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Preliminary description of two new species of Cephalopods (Cephalopoda: Brachioteuthidae) from South Atlantic and Antarctic waters

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Abstract. Two species of cephalopods belonging to the squid family Brachioteuthidae are described for the first time. *Brachioteuthis linkovskyi* sp. nov. is a large brachioteuthid (120 mm mantle length [ML], mature male) collected at night in 720 m water depth using a krill trawl about 600 miles south-east of Montevideo (South Atlantic). Characters differentiating it from other brachioteuthids include: a fibrous net covering the head and arms (at least in mature males), sucker dentition on arms and tentacular clubs, and tentacular club and stalk morphology. *Slosarczykovia circumantarctica* gen. *et* sp. nov. is a large brachioteuthid (150 mm ML, but 170 mm has been reported in the literature), which has often puzzled teuthologists and has been reported previously from the Antarctic waters. Characters of the new genus include subequal suckers on the tentacular clubs and a delicate net of fibrous tissue covering the entire bodies of both sexes for individuals of about 60 mm and longer. The holotype for the new genus and species was collected by a krill trawl in the waters adjacent to the Wilkes Land (Antarctica) in January 1978. *Slosarczykovia circumantarctica* is one of the most common squids in the Antarctic waters and occurs around the Antarctic.

Key words: Systematics, squids, new genus, two new species, SW Atlantic, Antarctic waters

INTRODUCTION

Chaos in the systematics of the family Brachioteuthidae and Architeuthidae (giant squids) is probably greater than in any other squid family. Although giant squids are huge, they break up easily resulting in missing body parts, and they are relatively scarce in the collections. Brachioteuthidae are relatively small and easy to work with, and are relatively common worldwide. Unfortunately, first new species within this family were described from juveniles (*Tracheloteuthis riisei* Steenstrup, 1882 and *T. behni* Steenstrup, 1882) or from damaged specimens (*Brachioteuthis beani* Verrill, 1881). Of the later additions, only *B. picta* Chun, 1910 was well described and illustrated. Russel's type (*Brachioteuthis bowmani* Russel, 1909) went missing and cannot be traced in either English or Scottish museums (C.F.E. Roper, pers. comm.; M.R. Lipinski, in correspondence). Early descriptions, with the notable exception of Chun 1910, have concentrated on poor and/or variable characters. Consequently, all subsequent authors were reluctant to redescribe existing species or describe new ones, (e.g. Nesis 1987,

p. 222-223). This reluctance was understandable, because descriptions of new species without clarifying their relations to those already described would have added to the existing confusion.

The present author has been working intermittently on the family Brachioteuthidae since 1979, planning first to publish redescriptions of good species (*Brachioteuthis riisei* (Steenstrup, 1882) and *B. picta* Chun, 1910), while simultaneously determining the validity of doubtful species and compiling the synonymy. Descriptions of new species were to be published later, because of the possible change of the generic name (from *Brachioteuthis* Verrill, 1881 to *Tracheloteuthis* Steenstrup, 1882). Unfortunately, the author has learnt about the possible publication of a new species of *Brachioteuthis* by two students of cephalopod systematics: Dr A. Salcedo-Vargas and Dr J. Guerrero. This species may be identical with *Slosarczykovia circumantarctica*. However, they are intending to publish their findings under the genus *Lepidoteuthis*. The discussion with them concerning these difficult matters was fruitless. Therefore, it was decided to publish the results somewhat hastily in order to pre-empt further confusion (even if the systematic priority cannot be assured).

MATERIALS AND METHODS

A single individual of *Brachioteuthis linkovskyi* was collected at night on board the R/V PROFESSOR SIEDLECKI in May 1978 using a krill trawl (WP-6) fished in a depth range 720-0 m, some 600 miles south-east of Montevideo (Fig. 1).

Materials for describing *Slosarczykovia circumantarctica* were collected mainly by the late Dr Wiesław Ślósarczyk on board the R/V PROFESSOR SIEDLECKI and the R/V PROFESSOR BOGUCKI during the period of 1978-1984. Some material was collected on board the M/T TAZAR by Dr Z. Witek. Detailed lists of materials (with accurate distribution of samples) will be given in a subsequent publication. Only a small part of the existing collections is used here. The holotype was found opposite of Wilkes Land (Fig. 1) in January 1978 (Station 171 of R/V

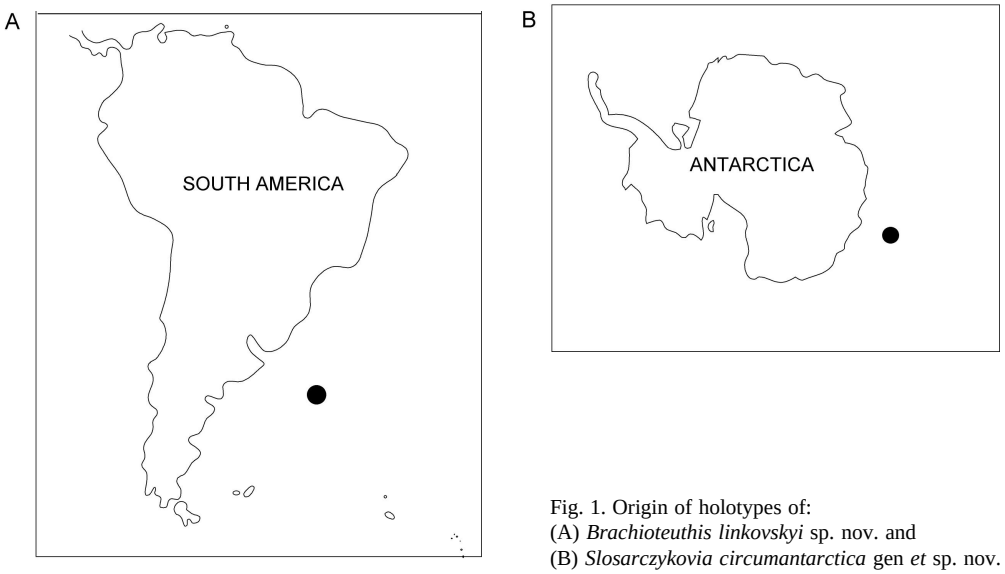


Fig. 1. Origin of holotypes of:
(A) *Brachioteuthis linkovskyi* sp. nov. and
(B) *Slosarczykovia circumantarctica* gen *et* sp. nov.

PROFESSOR BOGUCKI). Paratypes were collected as follows: Sta. 171 (same as the holotype): females 135, 95 and 88 mm ML; Sta. 47 and 48: female 133 mm ML, two males 111 and 114 mm ML; Sta. 175: female 118 mm ML and two males 81 and 82 mm ML; Sta. 168: female 110 mm ML; Sta. 119/08: male 88 mm ML, ?male 75 mm ML and 57 mm ML (sex undetermined). All this material was collected on board the R/V PROFESSOR BOGUCKI. Additional paratypes (all from the FIBEX Expedition January – April 1981): Sta 7/2 (17 Feb. 1981): male 100 mm ML; Sta. 7/2 (15 Feb. 1981): female 145 mm ML, male 103 mm ML, two juveniles 58 and 64 mm ML; Sta. 157/8 (21 March 1981, Admiralty Bay): two females 147 and 150 mm ML.

The new species was described and abbreviations and definitions used were according to Roper and Voss (1983).

DESCRIPTIONS

Familial characteristics

Small squids (up to 20 cm mantle length [ML]) with firm (not gelatinous) body, often muscular. Tentacles, simple funnel locking cartilage, biserial suckers on arms I-IV, DDVV buccal attachments present. Club bears many suckers, at least 50 of them in the proximal part of manocarpal area. Parts of the club are not clearly differentiated. Liver is drawn out ventrally, with relatively sharp anterior apex. Gladius with narrow straight rhachis and relatively wide conus, which forms roughly one-third of the gladius length.

Generic diagnosis

***Brachioteuthis* Verrill, 1881**: skin smooth; reticulate structure and/or warts may occur in mature males (or at least in those approaching maturity). Tentacular club with sharply differentiated suckers; largest from the proximal manus are at least one-half smaller than those from the proximal dactylus. Fixing apparatus usually present (not all species were checked in detail concerning this character).

***Slosarczykovia* gen nov.**: skin in both sexes (from about 60 mm ML) forms a fibrous, delicate net, which covers the whole body (fins, mantle, head and arms). Tentacular club with weakly differentiated suckers; largest from the proximal manus are about one-third or larger than those from the proximal dactylus. Fixing apparatus absent.

Brachioteuthis linkovskyi sp. nov.

