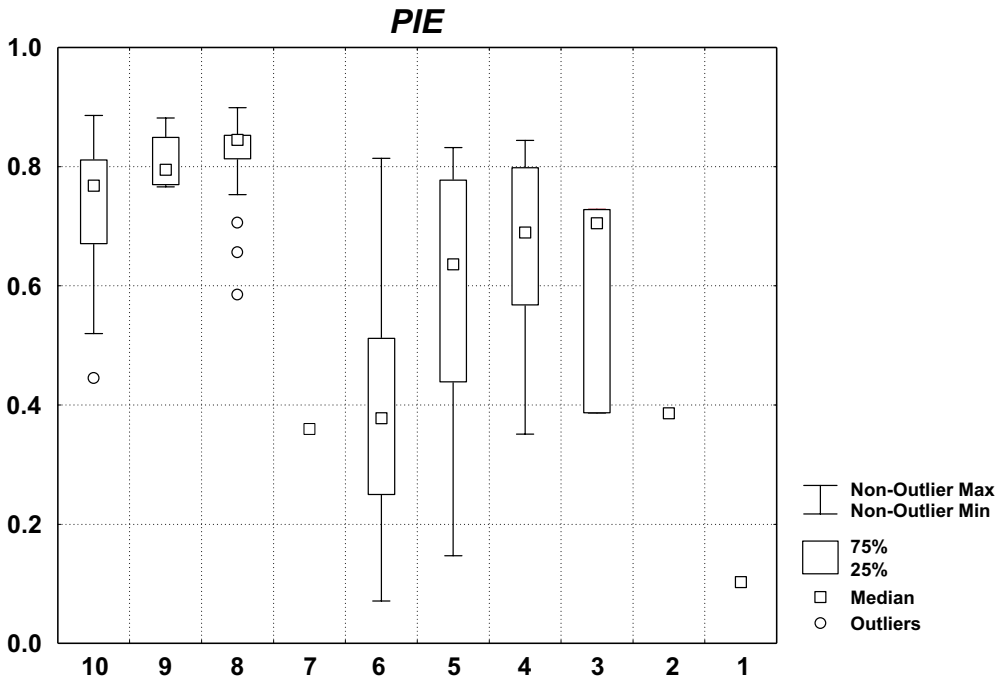

Fig. 4. Distribution of the *PIE* index in each of the identified groups

frequency of each taxa in the group. Figure 4 presents the distribution of the probability of interspecific encounters (*PIE*) diversity index for each of the distinct groups.

The most distinct phytoplankton sample found in the material analyzed was the sample from station 37 collected during the May 1997 cruise in the Gulf of Gdańsk. Station 37 is located in the central part of the gulf and is relatively distant from the shore (about 25 km, Fig. 1). The clear distinction of the sample from station 37 (with a similarity level to other samples not exceeding 21%) was due to the dominance of dinoflagellate *Peridiniella catenata* which comprised 94.7% of the sample. Additionally, the phytoplankton biovolume of this sample was the highest of the samples taken during the cruise (3.3 $mm^3 \cdot dm^{-3}$) and it had the minimum value of the *PIE* diversity index (0.10) of all the samples from all the cruises. This single sample is described in Figure 3 as group 1**.**

Four samples from the remaining material were included in the next division of samples, those with a similarity level of 25%. They were collected in the closest vicinity of the Vistula River mouth at stations where very low salinity was observed (0.92-2.67 PSU). The samples were collected during cruises which took place in different seasons, i.e. in April, July and November 1994 and in July 1996. No other samples were collected in such close vicinity to the Vistula River mouth or at stations with such low salinity during the other cruises in the Gulf of Gdańsk. Small diatoms from the group Centrales, mainly *Cyclotella* spp. comprised the highest percentage (on average 63.1%) of the phytoplankton biovolume in these samples. Only in this group diatoms: *Aulacoseira granulata*, representatives of Pennales and green algae: *Pediastrum boryanum*, *P. duplex*, *Crucigenia quadrata, C. tetrapedia, C. rectangularis* were observed

the dominant phytoplankton species. Also, the maximum phytoplankton biovolume values were observed at these stations in each cruise. Samples from the vicinity of the Vistula River at a similarity level of 47% were divided into two groups. The second group included only one sample from April 1994 which was characterized by a clear domination of diatoms and a low *PIE* value (0.39), and the third group, which consisted of samples from July and November 1994 and one sample from July 1996. The phytoplankton composition in both July samples was characterized by high species diversity (0.71-0.73), while, the *PIE* observed in November was the same as the value of the index obtained in the second group.

The next two divisions (at similarity levels of 31 and 32%) split the remaining samples from both basins into three sections which correspond approximately to the different seasons of the vegetation cycle. One consists of the winter and spring samples, the second of autumn samples, and the third of summer samples.

A high percentage of dinoflagellates *Peridiniella catenata*, ciliate *Mesodinium rubrum* (with autotrophic endosymbionts) and Cryptophyceae in the phytoplankton biovolume and a low *PIE* index value (median 0.64-0.69) is characteristic of the samples from the winter-spring section. Samples from the winter-spring section were divided , at a similarity level of 43%, into groups four and five. The fourth group consists of samples from the cruise in the first half of May 1997 in the Gulf of Gdańsk to which *P. catenata* made the highest percentage contribution (on average 34.7%) to the biovolume, followed by *M. rubrum* and Cryptophyceae. Other characteristic species included nanoplanktonic flagellats, green-algae of the genus *Pyramimonas* and a dinoflagellate *Heterocapsa rotundata*. In the fifth group, with samples from the cruises which were carried out in February 1996 and April 1994 in the Gulf of Gdańsk and in March 1996 in the Pomeranian Bay, the diatoms Centrales, mainly *Thalassiosira* spp. (on average 43.5%), then *P. catenata*, *M. rubrum* and Cryptophyceae were dominant. In addition to the above taxa, characteristic species of other diatom representatives were observed, such as *Skeletonema costatum* and *Chaetoceros* spp.

Group six was comprised of samples from the autumn section. This group consisted of samples from the November 1994 cruise in the Gulf of Gdańsk and the October 1997 cruise in the Pomeranian Bay. During both cruises, at low species diversity index (median of about 0.38) values, the phytoplankton was characterized by the domination of large Centrales diatoms, such as: *Coscinodiscus granii* (on average 73.2%) and *Actinocyclus octonarius* (on average 7.3%). A high percentage in the phytoplankton biovolume was also characteristic for Cryptophyceae and *Mesodinium rubrum*.

The third, summer section was divided into four groups, from the seventh to the tenth. All of them were characterized by the high biovolume percentage of nanoplanktonic species that belong to undetermined monade and coccal forms, Cryptophyceae and coccal blue-green algae, and maximum values of the *PIE* index (median about 0.77-0.85) with the exception of the seventh group. The seventh group, with a low *PIE* index (0.36), contained one sample from the Gulf of Gdańsk; it was collected in July 1996 at station 63 located in the coastal area near the Dead Vistula mouth. The dinoflagellate *Heterocapsa triquetra* (79.5%) dominated here. This group was separated from its parent cruise and put closer to the eighth group due to its greater contribution of blue-green algae *Aphanizomenon* sp. and Aphanothecoideae too. The eighth group consisted of samples from two cruises in the Gulf of Gdańsk in July 1994 and August 1995 when there were real summer temperatures ranging from 16.6 to 23.9ºC. Blue-green algae, mainly from the subfamily Aphanothecoideae (on average 14.9%), *Aphanizomenon* sp. (on average 11.2%), *Nodularia spumigena* (on average 10.9%) and Gomphosphaerioideae, dominated here. The ninth group, separated from group ten at a similarity level of nearly 50%,

consisted of four samples from the July 1996 cruise in the Pomeranian Bay that had been collected near the Świna River mouth. The salinity in this area were the lowest at 6.28 to 7.16 PSU. The highest contribution to the phytoplankton biovolume in this group was made by Cryptophyceae (on average 19%) and the diatoms *Coscinodiscus granii, C.* cf. *commutatus* (on average 18.8%) and *Cylindrotheca closterium* (on average 15.9%). Due to their similar size and difficulties in identification from the valve view, *Coscinodiscus granii* and *C*. cf. *commutatus* were put together for the cluster analysis. The tenth group consisted of samples from two summer cruises which took place in both basins in July 1996, when rather low water temperatures for summer were observed at 12.5-17.1°C, and samples from the second half of May 1997 which were collected in the Pomeranian Bay. The dominant forms in this group were nanoplanktonic, including Cryptophyceae (on average 36.3%), undetermined monadal and coccal forms (on average 20%), *Pyramimonas* spp. and *Heterocapsa rotundata*. Of the blue-green algae dominants, only *Aphanizomenon* sp. appeared.

Since the sample groups were divided based on algal taxonomic composition, the set of taxa characteristic for a particular group (Table 1) can be regarded as the natural phytoplankton assemblage, especially when the similarity of the taxonomic composition within the group exceeded 50%.

Environmental conditions related to phytoplankton assemblages

Among the analyzed environmental conditions (Figs. 5 and 6), salinity was determined to be significant only in the case of the assemblages near the Vistula River mouth (groups 2 and 3) where it did not exceed 3 PSU. In other cases, salinity varied in the range from about 5 to over 8 PSU, and it did not have a clear impact on the composition of phytoplankton assemblages.