Large muscular brachioteuthids (single mature male 120 mm ML after 23 years of preservation, first in formalin and then in ethyl alcohol). Mantle covered by reticulate skin with warts (Fig. 2, 9 and 10). The reticulate skin without warts covers fins, head and arms, but skin on the fins is damaged. Mantle long and slender (MW1I 20, MW2I 18, MW3I 11). Fins drawn into the tail, the reminder to *Todarodes angolensis* Adam, 1962 (FLI 42, FWI 42). Nuchal folds were not found. Olfactory papillae long and prominent. Characteristic but faint V-folds (or ridges) dorsally on the neck and head (from nuchal cartilage to the bases of arms I). Arms relatively short (A1I 45, A2I 61, A3I 56, A4I 50). Arms formula II>III>IV>I. Arm suckers globular and fleshy, stalks short. Sucker rings strong. The largest suckers on the arms have 9-12 teeth (Fig. 3),

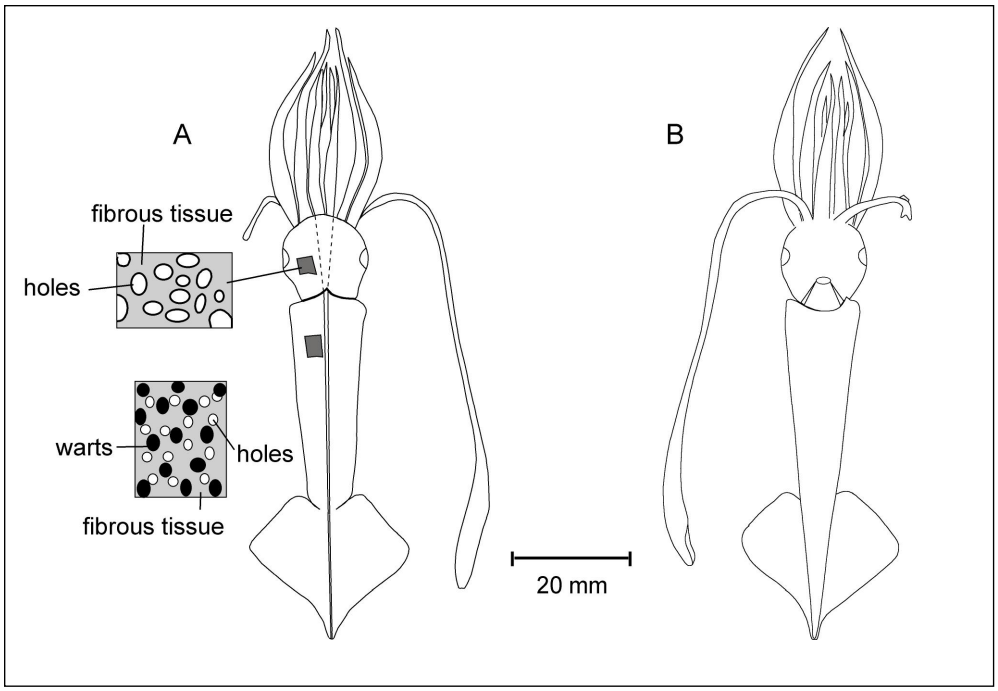


Fig. 2. Holotype of *Brachioteuthis linkovskyi* sp. nov: (A) dorsal view and (B) ventral view.

which may be low and flat, or long and pointed (on arms IV). No apparent sucker enlargement and modification (hectocotylus). Protective membranes on arms damaged, but remnants indicate that they are well developed on the ventral side, with long filiform trabeculae that originate from the bases of the stalks. Each arm has a medial groove instead of a keel. Buccal membrane 8-membered, smooth and without papillae. Lappets attachment DDVV. Tentacles long (TLI 142) and club long (CLI 37). Parts of the club not clearly differentiated (Fig. 4 and 11). Protective membranes strongly developed, with long trabeculae; swimming membranes well developed. Fixing apparatus present, but it could not be adequately described because of the damage to the stalks. About 15 of densely packed rows of minute suckers on manus. Characteristic sucker pad on the tip of the club (Fig. 4). Suckers on a proximal dactylus much larger, x2.5-4 than largest suckers on proximal manus. Largest sucker ring has 14 sharp, long, fairly uniformly spaced teeth (Fig. 3). Thick luminous tissue on the ventral side of the eyeball (Fig. 5). Eye sinus present. Funnel organ with very large ventral pads and relatively short papilla on the dorsal component. Anal papilla attached between and around mid-length of the dorsal pads (Fig. 6). Liver relatively flat, covered ventrally (Fig. 5).

Beaks, gladius and spermatophores will be described in the subsequent paper. Basic measurements are provided in Table 1.

Slosarczykovia circumantarctica gen. *et* sp. nov.

Large muscular brachioteuthids (largest measure female 150 mm ML, largest measured male 95 mm ML after 20-23 years of preservation, first in formalin and then in ethyl alcohol). Fins, mantles, heads and arms in both sexes (excluding juveniles smaller than 60 mm ML) covered

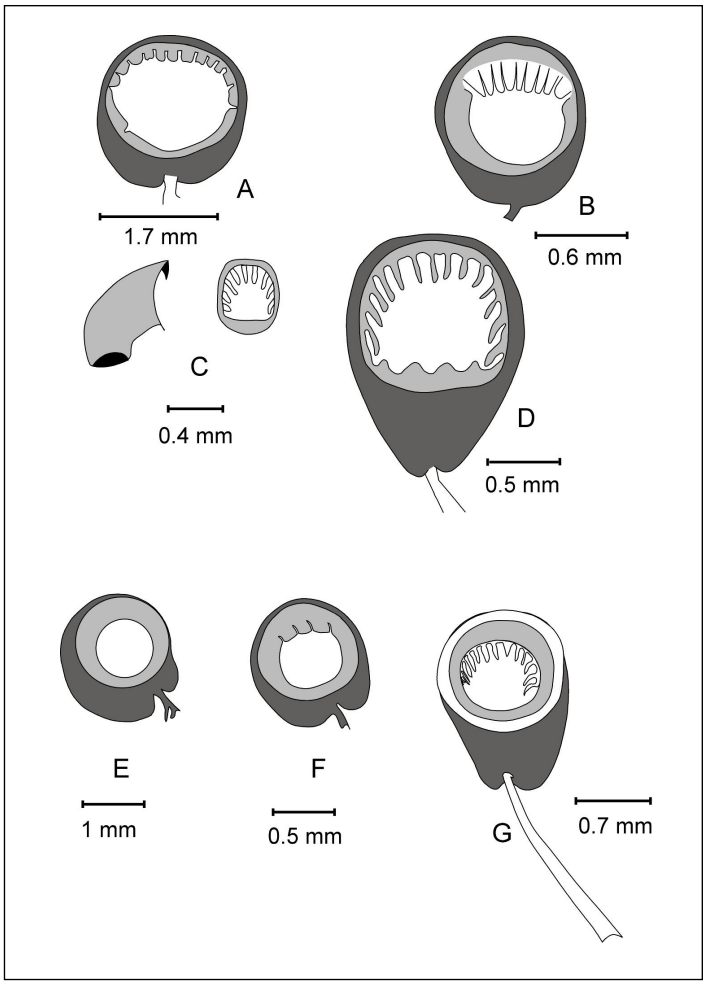


Fig. 3. Suckers of *Brachioteuthis linkovskyi* sp. nov. (A-D) and *Slosarczykovia circumantarctica* gen. *et* sp. nov. (E-G): (A) 14th sucker from A2; (B) 12th sucker from A4; (C) sucker from the middle of the proximal manus on tentacular club; (D) largest sucker from the proximal dactylus on tentacular club; (E) 10th sucker from A2 (female); (F) 10th sucker from A4 (male); (G) largest sucker on the proximal dactylus on tentacular club. All suckers taken from the left arms/tentacular clubs.

by the reticulate skin, looking like delicate fish-net (Fig. 7, 9 and 10). No warts on mantles of maturing males (III-IV according to scale by Lipinski and Underhill 1995). Mantle long and relatively slender (MW1 19, MW2I 21, MW3I 19). Fins romboid (FLI 40, FWI 55). Olfactory organ in the form of small and flat protuberance. Nuchal folds straight and inconspicuous. Characteristic and strong V-folds (ridges) dorsally on the neck and head, from nuchal cartilage to the bases of arms I. Arms short (females: A1I 34, A2I 46, A3I 42 A4I 36; males: A1I 35, A2I 47, A3I 42, A4I 40.). Arm formula II>III>IV>I. In females, sucker rings of arms I-IV smooth (Fig. 3). In males, 1-4 low, inconspicuous teeth may be present. Suckers on arms globular and fleshy. Sucker rings strongly developed. Stalks short. No sucker enlargement and/or modification (no hectocotylus). Protective membranes low dorsally and well developed ventrally, with long

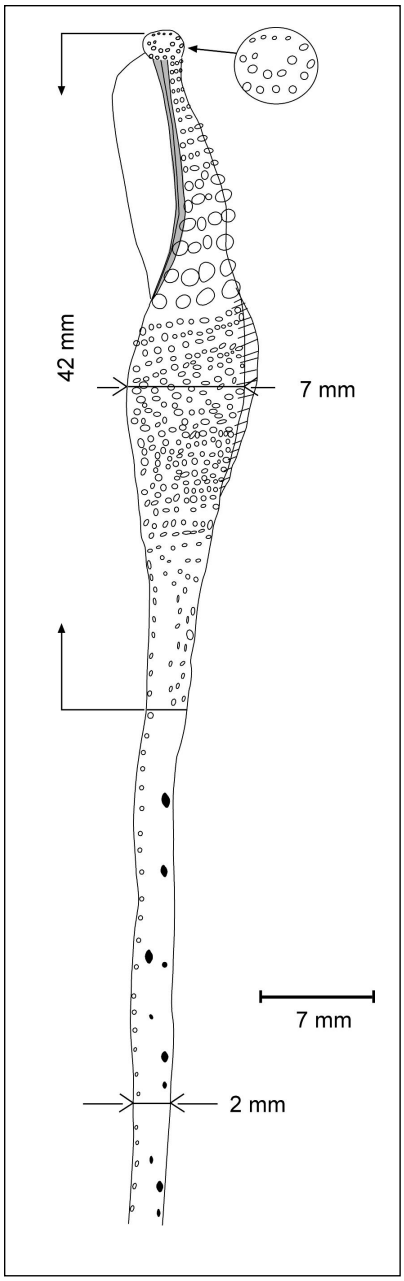
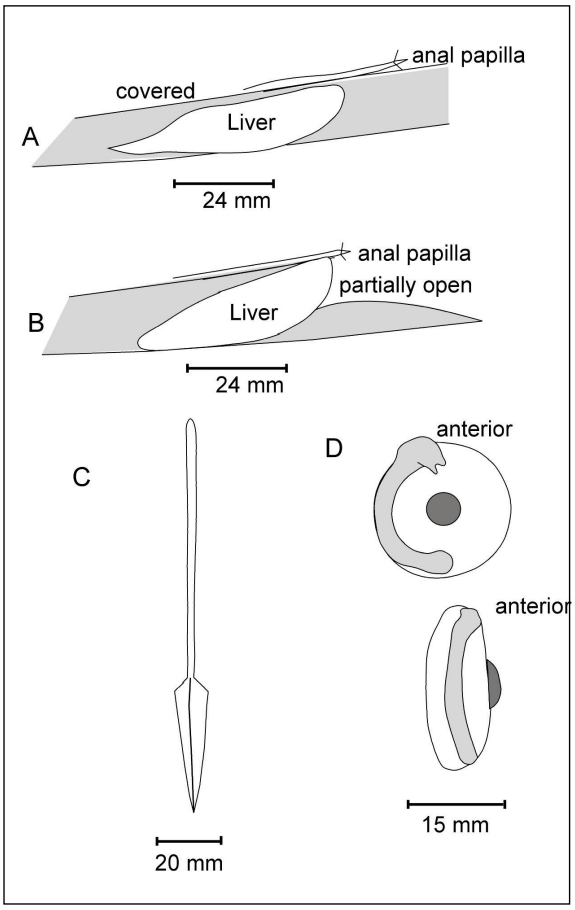


Fig. 4. Left tentacular club of *Brachioteuthis linkovskyi* sp. nov.

Fig. 5. (A) Liver of *Brachioteuthis linkovskyi* sp. nov.; (B) Liver of *Slosarczykovia circumantarctica* gen. *et* sp. nov.; (C) Gladius of *Slosarczykovia circumantarctica*; (D) Eyeball of *B. linkovskyi*



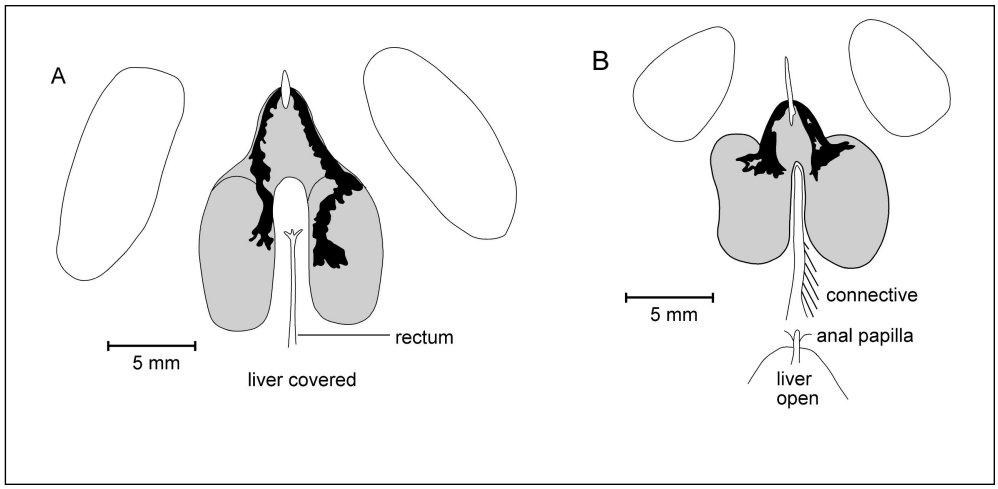


Fig. 6. Funnel organs of:
(A) *Brachioteuthis linkovskyi* sp. nov. and (B) *Slosarczykovia circumantarctica* gen. *et* sp. nov.

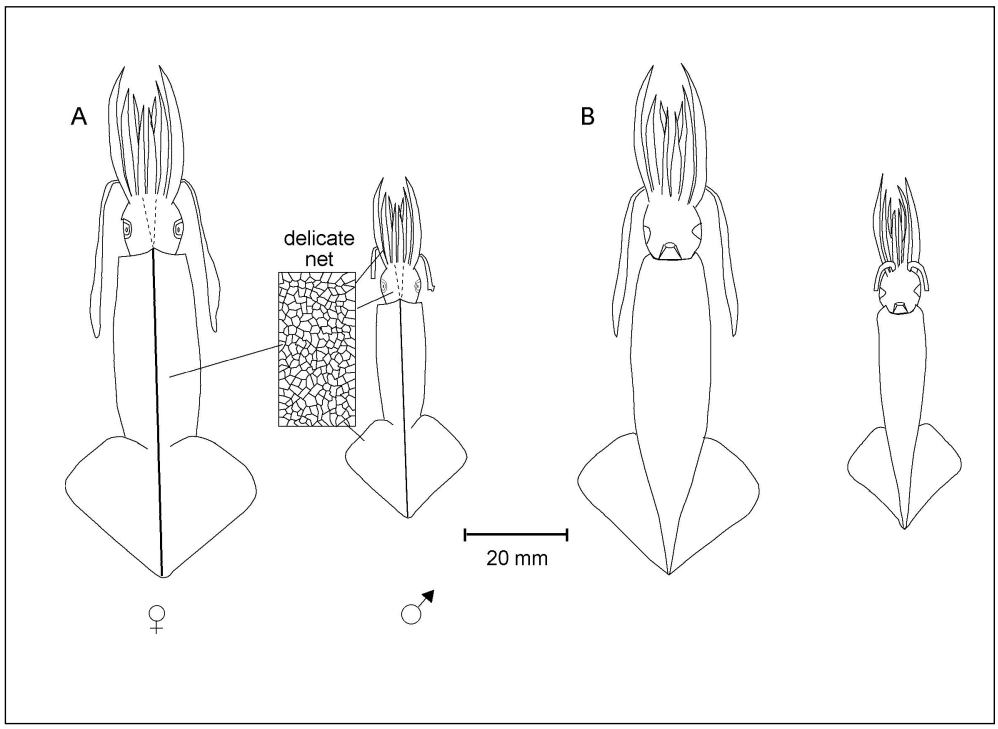


Fig. 7. *Slosarczykovia circumantarctica* gen. *et* sp. nov.:
(A) dorsal view and (B) ventral view of a female and a male

Table 1. Basic measurements [in mm] of the holotypes and paratypes of the *Brachopteuthis linkovskyi* sp. nov. and *Slosarczykovia circumentartica* gen. et sp. nov. Maturity II-III (Lipinski and Underhill 1995).

	B. linkovskyi holotype	*S. circ.* holotype Sta. 171B	FIBEX Sta.7:2 female	FIBEX Sta. 7:2 male	Sta. 171B female	Sta. 171B female	Sta. 168B female	FIBEX Sta. 7:2 male	Sta. 119:8 B male	Sta. 119:8 B male??	Sta. 119:8 B juv.	FIBEX Sta. 157:8 female	FIBEX Sta. 157:8 female	Sta. 175B female	Sta. 175B male	Sta. 175B male	Sta. 47:48 B female	Sta. 47:48 B male	Sta. 47:48 B male
ML	120	128	147	101	134	90	110	97	88	74	58	150	147	117	80	79	133	113	115
MW1	24	n. meas.	28	21	n. meas.	n. meas.	n. meas.	21	18	16	10	30	30	26	16	19	27	23	n. meas.
MW2	22	n. meas.	29	23	n. meas.	17	n. meas.	21	18	15	10	34	32	32	17	16	34	23	n. meas.
MW3	13	n. meas.	25	18	n. meas.	15	n. meas.	16	17	13	8	26	26	23	12	13	27	19	n. meas.
FL	50	52	65	45	60	38	43	46	43	37	29	66	60	50	36	38	55	50	51
FW	50	76	80	55	80	56	60	52	49	46	35	85	73	70	48	51	75	62	60
A1	54	46	48	34	43	36	30	34	35	22	15	50	50	42	28	25	44	36	38
A2	73	55	63	49	58	47	48	45	39	33	28	64	64	57	38	34	57	49	46
A3	67	51	60	46	55	45	43	42	37	31	27	57	58	56	35	34	54	44	42
A4	60	48	48	43	47	38	37	39	33	28	20	54	52	49	31	30	46	38	40
TL	pt missing	90	90	missing	missing	missing	missing	missing	missing	65	55	missing	missing	missing	missing	missing	missing	missing	missing
TR	120	80	90	missing	missing	missing	missing	missing	missing	missing	58	missing	missing	missing	missing	missing	damaged	missing	missing
CL	45	42	50	missing	missing	missing	missing	missing	missing	27	25	missing	missing	missing	missing	missing	damaged	missing	missing
CW	7	7	5	missing	missing	missing	missing	missing	missing	4,5	3	missing	missing	missing	missing	missing	damaged	missing	missing
HL	23	n. meas.	27	24	25	23	22	19	19	17	13	25	21	25	19	17	damaged	20	22
HW	25	n. meas.	24	21	20	15	22	20	20	16	13	24	22	25	16	12	damaged	18	22
S2	1,7	1	n.meas.	n.meas	n.meas	n.meas	n.meas	n. meas.	n. meas.	n. meas	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.
ST	1	0,7	n.meas	n.meas	n.meas	n.meas	n.meas	n. meas.	n. meas.	n. meas	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.
STM	0,4	0,5	n.meas	n.meas	n.meas	n.meas	n.meas	n. meas.	n. meas.	n. meas	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.
GL	n. meas.	n.meas.	n.meas	n.meas	n.meas	n.meas	120	n. meas.	n. meas.	n. meas	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.	n. meas.