A clear relationship between assemblage composition and temperature was observed. The winter-early spring assemblage (group 5) occurred at the lowest temperatures that did not exceed 5°C. The late spring assemblage with *Peridiniella catenata* and *Mesodinium rubrum* (group 4) occurred at slightly higher temperatures, from 5 to 8°C. The summer, cold water flagellates assemblage (group 10) occurred at temperatures from 6 to 16°C, and the summer-warm water multispecies assemblage, dominated by blue-green algae (group 8), occurred at temperatures from 17 to 23°C. The autumn assemblage, dominated by *Coscinodiscus granii* (group 6), occurred at temperatures from 8 to 12°C. Near the Vistula River mouth the early spring assemblage (group 2) occurred at much lower temperature (4°C) than the summer and autumn assemblages (group 3; from 10 to 21°C).

In terms of day length, a significant difference occurred only between the winter-early spring and autumn assemblages (9 to 13.5 hours) and the late spring and summer assemblages (13.5 to 17 hours). The daily radiation varied widely during the investigation periods. Thus, despite generally lower values in winter, early spring and autumn than in late spring and summer, the ranges of radiation partly overlapped, which indicated that this parameter was not very significant with regard to the differentiation of algae assemblages.

The thickness of the mixed surface layer, despite showing some seasonal regularities, was very differentiated in the investigation periods and no relationship with the phytoplankton composition could usually be determined. For example, the greatest average thickness of the mixed layer was observed in the Gulf of Gdańsk in February 1996 (median 18 m), while, the thickness of the mixed layer observed in this gulf in April 1994 was the smallest (median 3.5 m). However, the phytoplankton composition in both periods was similar, and the samples

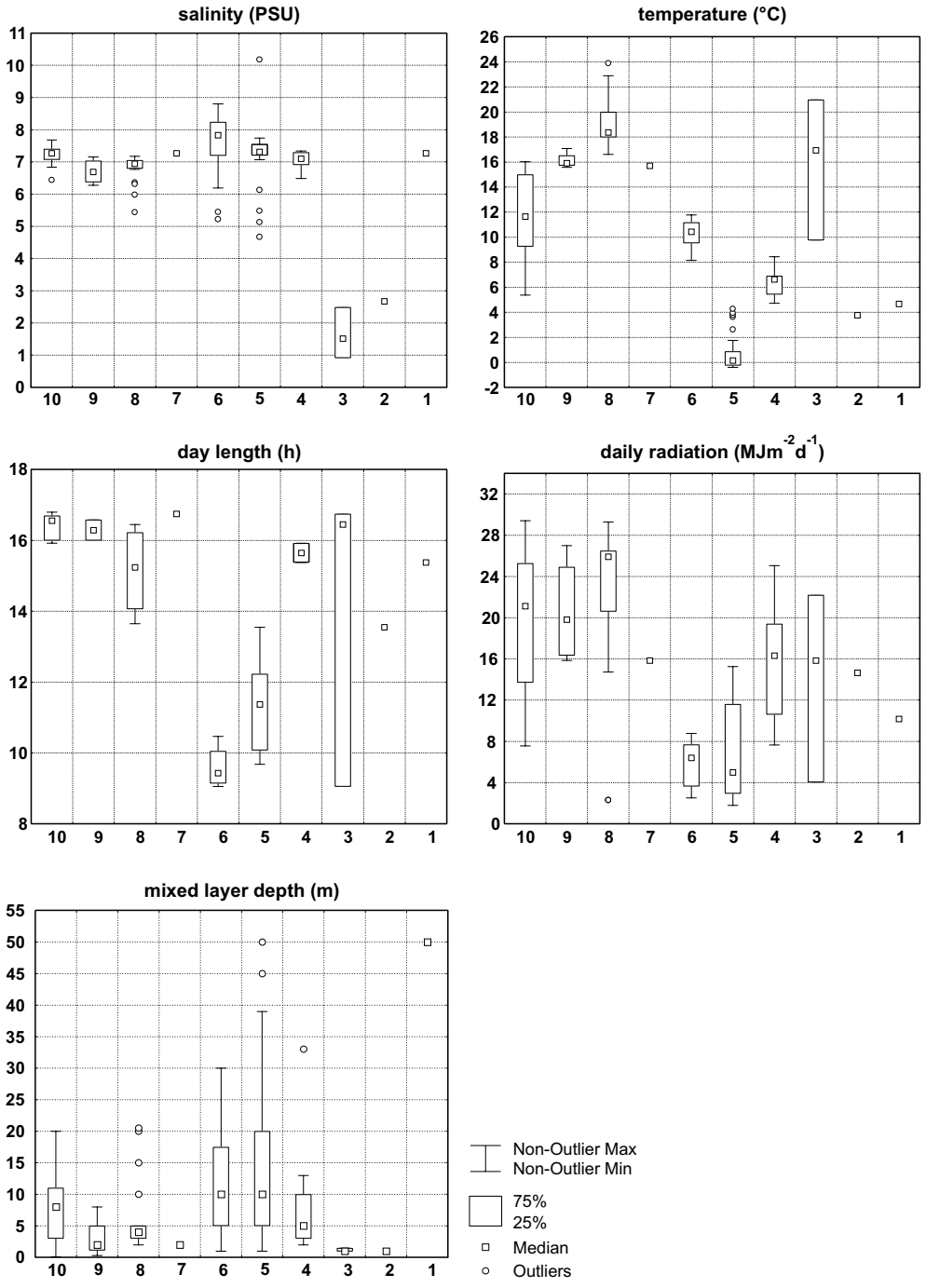

Fig. 5. Statistical characteristics of salinity, temperature, day length abd daily radiation and the depth of the mixed layer in the identified groups of samples

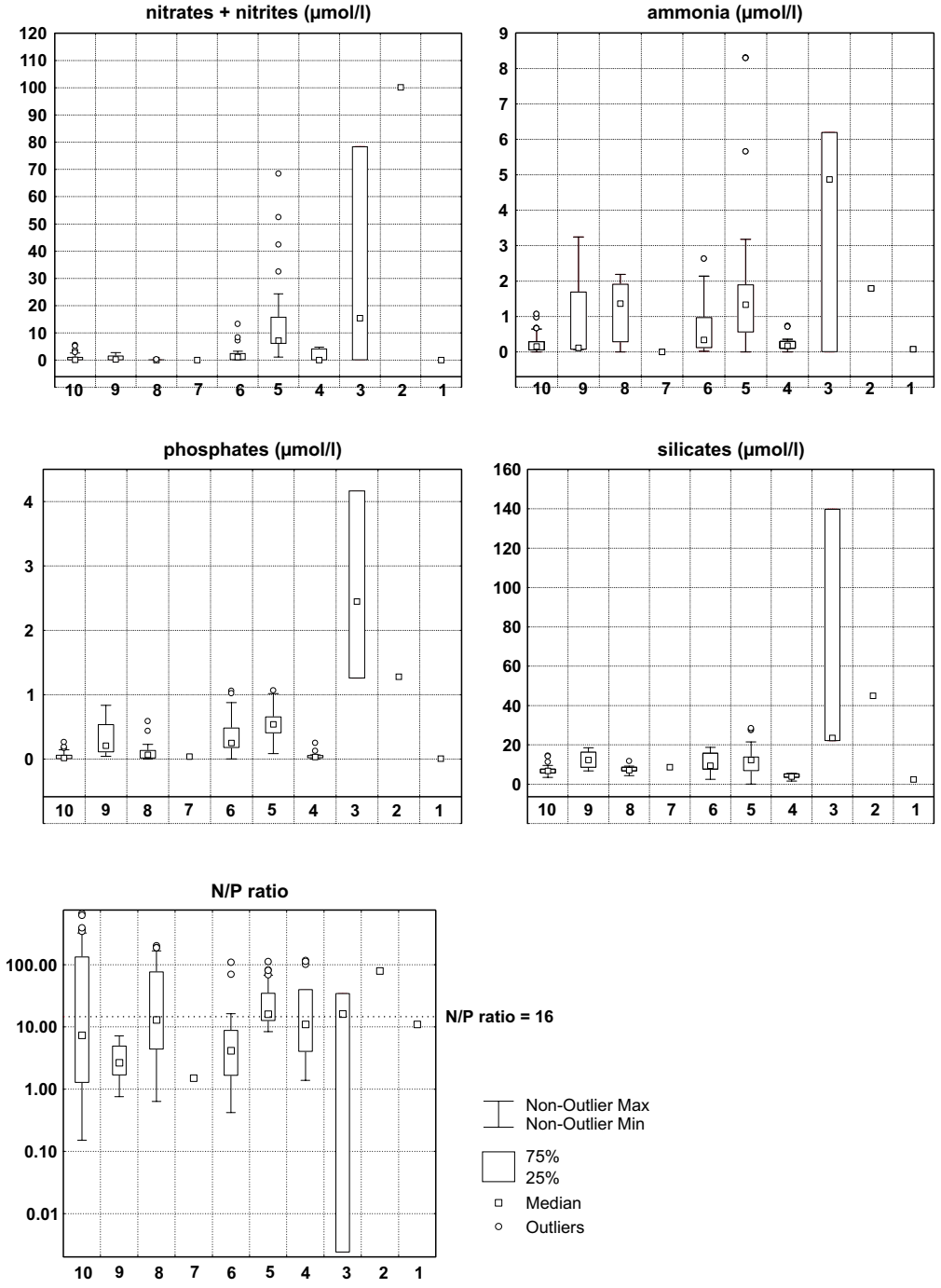

Fig. 6. Statistical characteristics of salinity, temperature, day length and daily radiation and the depth of the mixed layer in the identified groups of samples.

were put into the same assemblage. A relationship between the thickness of the mixed layer and phytoplankton composition was observed for the Vistula River mouth assemblages; they were present with a very thin layer (< 2 m), which was rarely observed in other areas. The assemblage dominated by *Peridiniella catenata* (group 1), which occurred in a very deep mixed layer (50 m), is also significant.