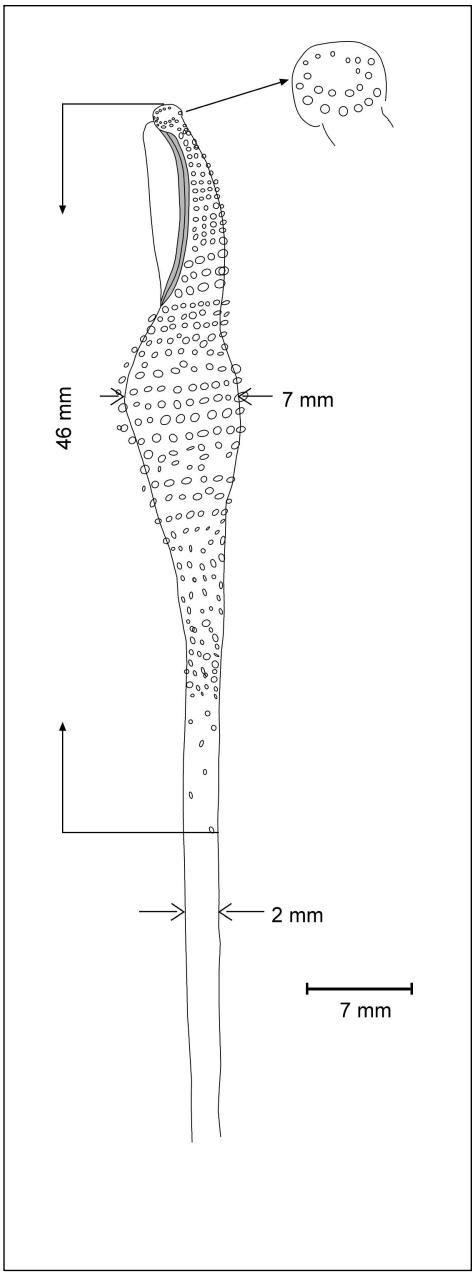


Fig. 8. Left tentacular club of *Slosarczykovia circumantarctica* gen. *et* sp. nov.

filiform trabeculae that originate from the bases of the stalks. Each arm has a median groove instead of a keel. Buccal membrane fleshy, with many papillae in females, or smooth in males. This may indicate that spermatophores are attached there. Buccal lappets attachment DDVV. Buccal membrane 8-membered. Tentacles short (TLI 75) and club long (CLI 33). Parts of the club not clearly differentiated (Fig. 8 and 11). No apparent fixing apparatus. Seven small suckers at the base of the club (on the stalk). Approximately 10 loose rows of suckers on manus (not crowded, but rather sparsely distributed). Diameter of the largest sucker on the proximal dactylus only about one-third larger than the largest sucker on manus. Overall, suckers on the club appear subequal, except on marginal row dorsally and on the stalk, where suckers are minute. There are 11-13 sharp, long teeth on the rings of largest suckers on the club (Fig. 3). Thin luminous tissue around the lens, but not on the ventral side of the eyeball. Eye sinus prominent. Funnel organ very distinct, with relatively small ventral pads and very long papilla on the dorsal component (Fig. 6). Anal papilla far away from the funnel organ. Gladius with long, narrow, straight rhachis and well developed conus (33% of the GL) (Fig. 5). Liver globular, partially open ventrally (Fig. 6). Basic measurements are provided in Table 1.

Etymology

Following a long tradition, *Brachioteuthis linkovskyi* is named after Dr T. B. Linkowski (Sea Fisheries Institute, Gdynia), who found the specimen from collections taken on board the R/V PROFESSOR. SIEDLECKI during the Open Ocean Expedition in 1978. The generic name *Slosarczykovia* was derived from the surname of the late Dr Wiesław Ślósarczyk, who collected almost all the material, and the specific name *circumantarctica* denotes the circumantarctic distribution of the species.

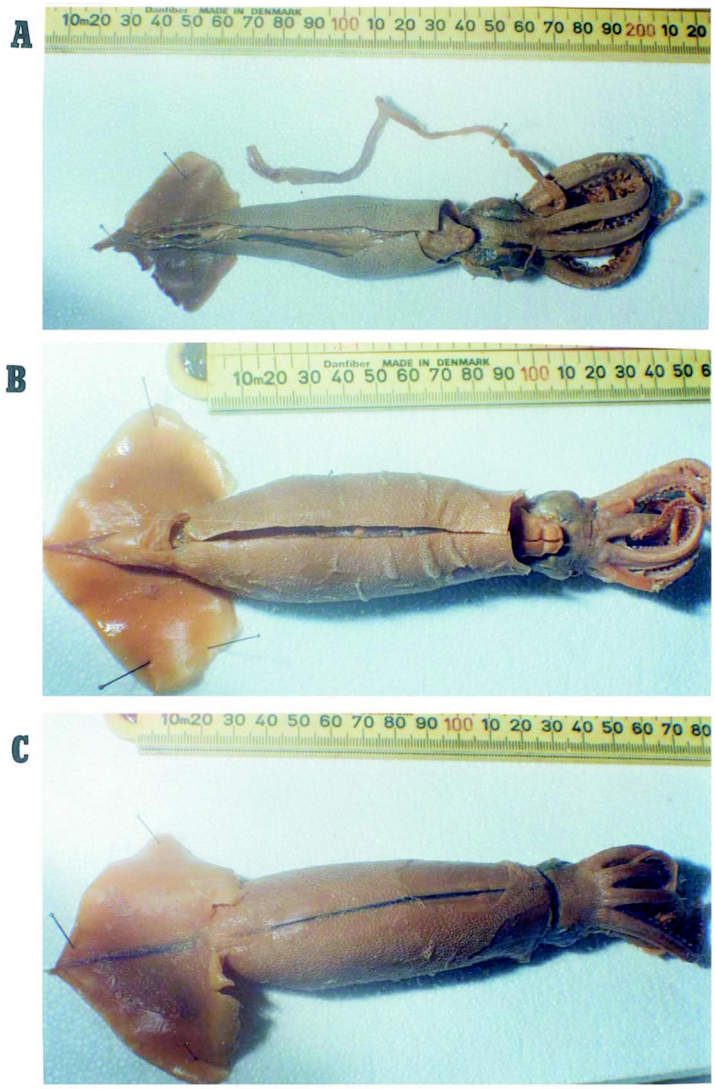


Fig. 9. Photographs of: (A) *Brachioteuthis linkovskyi* sp. nov., ventral view; (B) *Slosarczykovia circumantarctica* gen. *et* sp. nov., female, ventral view; (C) *Slosarczykovia circumantarctica*, female, dorsal view.

Deposition

Both holotypes and paratypes of *Slosarczykovia circumantarctica* are deposited in the South African Museum, P.O. Box 61, Cape Town 8000, South Africa. The collection register numbers are as follows: *Brachioteuthis linkovskyi*: S-3948; *Slosarczykovia circumantarctica*: S-3949 (holotype) and S-3950 (paratypes).

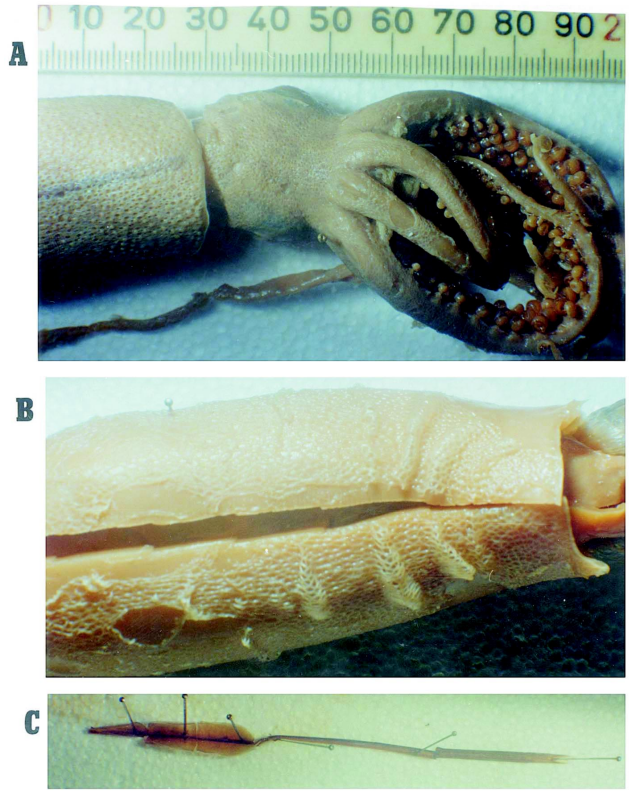


Fig. 10. Photographs of: (A) *Brachioteuthis linkovskyi* sp. nov., anterior mantle, head and arms dorsally, showing warts on the mantle and the reticulate structure on the head; (B) *Slosarczykovia circumantarctica* gen. *et* sp. nov., mantle ventrally, showing the reticulate skin; (C) *Slosarczykovia circumantarctica*, gladius.