The nutrient concentrations which accompanied the different phytoplankton assemblages often occurred in overlapping value ranges. Much higher concentrations of nutrients near the mouths of the Vistula River were exceptional; however, mineral nitrogen was almost entirely depleted in this area in July 1994. Concentrations of nitrates and phosphates in winter early-spring assemblage and concentrations of phosphates in the autumn assemblage were also higher than the concentrations in other assemblages. The summer assemblages occurred at almost undetectable nitrate concentrations, and the late spring assemblage in the Gulf of Gdańsk occurred at very low concentrations of phosphate and the lowest concentrations of silicates. The highest N:P ratio was observed in the assemblages near the Vistula River and those in winter-early spring, while the lowest ratios were found in the assemblage near the mouth of the Świna River in July 1996 (group 9), the autumn assemblage and the assemblage dominated by *Heterocapsa triquetra* (group 7) in the coastal zone of the Gulf of Gdańsk in July 1996.

DISCUSSION

Seven algae assemblages in which the similarity of phytoplankton composition among the samples was > 50% (Bray-Curtis formula) were identified by comparing the phytoplankton composition of 156 samples collected over the course of 11 cruises in two Baltic basins. Additionally, three assemblages were represented by single samples.

Unfortunately, the intended objectivity of the clustering analysis was not fully achieved since many algae were not identified to the species level. There was also a significant contribution of the group referred to as 'other non def.', which included unidentified monadal and coccal forms. Taxa such as genus, family or the 'other non def.' group included a variable number of species. Therefore, the similarity values, which determined which sample groups would be considered assemblages, are applicable only to the present paper and should not be compared with the values obtained by other authors without comparing the methodologies of phytoplankton identification. The incomplete phytoplankton identification, however, does not seem to have had a greater impact on the fundamental conclusions of this paper since the same degree of detailed phytoplankton analysis has been applied to all the samples investigated.

Seasonal phytoplankton assemblages

Despite the fact that the materials for this work were collected in each of the four seasons, the samples obtained still did not include all the stages of the annual phytoplankton developmental cycle. Based on weekly investigations carried out for a seven-year period in the coastal area near the eastern Swedish coast, Hobro (1979) described seven stages in the annual cycle of phytoplankton succession: 1 – winter with low phytoplankton biomass and composition similar to spring, 2 – spring maximum with the domination of diatoms and *Gonyaulax* (*Peridiniella*)

catenata, 3 – post spring stage with the domination of dinoflagellates, 4 – summer minimum with dinoflagellate *Heterocapsa triquetra* and blue-green algae *Aphanizomenon flos-aquae*, 5 – summer maximum with filamentous blue-green algae and monads, 6 – early autumn stage with the domination of *H. triquetra*, and 7 – late autumn stage with large forms of diatoms and blue-green algae *A. flos-aquae*.

Bralewska (1992) collected samples in the Gulf of Gdańsk at 2-3 week intervals for a period of almost two full years and identified 5 stages in the annual phytoplankton development cycle: 1– early spring diatom maximum; 2 – late spring dinoflagellate maximum; 3 – summer blue-green algae-flagellate stage; 4 – autumn maximum, consisting of large forms of diatoms and *Mesodinium rubrum* and 5 – winter resting period, which is characterized by very low biomass and the presence of various survival stages of algae. Niemi (1975) identified a similar number of phytoplankton succession stages in the Gulf of Finland, as did Smetacek (1977) in the Kieler Bucht. The stages described by Bralewska (1992) can be easily identified with the seasonal assemblages described in this work, the only difference being that the application of an objective comparison method in this work suggests the existence of a greater similarity of winter and early spring phytoplankton than results from the division suggested by Bralewska (1992). However, the results we obtained are in accordance with those obtained by Niemi (1975) and Hobro (1979).

Bralewska (1992) carried out her research in 1987-1988; the majority of her material originated from 1987 which was the coldest year in several decades. Thus, one could assume that the annual phytoplankton succession as determined under such unusual weather conditions did not fully describe phytoplankton development under average conditions. Investigations which were carried out in the Gulf of Gdańsk by various scientists, both before and after 1987, also identified different algae assemblages than those described by Bralewska. Disregarding very early investigations, which had been carried out when Baltic water eutrophication was much lower and with different methodology (Rumek 1948, Ringer 1970; 1973, Malewicz *et al.* 1974, Pliński *et al.* 1982), the investigations which were carried out in the 1980s and the 1990s in the Gulf of Gdańsk indicated the following: summer and autumn phytoplankton assemblages with a significant contribution of green algae (Pliński *et al.* 1982); June and July assemblages dominated by the dinoflagellate *Heterocapsa triquetra* (Pliński *et al.* 1985, Witek 1986); spring and summer assemblages with a significant contribution of dinoflagellates of the genus *Dinophysis* (Wrzołek 1996, Niemkiewicz and Wrzołek 1998); late summer assemblages dominated by dinoflagellate *Prorocentrum minimum* (Hajdu *et al.* 2000, Witek and Pliński 2000). It is difficult to predict what the strength of such assemblages would have been if cluster analysis had been applied. The most likely seems to be the identification of a separate late summer assemblage dominated by the dinoflagellate *Prorocentrum minimum*. In the 1990s, such an assemblage was observed between August and September in both the Gulf of Gdańsk (Hajdu *et al.* 2000, Witek and Pliński 2000), and the Pomeranian Bay (Ochocki *et al.* 1995a, Gromisz *et al.* 1999). However, it must be emphasized that the most distinct division in our investigations, at a similarity level slightly over 30%, which divided phytoplankton into assemblages according to season (winter-spring, summer, autumn), had previously been observed by Rumek (1950), Ringer (1970, 1973) and Pliński and Picińska (1986). The distinct features of phytoplankton in the main seasons throughout the southern Baltic Sea are described by Wasmund *et al.* (2000).

In this work, two summer assemblages are strongly diversified: the cold water assemblage of flagellates of July 1996, and the warm water, multispecies assemblage with dominant blue-green algae of July 1994 and August 1995 (similarity < 40%). The summer of 1996 was

one of the coldest of the last decade, while the summer of 1994 was one of the warmest; this must have resulted in differences between the assemblages of both summers. An important role was played by filamentous blue-green algae (e.g. *Nodularia spumigena*, *Anabaena* sp.) in the warm water multispecies assemblage. These taxa were non-existent among those characteristic for cold water flagellates assemblage. Only the filamentous blue-green algae species *Aphanizomenon* sp. occurred in both types of summer phytoplankton. The limiting temperature between both assemblages was 16-17°C (Fig. 5). It seems probable that the flagellates assemblage appears every year at the beginning of summer or even at the end of spring (e.g. May 1997 in the Pomeranian Bay). This assemblage may occur throughout the entire summer season in cold years, until it is replaced by the autumn assemblage. The warm water assemblage occurs when water temperature exceeds the threshold value, and it may occur after the flagellates assemblage. Despite differences in the species composition of dominants, both assemblages were characterized by maximum *PIE* values, and the significantly smaller range of its values than in the winter-spring and autumn assemblages.

Assemblages dominated by one species

Assemblages which were strongly dominatedby one species (> 75% contribution to the biovolume) and had minimum or low *PIE* values occurred several times in the analyzed material. Most often, this phenomenon occurred in autumn, when large diatoms *Coscinodiscus granii* dominated in the assemblage. In November 1994, the contribution of this species to the phytoplankton biovolume in the Gulf of Gdańsk ranged from 78 to 96%, while in the Pomeranian Bay in October 1997 it ranged from 64 to 89%, with the exception of three stations located near the Świna River mouth). In addition to *C. granii*, dinoflagellates created single species assemblages. In our material, it was an assemblage dominated by *Peridiniella catenata* and one dominated by *Heterocapsa triquetra*. In both cases, they were single samples, which indicated the limited spatial range of the phenomenon in the Gulf of Gdańsk. However, the mass occurence of *P. catenata* is well documented from the whole Baltic Proper (HELCOM 1996, Wasmund *et al*. 1998, 2000). Beside the assemblage dominated by *C. granii*, single species assemblages have begun to appear in the Gulf of Gdańsk and the Pomeranian Bay only recently, they are most frequent in the coastal area and usually consist of one of the dinoflagellate species (*Heterocapsa triquetra* – Pliński *et al.* 1985, Witek 1986, *Peridiniella catenata* – Bralewska 1992; *Prorocentrum minimum* – Ochocki *et al.* 1995a, Witek and Pliński 2000) and are often associated with the mass algal occurrences.