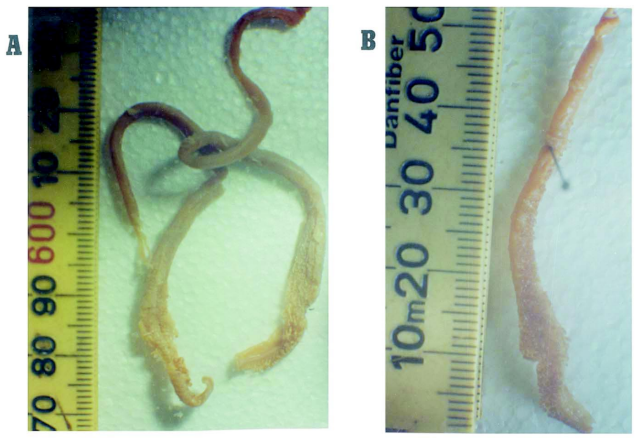


Fig. 11. Tentacular clubs of: (A) *Brachioteuthis linkovskyi* sp. nov.; (B) *Slosarczykovia circumantarctica* gen. *et* sp. nov.

DISCUSSION

The revision of the family Brachioteuthidae presents interesting challenges. There are some surprising results, such as the fact that it is not the family of "circumglobal" species as generally believed. Most species seem to be rather localized. Also, it is not a family without characters of systematic significance as is often thought. In this paper, attention is drawn to the following: body cover; tentacles and tentacular club (probably the single most important diagnostic character in the family); sucker dentition; funnel organ; and internal anatomy (e.g. liver). There are some other characters, such as the hectocotylus (well-developed in *Brachioteuthis riisei*), the gladius (see the excellent gladius drawing of *Brachioteuthis riisei* in Bizikov, 1996 p. 55, which is markedly different from the gladius of *Lepidoteuthis* that is illustrated on the same page) and anatomy of the reproductive organs, among others.

To the author's knowledge, there are no previous records of *Brachioteuthis linkovskyi* in the literature. There are, however, numerous references to *Slosarczykovia circumantarctica*. The earliest was probably in Roper, (1969, p. 193-194) under *Brachioteuthis picta* Chun, 1910. Filippova (1972) and Nesis (1987) clearly identified *Slosarczykovia circumantarctica* as a new species. Rodhouse (1989) also recorded it under *Brachioteuthis ? picta*, with the short discussion pointing out its common occurrence around the Antarctic Peninsula.

Acknowledgements. *Many people contributed to this work over the years, but I would like to particularly acknowledge the great input of the late W. Ślósarczyk who collected many specimens for this work, most of them from the Antarctic. C. Boucher, J.H.M. David and S. Pillar helped with manuscript preparation.*

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Status of arrow worms (Chaetognatha) in the southern Baltic Sea

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Abstract. The occurrence of chaetognaths (*Sagitta elegans* and *Sagitta setosa)* was analyzed in three regions of the southern Baltic Sea: the Bornholm Deep, the Słupsk Furrow and the Gdańsk Deep. It was confirmed that chaetognaths are brought into the Baltic with inflows of saline waters from Kattegat. From the moment of inflow chaetognaths do not feed, or do so sporadically, and neither their size structure nor their gonadal development stage change. Based on this information, it can be stated that chaetognaths in the Baltic are allochthonous and that they constitute a pseudo-population which is renewed with saline water inflows from Kattegat.

Key words: Chaetognatha, *Sagitta elegans, Sagitta setosa,* southern Baltic Sea.

INTRODUCTION

Despite the fact that investigations of Baltic fauna date back over a hundred years (Moebius 1887, Aurivillius 1896, Brandt 1897), the status of certain Baltic species has still not been completely described. The best example of this is the Baltic Sea chaetognaths (genus *Sagitta*).

There are two species of this planktonic predator in the Baltic Sea: *Sagitta elegans* Verril and *Sagitta setosa* J. Mueller (Mańkowski 1950, Różańska 1978, Maciejewska 1992).

In general, chaetognaths are oceanic animals which most often inhabit the epipelagic zone (Sameoto 1966, Kuhlmann 1977, Terazaki *et al.* 1995). Due to the low salinity of its surface waters (5-7 PSU), the Baltic Sea lies at the periphery of waters in which chaetognaths occur. In the southern Baltic Sea they can be found in the more saline near-bottom waters that flow into the Baltic Sea through the Danish Straits from Kattegat (Różańska 1971, 1978, Mańkowski 1978). Baltic Sea chaetognaths differ from the same species which inhabits the North Sea. Two Baltic subspecies have even been identified: *Sagitta elegans elegans* and *Sagitta elegans baltica* (Ritter-Zahony 1911, Mańkowski 1950, 1959, Różańska 1978, Maciejewska 1992). Their distribution in the water column also differs from that of chaetognaths in highly saline waters (Maciejewska 1992).

Features such as morphological changes, atypical gonad development, the absence of the youngest age groups and breeding specimens and the lack of food in the digestive track (Różańska 1971, 1978, Maciejewska 1992) may indicate that Baltic Sea chaetognaths neither form local populations or local subspecies nor are they endemic to the Baltic Sea. Rather, they are an

allochthonus element brought in from the North Sea to the Baltic Sea where they form short-term pseudo-populations.

The aim of this work was to verify the hypothesis that chaetognaths (*Sagitta elegans* and *Sagitta setosa*) are not an autochthonous element of the Baltic fauna. They are brought into the Baltic with inflows of saline waters from Kattegat and that they are non-reproductive pseudo-populations.

MATERIALS AND METHODS

Chaetognath specimens were collected during six cruises of the R/V BALTICA in July 1993, August and September 1994, June and September 1995 and September 1996. The material was collected in regions of potential chaetognaths occurrence, i.e. the Bornholm Deep, the Słupsk Furrow and the Gdańsk Deep (Fig. 1).

Bongo nets with 333 and 500 µm mesh sizes were used. Oblique hauls were applied which sampled the waters from the surface to a depth of about 5 meters above the sea bottom. Other types of fishing gear used included 2-meter diameter MIK with 2 mm mesh-size net

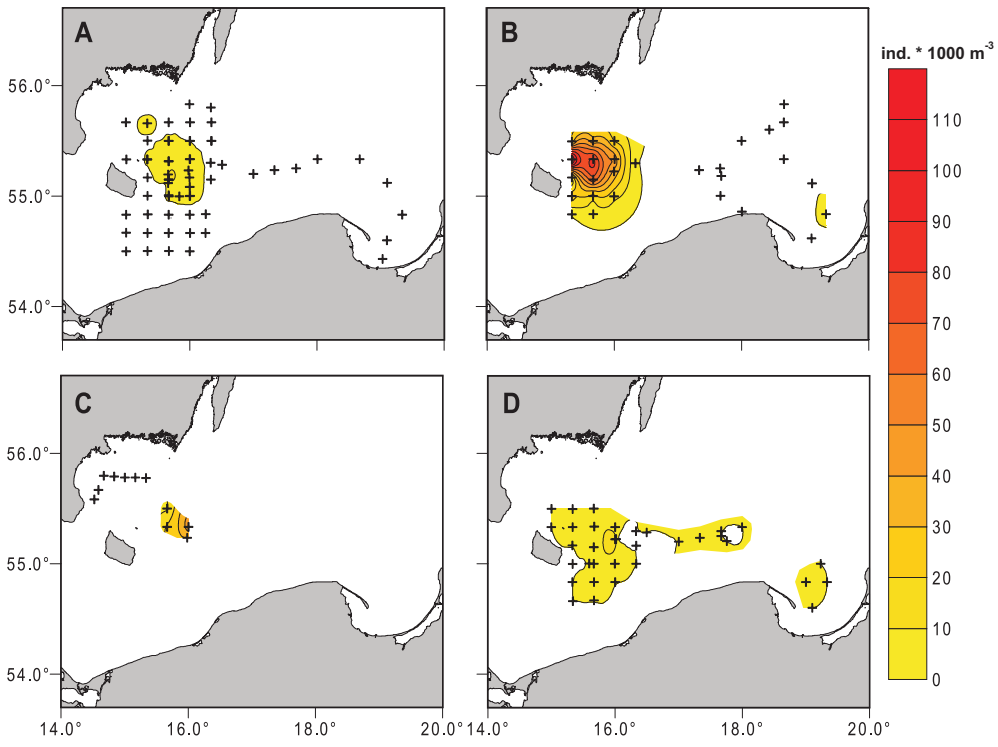

Fig. 1. Occurrence of chaetognaths in the southern Baltic Sea (Bongo 333 µm) and their abundance (ind. · 1,000 m^{-3}) in 1993-1996. Crosses denote catch sites.
A – July/August 1993; B – August 1994; C – September 1994, D – June 1995.

(500 µm in the cod-end) and a Multinet net with a 0.25 m^2 opening and 300 µm mesh nets. The latter was used to collect stratified samples in ten meter water layers to a depth of 80 m. The volume of filtered water was measured using a flowmeter.

The plankton material collected was preserved in 4% formaldehyde and the chaetognaths were separated out and, based on their numbers in the sample and the volume of filtered water, the animal abundance was determined (ind. · 1,000 m^{-3}).

The length and maturity of the animals were determined. The four-degree scale applied by Russel (1932), Różańska (1971) and Maciejewska (1992) was used to determine the stage of gonadal development. On this scale, 0 denotes larvae, 1 specimens without visible gonads, 2 specimens with small oocytes and 3 animals with mature oocytes. Since the ovaries of Baltic Sea chaetognaths can be anomalous (Maciejewska 1992), the third stage for *Sagitta elegans* was divided into groups 3a and 3b, where only the latter denotes sexually mature specimens.

The level of digestive tract fullness was determined through microscope observations.

Data regarding saline water inflows from Kattegat into the southern Baltic Sea, their ranges and duration, as well as the hydrological conditions in the areas of their impact were taken from the paper of Wojewódzki (1996).

RESULTS

Area of chaetognath occurrence

A total of 921 plankton samples collected in the 1993-1996 period in areas of potential chaetognath occurrence were analyzed. The regions were the Bornholm Basin, the Słupsk Furrow and the Gdańsk Deep (Fig. 1).