The toxicity of single species algal blooms in Baltic coastal waters (Larsen and Moestrup 1989, Edler *et al.* 1996) as well as in the waters of other regions (Gowen 1987, Boalch 1987, Hallegraeff 1995, Codd 1999) is known; thus, attention has already been paid to the conditions which facilitate their occurrence. Currently, it is believed that, in addition to eutrophication and the intensive use of coastal waters for aquaculture, unusual hydrologic and climatic conditions, which often occur in limited areas, also favor single species algae blooms. Included among these phenomena are unusual thermal or saline stratification, upwelling, or elevating nutrients above the picnocline, all of which can be caused by winds, tides, eddies and internal waves (Holligan 1987, Hallegraeff 1995).

However, in the case of single species assemblages dominated by dinoflagellates that we identified, none of the factors described above was confirmed. Perhaps the environmental conditions which had led to intensive dinoflagellate development had already subsided by the time of sampling. Due to this, it is currently difficult to pinpoint the main factor in the creation

of these assemblages. A result of similar, unobserved factors, might have been the significant depth of the mixed layer in the case of the assemblage dominated by *Peridiniella catenata*. The station at which *Heterocapsa triquetra* dominated was located near the mouth of the port of Gdańsk canal where higher nutrient concentrations were noted due to the input of communal and municipal sewage (Nowacki and Jarosz 1998). This location might have stimulated the development of this dinoflagellate.

Regional differences

The region adjacent to the Vistula River mouth was the most distinctive basin in the whole of the investigated area. The phytoplankton composition in this area showed significant stability and the samples which were collected in July 1994, July 1996 and November 1994 were classified as the same assemblage (phytoplankton similarity > 50%). A sample collected in April 1994 was segregated from the other samples from near the Vistula River mouth with a similarity level of 47%.

The second outstanding basin in terms of phytoplankton composition was the area near the Świna River mouth. This basin was distinguished on the phytoplankton similarity level of < 50 % only during one of four research cruises, July 1996. In the other research seasons, the region near the Świna River mouth was also different from the remaining area; however, then the phytoplankton similarity was greater (Gromisz *et al.* 1999).

The significance of the differences in phytoplankton composition between the Gulf of Gdańsk and the Pomeranian Bay was relatively small since in the same stages of the biocenosis development the phytoplankton similarity in both basins exceeded 50%. However, the differences between the basins were clearer on a slightly higher level of similarity, e.g. 54% in the winter-spring assemblage, 55-65% in the summer cold water assemblage and 64% in the autumn assemblage. Among the most significant differences was the lack of *Peridiniella catenata* among the species dominating in spring in the Pomeranian Bay. However, in May 1997, the phytoplankton in the Gulf of Gdańsk created a separate late spring assemblage, in which *P. catenata* made the greatest contribution to the biovolume. In the Pomeranian Bay, phytoplankton from the same month was classified as the summer, cold water type along with phytoplankton from July 1996 in both basins. In the summer, cold water assemblage samples from July 1996 collected in the Pomeranian Bay, there was the dominant presence of large diatoms, typical for autumn phytoplankton, such as: *Coscinodiscus granii*, *C*. cf. *commutatus* and *Actinocyclus octonarius*. These species occurred in the Gulf of Gdańsk only in autumn, and *A. octonarius* never played such a significant role as it did in the Pomeranian Bay. In the assemblages located near river mouths in the Gulf of Gdańsk, the diatom *Skeletonema subsalsum* was not observed, even though it was characteristic for the phytoplankton composition at the points located near the mouths of the Świna and Dziwna rivers. The presence of this species in the Szczecin Lagoon and the Pomeranian Bay was also observed by Zembrzuska (1973) between 1956 and 1958.

The material analyzed for this paper did not include samples from the open Baltic Sea; thus, it is difficult to determine the differences in the phytoplankton composition between both basin, and the open sea. However, based on several peripheral samples, it can be stated that during the early spring phytoplankton bloom, diatoms dominated in both basin, while at the stations located beyond the 20 m isobath in the Pomeranian Bay and in the north-east region of the Gulf of Gdańsk, dinoflagellates comprised a larger percentage of the biovolume. Wrzołek (1996) did not mention any diatom representatives among the five dominants in the composi-

tion of the spring phytoplankton in the Gdańsk Deep in 1989-1993. A similar tendency of dinoflagellates to replace diatoms in the spring bloom in the Baltic Proper, while diatoms still dominated in the estuaries, was described by Wasmund *et al.* (1998, 1999, 2000).

Environmental conditions versus phytoplankton composition

From the analysis of the relationship between phytoplankton assemblages and environmental conditions (Figs. 5 and 6), it may be stated that low salinity and high nutrient concentrations were characteristic in the assemblages found in the waters near the Vistula River mouth. In the other areas, the most evident relationship was that between phytoplankton composition and temperature (and, to some extent, with day length). Special attention must be paid to the fact that the composition of summer phytoplankton assemblages is dependent on temperature. Above 16-17°C, two species of filamentous blue-green algae, *Aphanizomenon* sp. and *Nodularia spumigena*, occurred among three main dominant species. This fact was confirmed by long-term observations carried out by Pliński and Jóźwiak (1999) in the Gulf of Gdańsk, which indicate that *N. spumigena* needs higher temperature for its optimum development than *A. flos-aquae*, and both species develop intensively at temperatures exceeding 18°C. The phenomenon of *N. spumigena* blooms during warmer summer seasons was also observed in the open Baltic Sea (Kononen 1992, Kononen *et al.* 1996, Brandt *et al*. 1998).

When analyzing the relationship between phytoplankton assemblages and growing conditions, relatively high concentrations of phosphates and nitrates, which accompanied the winter-spring assemblage, and rather high phosphate concentrations at the same time as the autumn assemblage are notable. The depletion of nitrates which occurred together with the late spring and summer assemblages as well as the depletion of phosphates and the decrease of silicate concentrations during the late spring assemblage in the Gulf of Gdańsk was also characteristic. Hobro (1979), while carrying out research on the east coast of Sweden, also observed the highest nutrient concentrations during the winter and spring maximum of phytoplankton development, and the lowest – in late spring and summer. The depletion of phosphates, similarly to the Gulf of Gdańsk, occurred in late spring. The variations of nitrate concentrations described by Olli (1996), in Pärnu Bay (NE Gulf of Riga) in 1991, which were observed in spring assemblages dominated by diatoms and dinoflagellate *Peridiniella catenata*, and in the summer assemblage, dominated by blue-green algae (*Aphanizomenon flos-aque*, *Nodularia spumigena*), were also similar. The differences between this basin and the basins which were investigated by the authors appeared in phosphate concentrations. In Pärnu Bay, phosphate concentrations remained at a constant and relatively high level (0.5-1 $\mu mol \cdot dm^{-3}$) from late spring until the end of September. In the Gulf of Gdańsk and the Pomeranian Bay, their average concentrations exceeded 0.5 $\mu mol \cdot dm^{-3}$ only in the near river mouth and winter-spring assemblages.

Poder and Jaanus (1997), in July 1994, also described a similar summer warm water assemblage in the Gulf of Riga in which *Aphanizomenon flos-aquae*, *Nodularia spumigena* and Cryptophyceae and *Pyramimonas* spp. dominated with nutrient concentrations corresponding to concentrations observed in the Gulf of Gdańsk in July 1994 and August 1995. In these cases the depletion of nitrogen compounds most likely facilitated the domination of filamentous blue-green algae in phytoplankton assemblages, which are able to assimilate molecular nitrogen.

Acknowledgements. *The authors would like to thank M. Kownacka and T. Mackiewicz for their analysis of a portion of the phytoplankton samples, and A. Grelowski, M. Pastuszak and M. Zalewski for carrying out hydrological and hydrochemical measurements. We would also like to thank P. Komorowski and A. Grelowski for help with the graphic presentation of the paper. The research was funded by KBN through the statutory activities of the SFI. The portion of the paper which refers to the Bay of Pomerania was funded by the Polish-German Cooperation Foundation, grant no. 1567/94/LN.*

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BULLETIN OF THE SEA FISHERIES INSTITUTE
2 (153) 2001

Energy budget in early stages of smelt *Osmerus eperlanus* (L.)

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Abstract. To estimate the influence of the smelt *Osmerus eperlanus* (L.) on the zooplankton in the Vistula Lagoon the consumption rate of this fish was calculated. The direct method for estimating production *P*, respiration *R* and egestion *F* was used. The daily fish food ration *C* was calculated as the sum of the above parameters of the energy butget: $C = P + R + F + U$. The energy budget of smelt weighing 7.6 mg dry weight (90.2 mg wet wt.) at the natural environmental temperature (17.5°C) is as follows (in cal per mg dry wt of fish per day): C (2.51 cal) = *P* (1.12 cal) + *R* (0.48 cal) + *F* (0.75 cal) + *U* (0.16 cal). The daily food ration of smelt larvae is thus 4.02 mg dry wt of zooplankton per individual (0.53 mg dry wt of zooplankton per mg dry wt of fish).