A total of 1,709 specimens of *S. elegans* were collected in the 1993-1996 period. This species occurred in the Bornholm Deep throughout the investigation period and in 1994 and 1995 it occurred in the Gdańsk Deep, although only single specimens were noted each time. This species was observed in the Słupsk Furrow in June 1995. The mean abundance of *S. elegans* observed in the Bornholm Deep dropped from 33.1 ind. · 1,000 m^{-3} in August 1994 to 0.1 ind. · 1,000 m^{-3} in August 1996 (Table 1).

Sagitta setosa occurred less frequently than *S. elegans*. A total of 116 specimens of this species were caught in the 1993-1996 period. Its occurrence was confirmed only in 1993-1995 and mostly in the Bornholm Deep. Its mean abundance ranged between 0.2 to 0.5 ind.· 1,000 m^{-3} (Table 1).

Vertical distribution of chaetognaths in the water column

The Multinet facilitated collecting plankton samples from discrete water layers. Single specimens of *Sagitta elegans* were noted in the 40-50 m layer. Their mean abundance increases with depth from 0.4 to 124.4 specimens in 1,000 m^3 (Table 2) with the maximum in the near bottom layers at 70-80 m.

The analysis of environmental conditions in water layers in which *S. elegans* occurred indicates that this species was found in low temperatures (8-3.8°C) and high salinity (15-17 PSU), although it may occur in waters with a salinity of 11-12 PSU. Only single specimens are noted at lower salinity levels (9.1 PSU in the 40-50 m layer) (Table 2).

Table 1. Number of plankton samples taken (Bongo 333 µm) in the Bornholm Deep, the Słupsk Furrow and the Gdańsk Deep in the 1993-1996 period, percentage of samples with no chaetognaths and their average abundance

			Sagitta elegans			*Sagitta setosa*		
Sampling area	Sampling period	Number of stations	Percentage of samples with no cheatognaths	Average abundance ($n \cdot$ 1,000 m^{-3})	SD	Percentage of samples with no cheatognaths	Average abundance ($n \cdot$ 1,000 m^{-3})	SD
Bornholm Basin	1993 July-August	53	69.8	1.9	5.7	100	0	
	1994 August	15	13.3	33.1	35.6	100	0	
	1994 September	11	63.6	9.7	16.1	90.9	0.5	1.6
	1995 June	23	56.5	2.5	4.5	95.7	0.2	0.9
	1995 September	24	12.5	0.2	0.6	100	0	
	1996 August	36	91.7	0.1	0.5	100	0	
Słupsk Furrow	1993 July	5	100	0		100	0	
	1994 August	4	100	0		100	0	
	1995 June	5	80.0	0.6	1.6	100	0	
	1995 September	1	100	0		100	0	
	1996 August	11	100	0		100	0	
Gdańsk Deep	1993 July	5	100	0		100	0	
	1994 August	7	85.7	0.2	0.4	100	0	
	1995 June	4	75.0	0.3	0.6	75.0	0.3	0.6
	1996 August	8	100	0		100	0	

Table 2. Average abundance of *Sagitta elegans* (ind. · 1,000 m^{-3}) and hydrological parameters at various depth strata in the Bornholm Deep

Depth (m)	Parameter	1993 July	1994 August	1994 September	1995 June	1996 August
0-40	T (°C)	12.3	12.6	13.0	9.0	11.1
	Sal (PSU)	7.5	7.4	7.4	7.6	7.2
	O_2 (ml · l^{-1})	6.8	6.2	6.1	7.8	7.0
	Abundance	0	0	0	0	0
	SD					
40-50	T (°C)	5.6	5.0	5.2	5.7	5.1
	Sal (PSU)	7.5	9.1	9.0	8.1	9.0
	O_2 (ml · l^{-1})	5.2	4.4	4.1	7.3	6.1
	Abundance	0	**0.4**	0	0	0
	SD		**1.0**			
50-60	T (°C)	8.0	6.4	6.9	5.0	5.1
	Sal (PSU)	12.0	12.7	12.4	9.6	11.9
	O_2 (ml · l^{-1})	3.5	3.6	2.8	5.4	5.0
	Abundance	**0.1**	**2.2**	**8.2**	**2.3**	**0.4**
	SD	**0.6**	**1.6**	**6.9**	**2.0**	**0.8**
60-70	T (°C)	5.2	4.2	5.5	5.0	3.8
	Sal (PSU)	14.8	15.2	15.4	13.8	14.1
	O_2 (ml · l^{-1})	3.5	2.4	1.9	1.7	2.5
	Abundance	**5.6**	**23.6**	**71.8**	**18.4**	0
	SD	**4.4**	**13.0**	**52.7**	**15.8**	
70-80	T (°C)	4.4	4.4	3.9	5.6	4.9
	Sal (PSU)	17.2	16.4	17.2	16.3	15.7
	O_2 (ml · l^{-1})	3.1	1.2	1.6	0.7	0.4
	Abundance	**27.6**	**56.4**	**124.4**	**41.1**	**0.4**
	SD	**30.2**	**24.5**	**17.6**	**47.8**	**0.9**

It appears that low oxygen levels in the water are well tolerated by *S. elegans*; the highest abundance was confirmed in the near bottom layer where oxygen levels even dropped below 1 ml · l^{-1}. The numbers of *S. elegans* were much lower (from 0 to 71.8 specimens in 1,000 m^3 – Table 2) in the 60-70 m layer at higher oxygen levels (1.7-3.5 ml · l^{-1}) and comparable temperatures (3.8-5.5°C) and salinity levels (13.8-15.4 PSU).

Sagitta setosa occurred in the upper layers of the water column and was found even in the 10-20 m layer where the temperature reached 15.2°C, the salinity was 7.4 PSU and the oxygen level was 6.6 ml · l^{-1} (Table 3). The highest abundance of this species (10.7 ind. · 1,000 m^{-3}) was found in the 40-50 m layer.

Analysis of the environmental conditions in which *S. setosa* occurs indicates that this species prefers temperatures in the 5-12° C range, salinity of 7-13 PSU and oxygen levels over 4 mg · l^{-1} (Table 3).

Since *S. setosa* was noted in the samples sporadically, the observations above refer to three series of samples (July 1993, August and September 1994) which may be affected by inter-seasonal influence.

The comparison of the occurrence of *Sagitta elegans* and *Sagitta setosa* in particular layers in the water column in the Bornholm Deep indicates that these species do not occur together. *S. setosa* occurs in the upper layers (10-60 m), while *S. elegans* occurs in the lower layers (40-80 m) of the water column (Table 4). Only in the 50-60 m layer were both species

Table 3. Average abundance ($n \cdot 1{,}000\ m^{-3}$) of *Sagitta setosa* and hydrological parameters at various depth strata in the Bornholm Deep

Depth (m)	Parameter	1993 July	1994 August	1994 September
0-10	T (°C)	15.8	18.1	16.5
	Sal (PSU)	7.3	7.3	7.3
	O_2 (ml · l^{-1})	6.9	6.5	6.5
	Abundance	0	0	0
	SD			
10-20	T (°C)	15.2	17.2	16.6
	Sal (PSU)	7.4	7.3	7.3
	O_2 (ml/l)	6.6	6.1	6.1
	Abundance	**0.5**	0	0
	SD	**2.1**		
20-30	T (°C)	11.7	10.5	12.1
	Sal (PSU)	7.5	7.3	7.3
	O_2 (ml · l^{-1})	6.7	5.8	6.0
	Abundance	0	0	**4.6**
	SD			**10.2**
30-40	T (°C)	5.9	6.6	6.5
	Sal (PSU)	7.8	7.5	7.5
	O_2 (ml · l^{-1})	6.8	5.9	5.7
	Abundance	**4.5**	**4.1**	0
	SD	**10.5**	**10.0**	
40-50	T (°C)	5.6	4.9	5.2
	Sal (PSU)	8.8	8.5	9.0
	O_2 (ml · l^{-1})	5.2	4.4	4.1
	Abundance	0	0	**10.7**
	SD			**10.0**
50-60	T (°C)	8.0	6.4	6.9
	Sal (PSU)	7.9	12.1	12.4
	O_2 (ml · l^{-1})	3.5	3.6	2.8
	Abundance	0	0	**5.7**
	SD			**12.8**
60-70	T (°C)	5.2	4.6	5.5
	Sal (PSU)	14.8	14.7	15.4
	O_2 (ml · l^{-1})	3.5	2.4	1.9
	Abundance	0	0	0
	SD			
70-80	T (°C)	4.4	3.8	3.9
	Sal (PSU)	17.2	17.0	17.2
	O_2 (ml · l^{-1})	3.1	1.2	1.6
	Abundance	0	0	0
	SD			

observed in September 1994. It seems that this was the result of the high salinity (12.4 PSU) in this layer which is tolerated by *S. setosa* and required by *S. elegans*. In 21 other cases of chaetognath occurrence in particular water layers, the presence of one species excluded that of the other (Table 4).

Table 4. Co-occurrence of *Sagitta elegans* (S.e.) and *Sagitta setosa* (S.s) in the Bornholm Deep

Depth	1993 July	1994 August	1994 September	1995 June	1995 September	1996 August
0-10						
10-20	S.s					
20-30			S.s			
30-40	S.s	S.s		S.s		
40-50		S.e	S.s			
50-60	S.e	S.e	S.e S.s	S.e		S.e
60-70	S.e	S.e	S.e	S.e		
70-80	S.e	S.e.	S.e	S.e		S.e

Length distribution of the chaetognath population

Length distribution analysis could only be carried out for *Sagitta elegans* based on the series of samples collected in July 1993, August and September 1994 and in June 1995. The very small number of animals caught in September 1995 (4 specimens) and in August 1996 (7 specimens) did not permit this kind of analysis (Fig. 2).

The smallest specimens of *S. elegans* caught were 6 mm long (September 1994, 3 specimens). Only 56 specimens shorter than 10 mm were caught in the 1993-1996 period. The largest number of animals were specimens 10-20 mm in length, while only 32 specimens caught were longer than 20 mm (21-22 mm). The 17-18 mm size classes were the most abundant ones – 25% in July 1993 and 32% in September 1994 (Fig. 2).

The length distibution of the *S. elegans* population were very similar in 1993 and 1994. However, the 18 mm class more clearly dominated in 1995 when 31% of the specimens belonged to it and 70% of the specimens were in the 17-19 mm classes (Fig. 2).

Sagitta setosa specimens ranged in length from 8 to 14-15 mm. Due to the small number of specimens caught, it is difficult to discuss the size structure of the population, however, in July 1993 and in September 1994 two abundance peaks are distinguishable in the 10 mm and 13 mm length classes (Fig. 3). The dearth of material does not allow for the formulation of any conclusions regarding the occurrence of two cohorts of this species.

Sexual maturity

Chaetognath gonadal development was determined using a four-degree scale. The presence of the youngest specimens of *Sagitta elegans* (gonadal development = 0) was noted only in 1993-1994 (48 specimens or 12.4% of all animals analyzed). Specimens in the second stage of gonad development dominated comprising from 49 to 67% of all the specimens. Only 3-4% of the population were mature specimens which were ready to spawn (Table 5). In 1995-1996 larvae and specimens which were ready to spawn did not occur at all.

Analysis of the maturity of *Sagitta setosa* is impossible due to the very small number of animals caught. *S. setosa* appeared only in 1993-1994 and animals in the second degree of gonad development dominated (Table 6). Sexually mature animals did not appear at all.

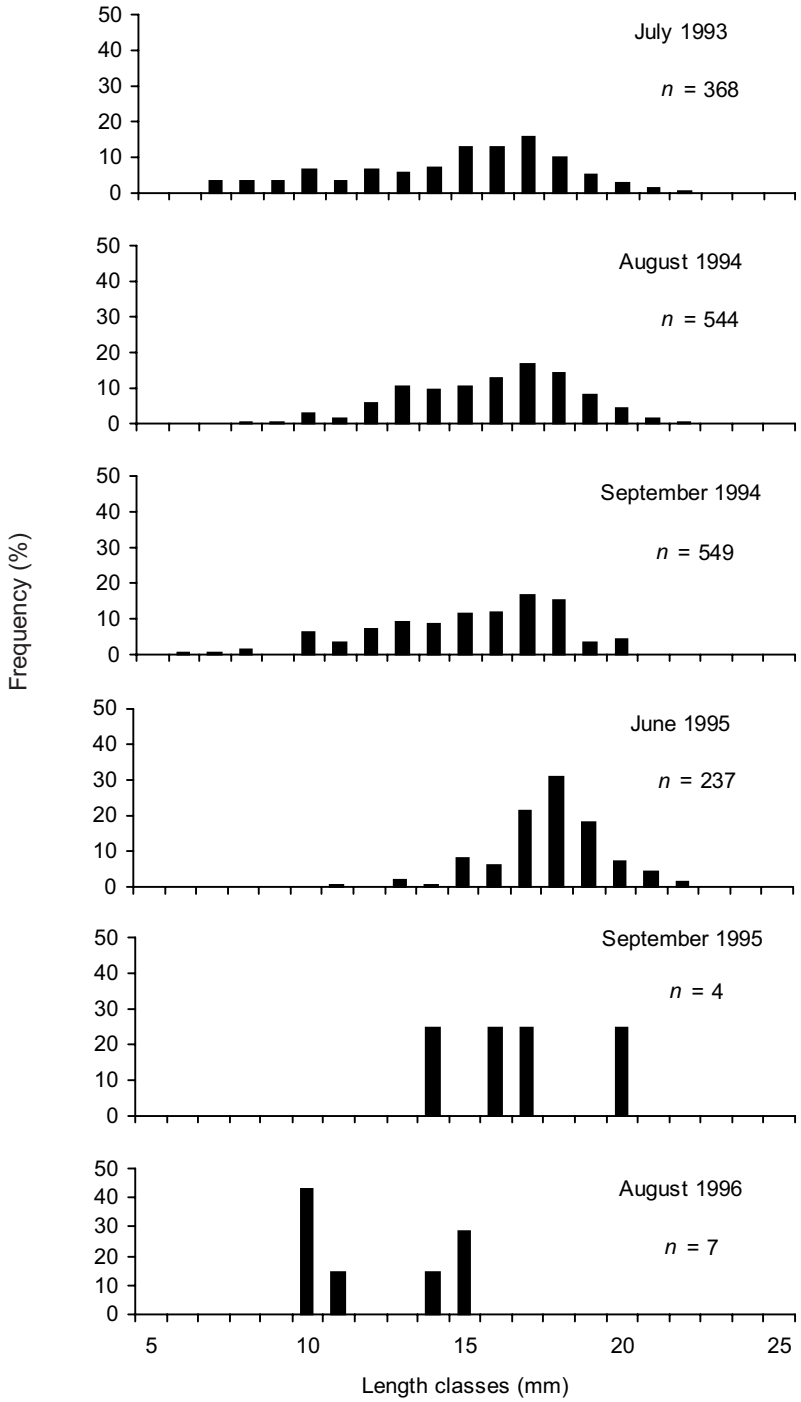

Fig. 2. Length distribution of *Sagitta elegans* in the Bornholm Deep in the 1993-1996 period (Bongo 333 µm).

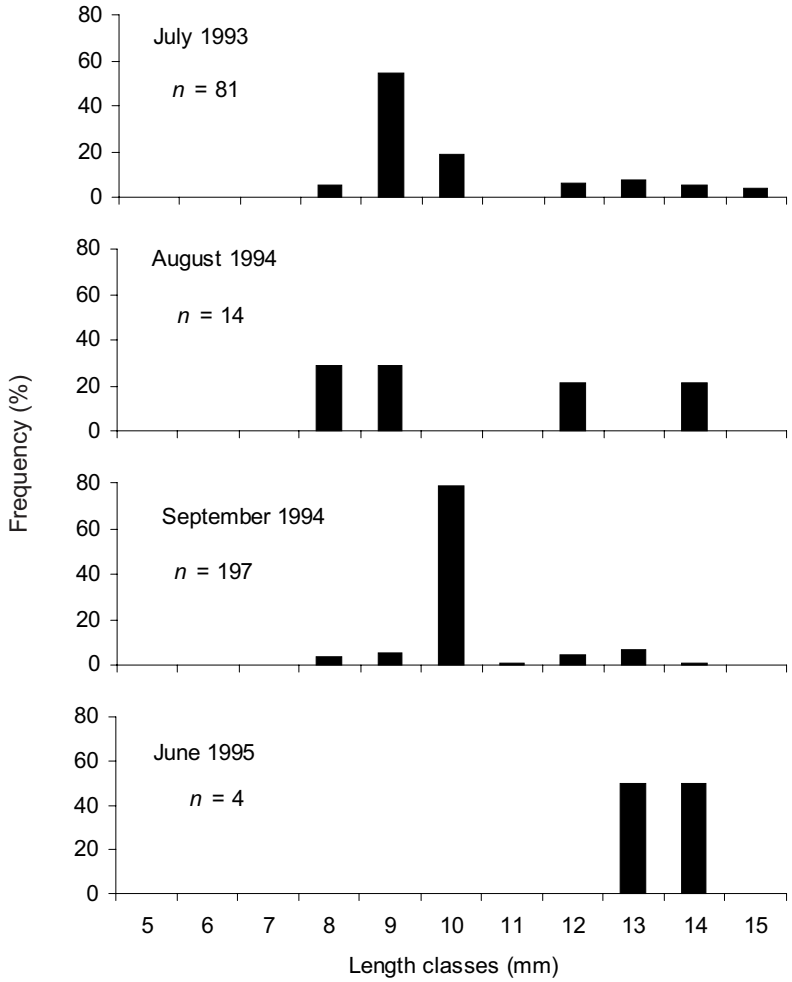

Fig. 3. Length distribution of *Sagitta setosa* in the Bornholm Deep in the 1993-1996 period (Bongo 333 µm)

Table 5. Stage of gonadal development in *Sagitta elegans* in the 1993-1996 period in the Bornholm Deep (based on Bongo, MPS and MIK net catches). Absolute number of specimens caught.

Year/month	Number of animals analyzed	Gonadal development stage (%)				
		0	1	2	3a	3b
1993/July	362	8.6	33.9	48.6	6.1	2.8
1994/August	735	0.8	17.6	60.8	16.6	4.2
1994/September	364	3.0	34.3	49.5	12.1	3.6
1995/June	63	0	30	60.3	9.5	0
1996/August	3	0	33.3	66.7	0	0

Table 6. Stage of gonadal development in *Sagitta setosa* populations in the 1993-1996 period in the Bornholm Deep (based on Bongo, MPS and MIK net catches)

Year/month	Number of animals analyzed	Gonadal development stage (%)				
		0	1	2	3a	3b
1993/July	37	8.1	78.4	13.5	0	0
1994/August	14	28.6	42.9	28.6	0	0
1994/September	10	0	10.0	60.0	30.0	0

Table 7. Number of chaetognaths with full digestive tracts caught in the 1993-1996 period (based on Bongo, MPS and MIK net catches).