Key words: *Osmerus eperlanus*, food ration, Vistula Lagoon.

INTRODUCTION

The daily food ration in terms of energy can be determined by several methods, e.g. the direct method either by measuring the amount of food eaten, as is done in the case of monophagous animals (for phytophagous fish see Fischer 1973), or by the indirect method which uses the energy budget equation *C* (food ration) = *P* (production) + *R* (respiration) + *FU* (excreta). The theoretical basis for calculating animal food rations using the energy budget are described by Kleiber 1967, Phillipson 1966, and Klekowski and Fischer 1993.

In recent years, the indirect method has been commonly applied to determine the food consumption and, thus, the role of larval and juvenile fish stages (yellow perch, silverside, lake trout, Baltic herring, pollock, zander, smelt) in freshwater and marine ecosystems (Kitchell and Stewart 1977, Letcher and Bengtson 1993, Stewart *et al*. 1983, Arrhenius and Hansson 1994, Cortes and Gruber 1994, Karjalainen *et al.* 1997, Cianelli *et al.* 1998, Worischka and Mehner 1998, Tolonen 1999). The methods of applying the energy budget to early fish stages are outlined by Kamler (1992). In applying the energy budget principle to estimate food rations, it must be remembered that this method has many limitations and sources for potential error, as described by Hansen *et al*. (1993).

The aim of this work is to determine the daily food ration of larval stages of smelt *Osmerus eperlanus* (L.) from the Vistula Lagoon using the indirect method as the sum of production, respiration and egestion. The determination of the amount of food consumed by smelt along

with data regarding fish abundance will facilitate determining the role of this species in the Vistula Lagoon trophic chain (impact on zooplankton community) and can give information about food competition between carnivorous species (fish larvae, macrozooplankton) in the Vistula Lagoon pelagic community.

MATERIAL AND METHODS

Fish

Fish (larvae) were caught in the 1.5 m surface layer of the Vistula Lagoon several hundred meters from the port in Tolkmicko. The catches were carried out from a boat using a 5 m long Neuston plankton net with 500 μm mesh and a 2 m^2 opening. Haul times varied from 2 to 8 minutes, depending on local fish concentrations.

After landing the net, the fish were transferred to thermoses with aerated water and then transported to the laboratory in Gdynia where they were placed in thermostats.

Procedures

Smelt larval production P was determined as the average increase of dry body weight of particular individuals between 25 June and 8 July 1999 (dates of subsequent smelt catches in the Vistula Lagoon). The production was determined in mg of dry weight per day (mg dry wt. d^{-1}). The production measurements were based on 78 measurements of fish dry weight (48 measurements in June and 30 in July).

Since production was measured only under natural conditions (17.5°C), the value of production at temperatures of 15 and 10°C were derived using the values measured at a temperature of 17.5°C and a temperature coefficient Q_{10} for egestion. The following formula was used: $P_{t2} = P_{t1}/(Q_{10})^{(t2-t1)/10}$ (Duncan and Klekowski 1975), where: P_{t2} – production at a temperature of 15ºC or 10ºC, P_{t1} – production measured, i.e. at a temperature of 17.5°C. The method described by Opaliński and Klekowski (1992) was applied to interpret the Q_{10} value as a measure of the influence of temperature on metabolic processes.

The respiration of smelt larvae R was determined by the closed vessel method at the temperature of their natural environment (17.5°C, 11 measurements) and under experimental conditions (10 and 15°C, 24 h adaptation period to thermal conditions of the measurements, 11 and 26 measurements taken, respectively).

Respirometric vessels with a volume of 50 ml were used. Exposition time was 2.5 hours. The oxygen concentration was measured using an oxygen sensor (Oxygenmeter XI 196 by WTW). Fish oxygen consumption R was expressed as $mm^3 \cdot ind.^{-1} \cdot h^{-1}$ and the metabolic rate MR as $mm^3 \cdot mg^{-1} \cdot h^{-1}$.

The amount of fish egestion F was determined by weight. Twenty-one fish (17.5°C), 33 fish (15°C) and 40 fish (10°C) were placed in glass aquariums with 8 liters of water. The aquariums were placed in water thermostats at temperatures of 17.5, 15 and 10°C, respectively. After 20 hours of exposition, the water was filtered through glass filters and the sediment obtained was regarded as fish egestion. A control tank without fish was used in which the same amount of water was exposed to the same temperatures for the same period of time. The amount of fish egesta production is expressed as mg of dry mass per individual per day.

Since the excretion products U of final nitrogen transformations were not investigated, their value was assumed as 10% of assimilation ($P + R$), which is consistent with the smelt data of Hewett and Johnson (1992) as quoted in Lantry and Stewart (1993).

Daily food ration (consumption) is the sum of production, respiration and egestion (egesta + excreta): $C = P + R + FU$. In order to calculate this value, all elements of the energy budget must be expressed in unified energy units, calories. Therefore, the following parameters were used: for P – the energy value of a smelt body was assumed to be 805.7 cal per g wet wt (according to Lantry and Steward, 1993); for R – the oxycaloric value of 0.0047 cal per mm^3 of oxygen ($RQ = 0.75$, see Kleiber 1961); for F – the energy value of excrement pellets as 3.63 cal per mg dry weight (data for salmon *Salmo trutta* according to Raciborski 1987 and for guppy *Lebistes reticulatus* based on the unpublished data of Urban-Jezierska).

Fish survival in particular temperatures was determined in an independent experiment, during which 40 fish in every temperature condition were investigated.

RESULTS

Production *P*

Average dry weight of smelt larvae on 25 June was 7.6 mg, after 13 days it increased to 30.6 mg (Table 1). Data in Table 1 facilitates calculations which reveal that the smelt larvae production in the investigation period, under natural environmental conditions, i.e. at a temperature of 17.5°C, amounted to 1.77 mg dry wt. $ind.^{-1} \cdot d^{-1}$ and 13.8 mg wet wt. $ind.^{-1} \cdot d^{-1}$.

Table 1. Wet *Ww* and dry *Dw* weight, dry matter content and production *P* in smelt larvae (Vistula Lagoon). Values represent mean ± standard error. *n* = number of individuals

Date	*n*	*Ww* ± S.E. [mg]	*Dw* ± S.E. [mg]	Dry matter content [%]
June 25, 1999	48	90.2 ± 13.2	7.6 ± 1.4	8.5
July 8, 1999	30	269.0 ± 13	30.6 ± 2.0	11.3
Production		178.8	23.0	

Respiration *R*

The oxygen consumption of smelt larvae at 17.5°C is 32.19 mm^3 $ind.^{-1} \cdot h^{-1}$. Oxygen consumption at experimental temperatures, metabolic rate and the dependence of oxygen consumption on body mass are presented in Table 2.

Oxygen consumption R, metabolic rate MR and regression intercept a decrease as temperature falls, however, the fall in the 15-10°C range is very fast: oxygen consumption R) – from 26 to 14 $mm^3 \cdot ind.^{-1} \cdot h^{-1}$, metabolic rate MR – from 0.352 to 0.172 $mm^3 \cdot mg\ wet\ wt^{-1} \cdot h^{-1}$, intercept a – from 1.10 to 0.52. The intercept a, which describes the dependence of oxygen consumption on body mass, is interpreted as the oxygen consumption of an individual of the unit body weight, which, in this case, is 1 mg.

The decrease in oxygen consumption, metabolic rate and the intercept a in the temperature range of 17.5-15°C is much lower. The comparison of the temperature influence on oxygen consumption by smelt larvae in the temperature ranges 17.5-15°C and 17.5-10°C using the

Table 2. Respiration *R* and Metabolic Rate *MR* in smelt larvae (June 1999, Vistula Lagoon): laboratory experiments

Parameter	Unit	Temperature		
		17.5°C	15°C	10°C
Number of measurement	–	11	26	11
Respiration *R versus* wet weight *Ww* dependence ($R = a \cdot Ww^b$	$mm^3\ 0_2 \cdot ind^{-1} \cdot h^{-1}$ $mg \cdot ind^{-1}$	$a = 1.23$ $b = 0.72$	$a = 1.1$ $b = 0.74 \pm 0.10$	$a = 0.52$ $b = 0.74$
r^2 of the regression	–	0.6460	0.7032	0.7056
R – respiration	$mm^3\ 0_2 \cdot ind^{-1} \cdot h^{-1}$	32.19 ± 4.60	25.59 ± 1.10	13.95 ± 1.79
Ww – wet weight	$mg \cdot ind^{-1}$	90.2 ± 13.2	74.5 ± 3.80	86.4 ± 13.6
Dw – dry weight	$mg \cdot ind^{-1}$	7.6 ± 1.4	6.6 ± 0.4	8.6 ± 1.3
Dry matter content	%	8.5	8.9	9.9
MR – metabolic rate (*Ww* basis)	$mm^3 0_2 \cdot mg\ Ww^{-1} \cdot h^{-1}$	0.381 ± 0.266	0.352 ± 0.009	0.172 ± 0.013
MR – metabolic rate (*Dw* basis)	$mm^3\ 0_2 \cdot mg\ Dw^{-1} \cdot h^{-1}$	8.46 ± 0.64	3.99 ± 0.21	1.74 ± 0.44
Mortality (in independent experiment)	%	9	21	72

Q_{10} coefficient indicates that in the first range of temperatures, which are close to diurnal temperature variations in the natural environment, the influence is insignificant, while in the second range the temperature influence is very strong (Table 3).

Fish survival decreased with decreasing temperatures; at 17.5°C it was 91%, at 15°C 79 of the fish survived and at 10°C only 26% of the fish survived (Table 2).

Egestion *F*

The amount of excrement egested by one smelt larva per day under natural conditions (17.5°C) was 1.57 mg, or, recalculated per fish weight unit, 0.207 mg $mg^{-1} \cdot d^{-1}$. At lower temperatures the values were also much lower: 1.08 mg at 15°C and 0.20 at 10°C (Table 4).

Table 3. The influence of temperature on metabolic rate (temperature quotient Q_{10}) in smelt larvae (June 1999, Vistula Lagoon) in laboratory experiments. General formula: $Q_{10} = (MR_{t2} : MR_{t1})^{10:(t2-t1)}$ where: *MR* – in $mm^3\ 0_2$ mg wet $wt.^{-1}\ h^{-1}$, , and *Ww* – in mg ind^{-1}, *t*1 and *t*2 – temperatures

Temperature interval	Measured Q_{10} value	Q_{10} value according to Krogh's „normal curve" [a]	Remarks
17.5-15°C	1.4	2.6	Insignificant temperature influence (relative temperature independence *sensu* Duncan and Klekowski 1975)
17.5-10°C	2.8	2.7	Insignificant temperature influence (compensation *sensu* Prosser 1976)
15-10°C	4.2	2.9	Significant temperature influence (overcompensation *sensu* Prosser 1976)

[a] after Duncan and Klekowski (1975)

Table 4. Egestion rate (F) in smelt larvae (June 1999, Vistula Lagoon) in laboratory experiments

Temperature [°C]	Exposition time [h]	Number of animals	Animal mean dry weight [mg]	Egestion [mg dry wt $ind.^{-1} \cdot d^{-1}$]	Egestion rate [mg dry wt mg dry $wt^{-1} \cdot d^{-1}$]
17.5	20	21	7.6	1.57	0.207
15	20	33	6.6	1.08	0.163
10	20	40	8.6	0.20	0.023

The data presented reveal that under natural conditions smelt larvae exert 1.57 mg of excrement pellets per day which constitutes about a fifth of their body weight. The production of excrement rapidly decreases as temperature falls; at 15°C excrement constitutes a sixth of fish body weight and at 10°C this figure is only a fortieth of body weight. This indicates a rapid decrease in the feeding rate as the environmental temperature drops.

Based on the data obtained, the temperature coefficient of the egestion rate Q_{10} for smelt larvae was calculated. In the 17.5-15°C temperature range it is 2.4 and indicates an insignificant temperature impact, at temperatures from 17.5-10°C it is 19 which indicates a significant temperature impact and in the range of 15-10°C it is 50, i.e. a very strong temperature impact on egestion.

Energy budget

Table 5 presents the measured parameters of the energy budget for smelt at temperatures of 17.5, 15 and 10°C calculated per individual. Since the energy budgets are usually calculated per animal body weight unit in the literature, Table 6 presents the values of the smelt energy budget recalculated to a mg of fish dry body weight.

The data from Table 6 reveal that at temperatures of 17.5 and 15°C all parameters of the smelt larvae energy budget are practically identical (of course, not in absolute values, those in lower temperatures are lower, but in relative values, i.e. as a percentage of the food ration). Therefore, assimilation ($A = P + R$) is also the same (64% at 17.5°C and 65% at 15°C). At a

Table 5. Energy balance of smelt larvae (in cal ind^{-1} d^{-1}) (June 1999, Vistula Lagoon)

Parameter	Energy equivalent	17.5°C	15°C	10°C
Mean animal weight				
mg wet wt		90.2	74.5	86.4
mg dry wt		7.6	6.6	8.6
Production *P*	4.83 cal mg dry wt^{-1} [a]	8.55 cal	6.91cal	0.92 cal
Respiration *R*	0.0047 cal mm^3 [b]	3.63 cal	2.89 cal	1.57 cal
Egestion *F*	3.63 cal mg dry wt^{-1} [c]	5.70 cal	3.92 cal	0.73 cal
Excretion *U*	10% P+R [d]	1.22 cal	0.98cal	0.25 cal
Daily consumption *C*		17.88 cal	14.70 cal	3.47 cal

[a] data after Lantry and Steward (1993), recalculated into dry weight
[b] for $RQ = 0,75$
[c] after Raciborski (1987) and Urban-Jezierska (unpublished data)
[d] after Hewett and Johanson (1992)

Table 6. Energy balance in smelt larvae (in cal. per mg dry wt. of fish).
In parentheses – percentage of each parameter in total food consumption

Parameter	17.5°C	15°C	10°C
Animal mean dry weight [mg dry wt]	7.6	6.6	8.6
Production *P*	1.12 (45%)	0.92 (44%) [a]	0.11 (28%) [a]
Respiration *R*	0.48 (19%)	0.43 (21%)	0.18 (45%)
Egestion *F*	0.75 (30%)	0.59 (29%)	0.08 (20%)
Excretion *U*	0.16 (6%) [a]	0.13 (6%) [a]	0.03 (7%) [a]
Consumption *C*	2.51 (100%)	2.07 (100%)	0.40 (100%)

[a] calculated values

temperature of 10°C, in comparison to higher temperatures, production decreases, respiration increases and assimilation increases to 73%.

The temperature impact on the smelt larvae food ration calculated using data from Table 6 (temperature coefficient Q_{10}) indicates that in the 17.5-15°C temperature range the food ration practically does not change (Q_{10} = 2.0) and it is independent of temperature, while when the temperature decreases to 10°C a rapid decrease in food consumption occurs (Q_{10} = 10). A similar situation occurs when the temperature decreases from 15 to 10°C (Q_{10} = 24).

DISCUSSION

A number of works regarding the feeding habits (food rations) and the ecological role of smelt in lakes and the Baltic Sea have appeared in recent years (Lantry, Stewart 1993, Karjalainen *et al.* 1997 a, b). These works are based on the so-called bioenergetic model. In most cases the parameters measured were the size distribution of the populations and the temperature, while the remaining energy budget parameters were taken from the work dedicated to the bioenergetics of the species by Hewett and Johnson (1992).

This work presents the basic bioenergetic parameters of smelt (production, respiration, egestion) that were measured directly and facilitated the construction of the energy budget.

The smelt energy budget parameters measured comply quite well with the energy budgets of salmonids investigated at similar temperatures (Table 7). While making such comparisons, the temperature at which the measurements were made (for which the calculations were made) is important; the measurements reveal that only small temperature variations (about 2.5°C) do not significantly affect the smelt energy budget (of course the range of this variations depends on temperature range). A temperature decrease of about 7.5°C results not only in a significant decrease of all fish energy budget parameters but also in a radical change in the proportions between particular parameters (Table 6). Kaufmann and Wieser (1992) believe that a significant decrease in the metabolic rate among larvae and juvenile stages of cyprinids when temperature drops from 20 to 15°C cannot be explained only by changes in water viscosity. The influence of temperature on the energy budget parameters in larval stages of fish is analyzed in detail by Kamler *et al*. (1994).

Table 7. Comparison of the energy balances in early stages of some salmonid fish species

Species	Animal wet weight [mg]	Temper-ature [°C]	*P* Produc-tion [a]	*R* Respira-tion [a]	*FU* excreta + egesta [a]	Author
Smelt						
Osmerus eperlanus	86.4	10	28	45	27	present paper
Osmerus eperlanus	74.5	15	44	21	35	present paper
Osmerus eperlanus	90.2	17.5	45	19	36	present paper
Sea trout						
Salmo trutta	175	11	39	35	26	Raciborski 1987
Salmo trutta	50 g	9.5	33	36	31	Brett, Groves 1979
Rainbow trout						
Salmo gairdneri	age 0+	?	30	50	20	Penczak *et al.* 1982

[a] as % of consumption

Table 8. Consumption rate *C* in larval and juvenile fish species

Species	Temp. [°C]	Animal wet wt. [mg]	Consumption [mg · mg^{-1} · d^{-1}]	Author
Smelt *Osmerus esperlanus*	17.5	90	0.44	present paper
Rainbow smelt *Osmerus mordax*	3	60	0.02	Lantry and Stewart 1993
Whitefish *Coregonus lavaretus*	4	90 g	0.03	Tolonen 1999
Sea trout *Salmo trutta*	11	175	0.48	Raciborski 1987
Coho salmon *Oncorhynchus kisutch*	11.1	35 g	0.037	Brodeur and Pearcy 1987
Coho salmon *Oncorhynchus kisutch*	13.7	100 g	0.024	Brodeur and Pearcy 1987
Yellow perch *Perca flavescens*	?	15	0.21	Worischka and Mehner 1998
Yellow perch *Perca flavescens*	16.6	22	0.653	Post 1990
Zander *Stizostedion luciperca*	?	6.9	0.31	Worischka and Mehner 1998
Baltic Sea herring *Clupea harengus*	17.4	40	0.13	Arrhenius and Hansson 1994

Assuming that the diurnal food ration of one smelt larva in June is 17.88 cal (Table 5), and the energetic value of zooplankton is 4.45 cal mg dry wt^{-1}, it is possible to calculate that one larva consumes about 40 mg wet weight of zooplankton per day. This means that the ratio of the amount of food consumed per day to smelt wet weight is 0.44.

Table 8 presents the diurnal smelt food ration in comparison with that of other fish with similar feeding habits which live in the same, or very similar, environment. The daily food ration of smelt (0.44 mg of food per 1 mg of fish) is comparable to that of perch (0.65) and much higher than that of herring (0.13) which live under the same or similar thermal conditions.

In order to eliminate the weight difference of the species compared, data regarding their relative food ration are presented in a plot of food ration *vs*. fish weight in Fig. 1. This dependence is described as follows: $C/W = 1.1\ W^{-0.27}$, where C/W – food ration, (mg · mg^{-1} · d^{-1}), *W* – fish wet weight (mg). This dependence is a modification of the Kitchell *et al.* (1977) equation for a temperature of 23°C and fish weight in grams. The modification involved the recalculation of intercept *a* of this equation to the temperature of 17.5°C using Q_{10} calculated

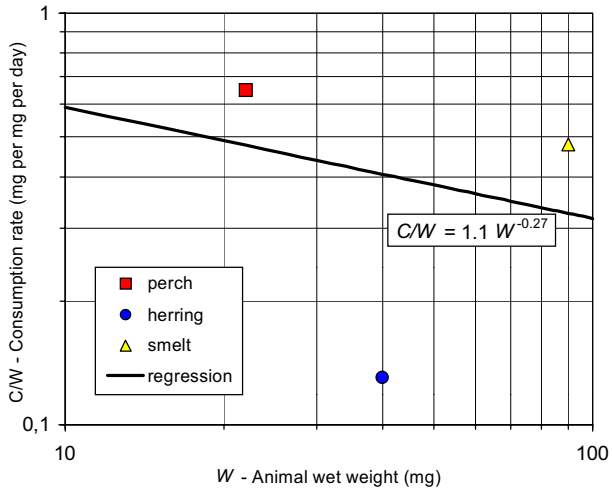

Fig. 1. General dependence between consumption rate (*C/W*, mg mg^{-1} · d^{-1}) and fish larvae wet weight (*W*, mg) as a regression line (after Kitchell *et al*. 1977, recalculated into units used in this paper). Data on consumption rate of the smelt (this paper, triangle), herring (after Arrhenius and Hanson 1994, circle), and perch (after Post 1990, square).

for smelt consumption. Also, the equation was transformed so that animal weight is in milligrams. The transformation method is described by Duncan and Klekowski (1975). The same value of regression coefficient *b* (–0.26) of the food ration to body weight for nine fish species larvae are given by Keckeis and Schiemer (1992).

After including the animal weight differences (Fig. 1), it can be concluded that the magnitudes of smelt and perch food rations are practically identical (placed along the regression line), while the herring food ration is about 3 times lower (much below the regression line).

It seems that herring fry loses out to smelt and perch in the food competition. However, the small food demand of early developmental stages of herring may be the mechanism which allows them to survive in an environment where food resources are shared with smelt and perch, which probably are the principal zooplankton consumers in the Vistula Lagoon. This hypothesis must be verified through the application of direct (or experimental) methods.

Acknowledgements. *Thanks are due Professor Janusz Uchmański for his scientific consultation and Professor Ewa Kamler for her critical review of the manuscript.*

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BULLETIN OF THE SEA FISHERIES INSTITUTE
2 (153) 2001

Fish larvae as food for age group 1 smelt *Osmerus eperlanus* (L.) in the Vistula Lagoon in spring 1998 and 1999

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Abstract. Investigations of the occurrence and species composition of fish larvae in smelt *Osmerus eperlanus* (L.) food were based on the analysis of the stomach contents of 365 and 1,240 specimens from age group 1 which were caught in April-June 1998 and 1999. The frequency that fish larvae occurred in smelt food (%F) increased with predator length, and it varied, on average, from 9.6% in 1998 to 4.7% in 1999. The length of the prey varied from 3.5-30 mm to 3.7-24.6 mm in 1998 and 1999, respectively. However, their species structure was different; in the majority of cases in 1998 prey consisted of the larvae and fry of percid fish (72.5%) and smelt (21.6%), while in 1999, herring larvae dominated (86.4%). The results of investigations of smelt food indicate that this fish has a rather insignificant role as a predator. The influence of smelt age group 1 on the mortality of herring larvae, which occur on a massive scale in spring in the Vistula Lagoon, is minimal and concerns only the early larvae developmental period, i.e. the yolk-sac stage.

Key words: smelt, feeding, fish larvae, predation, Vistula Lagoon.

INTRODUCTION

Smelt food includes a wide variety of smaller organisms (Scott and Crossman 1973). Due to its zooplankton consumption, smelt is a second order consumer in the trophic chain (Janchenko 1992). The predatory activity of smelt increases with age. The food of age group 0 includes almost only mesozooplankton crustaceans, i.e. Copepodaa and Cladocera, while the food composition of older smelt may include small zooplankton as well as larger organisms from the following groups: Mysidacea, Amphipoda, Crangonidae, Isopoda, Ostracoda and Insecta (larvae), depending on the basin which they inhabit (Filuk and Żmudziński 1965, Gąsowska 1962, Kühl 1970, Rogala 1992, Scott and Crossman 1973, Sterligova *et al.*1992, Wheeler 1969, Wiktor 1964). Staff (1950) reported that after exceeding a certain size smelt consumption habits switch from crustaceans to fish.

It is a fairly commonly belief that smelt prey on larvae and fry. However, this thesis is not confirmed by the results of investigations which reveal that fish rarely exceed 6-10% of smelt stomach content volume (Scott and Crossman 1973). The following species are observed in smelt food: sprats, herring, gobies, young gadids, and younger specimens of smelt (Wheeler 1969, Kühl 1970). In lakes, smelt is a predator which destroys the eggs and hatch of European whitefish (Szczerbowski 1993). Many authors emphasize a strong cannibalistic tendency among older specimens (Brylińska 1986, Gąsowska 1962, Staff 1950, Wiktor 1964).

In the Vistula Lagoon in spring the phenomenon of the coexistence of numerous herring larvae from the spring spawning (Margoński 2000) and young smelt from the previous year's generation, i.e. age group 1 which wintered in this basin, is observed. Therefore, there is the potential danger that herring larvae will be eaten by year-old smelt, especially between April and June. Later, when herring fry reach the length of 33 mm it migrates from the lagoon to the Baltic Sea (Janchenko 1992, Krasovskaja 1998).

The aim of the research was to confirm if and to what extent the diet of age group 1 smelt is based on herring larvae during the period when the latter is the most numerous, and if the coexistence of various developmental stages of smelt and herring has a significant impact on herring mortality.

MATERIALS AND METHODS

Smelt samples for the food investigations were collected during six cruises in 1998 and seven cruises in 1999 in the Polish part of the Vistula Lagoon. They were carried out at intervals of approximately two weeks between April and June (Table 1). Samples were collected at 15 stations using a neuston trawl with an intake area of 2 m^2 and a mesh size of 500 μm hauled at a speed of about two knots. The fish were collected at both coastal and centrally located stations and they belonged to age group 1 (Fey, personal communication).

The material was preserved with 4% buffered formaldehyde, and then placed in 95 % ethanol after 24-48 hours. All the fish were measured (SL – Standard Length and TL – Total Length) to the nearest mm, and, for the purpose of presenting the results, they were grouped in 5 mm length classes SL. The length range of the smelts caught varied from 53 to 106 mm in 1998 and from 44 to 110 mm in 1999. The stomach walls were cut, and the stomach contents were placed on microscope glass plates in a drop of glycerol with gentian violet spirit solution (Gamble *et al*. 1985). The stomach contents were examined focusing on the presence of larvae and fry. These were measured and marked according to Kryzhanovsky *et al.* (1953) and Urho (1992, 1996). The larvae were observed under polarised light which facilitated their identification (Nichols and Wood

Table 1. Date of sampling, length range and number of smelt *Osmerus eperlanus* (L.) specimens analyzed focusing on the presence of fish larvae in their food

Sampling date	Length range of analyzed smelt (SL, mm)	Number of analyzed specimens
1998		
20-21.04	53-80	40
07-08.05	56-106	263
18-19.05	55-80	24
27-28.05	61-78	3
08-09.06	68-80	14
17-18.06	66-105	21
Total	53-106	365
1999		
07-08.04	42-74	504
18-19.04	41-110	195
28-29.04	45-68	70
11-12.05	42-76	282
25-26.05	47-76	166
08-09.06	55-78	6
21-22.06	64-81	17
Total	44-110	1240
Total		**1605**

1976). The %F coefficient was determined, i.e. the frequency of occurrence (the percentage of smelt whose stomachs contained larvae or fry relative to all smelt analyzed) (Berg 1979). The zooplankton composition was not analyzed in detail.

RESULTS AND DISCUSSION

The number of specimens investigated and the frequency of fish larvae occurrence in the food of smelt *Osmerus eperlanus* (L.) in particular years and months of the investigations are presented in Table 2.

Table 2. Frequency of occurrence (%F) of fish larvae in smelt *Osmerus eperlanus* (L.) food by months of the investigations

	April		May		June		Total	
	98	99	98	99	98	99	98	99
Number of specimens analyzed	40	769	290	448	35	23	365	1240
Number of stomachs with fish larvae	0	48	22	6	13	4	35	58
%F	0.0	6.2	7.6	1.3	37.1	17.4	9.6	4.7

Larvae were confirmed in only 9.6% and 4.7% of the fish investigated in 1998 and 1999, respectively. The frequency of their occurrence (%F) increased as smelt size increased (Table 3), and it peaked during the final periods of the investigations (June, Table 2).

The prey were small larvae ranging in size from 3.5 to 30 mm in 1998 and from 3.7 to 24.6 mm in 1999. The smelt did not seem to have any size preferences. A maximum of eight larvae were confirmed in one stomach. In 1998, the larvae of percid fish constituted the largest group, i.e. 72.5%, followed by smelt – 21.6%. Herring larvae occurred only very sporadically – 2%. The situation was just the opposite in 1999, when herring were most common in the stomachs, i.e. 86.4%, while percid fish constituted only 4.9% and smelt only 2.5% of smelt stomach contents (Table 4). However, in both years the specimens which were most numerous either had a yolk sac or had one which was not entirely resorbed. In 1998, they constituted 67.6% of the percid fish larvae, and in 1999, 77.1% of the herring larvae. Obviously, the presence of the yolk sac, which causes problems with balance, significantly increased the larvae's potential of being preyed upon. Another factor which limits the ability of the larvae to escape at this stage are the small pectoral fin buds (Urho 1999). Herring larvae that are burdened with a yolk sac often swim on their sides or rotate around their body axis. As the size of the yolk sac decreases and other changes in body shape occur, the fish have better spatial orientation (Kryzhanovsky 1956). An increase in herring length from 6.5-8 to 12-14 mm doubles its swimming speed, thus increasing its ability to escape from predators (Blaxter 1969).

The greater number of herring larvae in the smelt food from 1999 in comparison with that of 1998 reflects the significant differences in numbers of larvae in the Vistula Lagoon in these

Table 3. Frequency of occurrence (%F) and size structure of fish larvae in smelt *Osmerus eperlanus* (L.) food by predator size.

	Years	Smelt length class (SL,mm)															
		40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100-104	105-109	110-114	Total
Number of analyzed	98			2	20	56	96	103	51	23	8	1	3		2		365
specimens	99	8	160	455	355	179	56	17	6	1			1		1	1	1240
Number of stomachs	98			0	0	0	4	13	7	6	2	1	2		0		35
with fish larvae	99	0	5	25	15	9	1	0	2	1			0		0	0	58
%F	98			0.0	0.0	0.0	4.2	12.6	13.7	26.1	25.0	100.0	66.7		0.0		9,6
	99	0.0	3.1	5.5	4.2	5.0	1.8	0.0	33.3	100.0			0.0		0.0	0.0	4,7
Number of larvae	98						6	11	9	8	4	5	5				48
measured in food	99		5	27	17	8	1		2								60
Length range	98						3.9-25.0	3.8-20.0	3.7-25.0	3.5-30.0	4.0-5.6	3.6-10.5	4.1-18.0				3.5-30.0
of larvae in food (mm)	99		4.0-6.2	3.7-7.5	4.7-9.7	4.0-24.6	6.0		22.9-23.2								3.7-24.6
Average length	98						7.9	8.0	13.6	12.2	4.9	6.7	8.8				9,4
of larvae in food (mm)	99		5.2	5.3	5.5	7.9	6.0		23.1								6,3

Table 4. Taxonomic structure of fish larvae in smelt *Osmerus eperlanus* (L.) food

	Years	Herring	Smelt	Percid fish	Unidentified	Total
Number of specimens	98	1	11	37	2	51
identified	99	70	2	4	5	81
Percentage of the total	98	2	21.6	72.5	4	
number of specimens	99	86.4	2.5	4.9	6.2	

years. A four-fold increase in their numbers was confirmed from 1998 to 1999 (Margoński 2000). Additionally, ichthyoplankton sampling in 1999 was begun two weeks earlier than in 1998 when the average herring larvae length was 4.8 mm; in 1998 their average length was 9.7 mm at the beginning of sampling (Margoński, interview by author). Many of them had no yolk sac and were thus under less pressure from smelt predation. Other authors present similar herring larvae lengths at which total resorption of the yolk sac occurs: 8.2 mm – Kryzhanovsky (1956); 8.6 mm – Dushkina (1988); 8.7 mm – Ojaveer (1988).

The predominant remaining portion of smelt food consisted of small crustacean plankton, i.e. Copepoda and Cladocera, dominated by *Eurytemora affinis* (Poppe) which is characteristic for the Vistula Lagoon, *Diaphanosoma brachyurum* (Liévin), and *Leptodora kindtii* (Focke), while *Neomysis vulgaris* (J.V. Thompson) and Diptera puppae and imagoes occurred sporadically.

Impact of age group 1 smelt on the mortality of herring larvae is mostly visible during the earliest larval developmental stage, i.e. the yolk-sac stage which lasts for about eight days in the Vistula Lagoon (Dushkina 1988). The numbers of larvae found (51 individuals in 1998 and 81 individuals in 1999) in comparison with the zooplankton mass in smelt stomachs, as well as the low %F coefficient prove that this type of food is consumed rather accidentally. This is confirmed by investigations which were carried out in the Russian part of the lagoon, where smelt feed mainly on plankton (Janchenko 1992). On the other hand, investigations that were carried out in the Elbe River estuary regarding all smelt age groups, revealed that fish are second in importance to mesozooplankton as components of the smelt diet, which makes them as important as macrozooplankton. The values of RI_a(%) (relative importance index) of these components were as follows: 43.87, 26.03 and 25.46, and smelt dominated among the fish consumed (RI_a = 23.74%) (Thiel 2000). Thirteen centimeters is the length at which smelt in the Szczecin Lagoon stop feeding on zooplankton and start to feed on fish and *Neomysis vulgaris* (Wiktor 1964).

The neuston trawl which was used for sampling the material used in the study made it impossible to catch older smelt specimens whose diet would surely be considerably higher in fish.

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6. Podziękowania należy ograniczyć do niezbędnego minimum (inicjały imienia i nazwisko osoby, do której są adresowane, bez wymieniania tytułów naukowych i nazw instytucji).

7. Bibliografię należy zestawiać w porządku alfabetycznym, podając bezpośrednio po nazwiskach autorów rok wydania i wymieniając tylko prace cytowane w tekście (np. Kowalski 1990). Tytuły czasopism – w pełnym brzmieniu. Tytuły prac – w językach oryginału (z wyjątkiem tytułów w języku rosyjskim wydrukowanych alfabetem niełacińskim, np. cyrylicą, które należy przetłumaczyć na język polski lub angielski).

8. Przypisy oznacza się cyfrą arabską we frakcji górnej (...[1]) i numeruje kolejno w całym tekście, z wyjątkiem tabel; treść przypisów – na osobnych stronach.

9. Tabele są dodatkowym źródłem informacji; nie należy powtarzać w nich danych występujących w tekście lub na rysunkach. Tabele numerowane, każda na osobnej stronie, muszą mieć tytuł; powołanie na nie należy umieścić w tekście. Każdą kolumnę w tabeli opatruje się tzw. „główką" wyjaśniającą zawartość kolumny. Przypisy w tabelach należy oznaczyć literami, kursywą, we frakcji górnej (np. Lata[a]), a ich objaśnienie umieścić pod tabelą.

10. Ilustracje. Obowiązuje kolejna numeracja z przywołaniem każdego numeru w tekście. Podpisy pod ilustracjami – na osobnej kartce. Stosowane na rysunkach skróty, terminy i symbole muszą odpowiadać użytym w tekście. Każdy rysunek, umieszczony na osobnej kartce oraz opisany kolejnym numerem i nazwiskiem autora, po wyskalowaniu musi zmieścić sie w kolumnie; trzeba to uwzględnić stosując odpowiednią grubość linii i wielkość opisów na rysunkach. Redakcja przyjmuje wyłącznie rysunki wykonane techniką komputerową (konieczny wydruk i dyskietka). Prace można ilustrować fotografiami (mogą być kolorowe). Łączna objętość rysunków i zdjęć nie może przekraczać 30% objętości pracy.

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Plik powinien być zachowany na dyskietce w takim formacie, aby umożliwić odczytanie go w programach przez nas stosowanych. Preferowanym formatem jest Word for Windows. Rysunki wykonane techniką komputerową prosimy zapisywać na dyskietce w formacie wykonania.

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