Year/month	*Sagitta elegans*		*Sagitta setosa*	
	Number of animals analyzed	Number of animals with full digestive tracts	Number of animals analyzed	Number of animals with full digestive tracts
1993/July	362	0	37	0
1994/August	735	8	14	0
1994/September	364	5	10	0
1995/June	237	0	0	0
1996/August	7	0	0	0

Feeding patterns

Of the 1,705 specimens of *S. elegans* which were analyzed only 13 (3.5%) had food in their guts, while none of the 61 specimens of *S. setosa* which were analyzed did (Table 7).

DISCUSSION

The aim of this work was to determine the ecological status of chaetognaths in the Baltic Sea. The most important information was data on the places and time of chaetognath mass occurrence, regardless of the type of fishing gear used. Different kinds of fishing gears have, of course, different possibilities to catch animals, but this study focused only on the mass occurrence of chaetognaths in a defined time, and not on the effect of the gear used.

Two chaetognath species were identified: *Sagitta elegans* and *Sagitta setosa. Sagitta elegans baltica* were not identified (they are regarded as endemic to the Baltic Sea) (Mańkowski 1951, Mańkowski *et al.* 1959, Demel and Mulicki 1959, Siudziński 1965). More and more often it is not regarded as a separate species, but rather *S. elegans* specimens which have undergone morphological changes due to the influence of the low salinity of the Baltic Sea waters. This opinion is held by David V. P. Convay from the Plymouth Marine Laboratory (personal communication).

In the 1993-1996 period inflows of saline waters from Kattegat to the southern Baltic were confirmed in January 1993, March and December 1994 and in May 1996. The inflow waters reached the Gdańsk Deep through the Bornholm Deep and the Słupsk Furrow within 75-90 days (Wojewódzki 1996, Lass and Matthaus 1994, Wojewódzki and Grelowski 1995, Grelowski and Wojewódzki 1993). Since the plankton samples in the Bornholm Deep and the

Słupsk Furrow were collected from 3 to 6 months after the saline waters reached the sampling area and from 1 to 4 months after their detection in the Gdańsk Deep (Table 8), it may be assumed that the sampling took place in the location and at the time of the saline water occurrence. Only in September 1995, 9 months after the last inflow of December 1994, while sampling zooplankton in the Gdańsk Deep, was the total extinction of the inflow effect confirmed by hydrochemical methods (Wojewódzki 1996), although the effect had still been detectable in May 1994. A slightly different situation occurred in August 1996 when the observed inflow from the Słupsk Furrow was advective (Wojewódzki 1996), and, thus, could not bring in water masses or fauna from Kattegat.

In 1993, zooplankton samples were collected 3 months after the saline waters reached the sampling area. The oxygen levels in the Gdańsk Deep decreased to 0.62 ml · l^{-1}, (Wojewódzki 1996) which is below the values tolerated by chaetognaths and they were not observed in this basin, although they were present in the Bornholm Deep (Table 8).

In 1994, samples were collected 3 and 4 months after the saline waters reached the sampling area (Table 8). The oxygen level in the Gdańsk Deep in August was about 0.89 ml · l^{-1}, and a small number of chaetognaths were noted. In September, when the oxygen level dropped to about 0.1 ml · l^{-1}, chaetognaths were not present.

Samples were collected in June 1995 during the final period of the December 1994 inflow effect. The oxygen level in the Gdańsk Deep was 0.79 ml · l^{-1} and very small numbers of chaetognaths were observed (Table 8). Additionally, some chaetognaths were observed in the Słupsk Furrow and this could indicate the way in which these animals are introduced to the Gdańsk Deep. However, in September 1995, 4 months after the detection of the inflow its influence became completely extinct and the oxygen level in the Gdańsk Deep decreased to 0.26 ml · l^{-1} and sulphuretted hydrogen appeared locally. No chaetognaths were observed.

In 1996, the inflow from Kattegat did not reach the Gdańsk Deep and, despite the fact that the oxygen conditions in this basin were very good (2.18 ml · l^{-1}), chaetognaths were not present in this basin.

Table 8. Inflow periods and appearance of Chaetognatha in the Gdańsk Deep in the 1993-1996 period.
Inflow periods and their observation in the Gdańsk Deep, Wojewódzki (1996)

Inflow period (year/month)	Inflow observation period in the Gdańsk Deep (year/month)	Sampling period	Period from detection of inflow to sampling (in months)	Conditions in the near bottom waters of the Gdańsk Deep			Chaetognath occurrence		
				Sal (PSU)	T (^oC)	0_2 (ml/l)	BD	SF	GD
1993/January	1993/April	1993/July	3	12	5	0,62	+	–	–
1994/March	1994/May	1994/August	3	13	4	0,89	+	–	+
		1994/September	4	13	4	0,10	+	–	–
1994/Decemb	1995/May	1995/June	1	13	5	079	+	+	+
		1995/September	4	12	5	0,26	+	–	–
1996/May	*	1996/August	–	12	3	2,18	+	–	–

BD – Bornholm Deep, SF – Słupsk Furrow, GD – Gdańsk Deep;
+ Chaetognatha occurrence confirmed,
– Chaetognatha occurrence not confirmed,
* advective inflow from the Słupsk Furrow.

Based on the comparison of the dates of saline water inflows from Kattegat into the southern Baltic Sea and the occurrence of chaetognaths in this basin, it can be stated that chaetognaths are brought in to the Baltic with the inflow of waters. Their abundance decreases as the distance from the inflow source increases; the highest abundance figures are from the Bornholm Deep while the lowest are from the Gdańsk Deep. This hypothesis is also supported by the fact that within the months after the inflow in June 1995 chaetognaths appeared in throughout the *stream* of the inflow water, from the Bornholm Deep, through the Słupsk Furrow to the Gdańsk Deep, while three months later, in September 1995, when the inflow waters had degraded (decreased salinity and oxygen level – Wojewódzki 1996, Wojewódzki and Grelowski 1995, Table 8), chaetognaths became extinct. A similar situation was observed in August 1996; the inflow from May 1996 did not reach the Gdańsk Deep, and despite optimum environmental conditions for chaetognaths (temperature 3°C, salinity 12 PSU, oxygen 2.18 ml · l^{-1} – Wojewódzki 1996 (Table 8), their occurrence was not noted.

Chaetognaths are planktonic animals and they occur in the surface water layers. In the southern Baltic Sea they appear at significant depths beginning at 20-30 m. However, their maximum concentrations occur right above the sea bottom at depths of 60-80 m in the place where the saline inflow waters are located. A gradual degradation of the inflow waters (decreasing salinity, decreasing oxygen level), separation from the productive euphotic layer which results in the lack of food input (only 2.5% of the animals analyzed had food in their guts) probably result in the extinction of the advected pseudo-population of chaetognaths which can only survive in inflow waters.

The size structure of the *Sagitta elegans* population in the Baltic Sea indicates the occurrence of only one cohort with one clear abundance peak in the 17-18 mm class. In open sea populations of *Sagitta elegans* 3 to 4 cohorts (sub-populations) occur (Sameoto 1971) which are characterized by clear abundance maximums in the 8, 10 and 22 mm classes.

The age structure of *S. elegans* observed in July and August in the Baltic Sea is very similar to the age structure described by Sameoto (1971) for January and March, thus during the inflows of saline waters from Kattegat to the Baltic Sea. This can lead to the conclusion that chaetognaths which are brought into the Baltic Sea with the inflow waters neither reproduce nor grow and because of the adverse environmental conditions (oxygen, salinity, food) their population structure becomes *preserved* in its state at the moment of inflow.

The lack of change in size structure during the 6 to 7 months between inflow and catch confirms that, in the case of *S. elegans*, theirs is not a true population but an advected pseudo-population composed of a group of non-growing, non-reproducing individuals.

In the Baltic population of *Sagitta elegans* in July 1993 and August and September 1994 sexually mature specimens comprised about 3 to 4%. According to data in the literature (Sameoto 1971), during these months the percentage of the sexually mature animals should have been 13%, 3% and 11% of all specimens, respectively. A small percentage of specimens in the third degree of maturity, 1-3%, was noted among the open sea population of *S. elegans* in January - March (Table 9).

The data presented in Table 9 reveal that the maturity structure of the open sea chaetognath population, which was introduced into the Baltic Sea with the inflows in January 1993 and March 1994, was preserved until late summer (July - September) when it was still similar to that of the inflow population (winter – January, March) and not to the structure characteristic for the summer-time open sea population.

A similar situation was observed in June 1995 (after the inflow from December 1994). The sexual maturity structure of *S. elegans* (especially the lack of sexually mature specimens)

Table 9. Gonadal development stages of *Sagitta elegans* in various periods of the year (data from the literature)

Sampling period	Stage I (%)	Stage II (%)	Stage III (%)	References
July-September 1993-1994 (after inflows in January and March)	28,6	64,6	3,5	present work
July-September	43,7	47,0	9,0	Sameoto (1971)
January-March	14,7	83,3	2,6	Sameoto (1971)
June 1994 (after the inflow in December)	30,0	69,5	0	present work
June	29	21	50	Sameoto (1971)
December	51	49	0	Sameoto (1971)

in that period was more similar to that for the open sea population in December (during the inflow), than in June (Table 9).

This leads to the conclusion that the development (maturity) of specimens which reach the Baltic Sea is halted and the specimens physiology is frozen in the state that it is in at the moment of the inflow. Therefore, they constitute a non-reproductive, pseudo-population which becomes extinct.

The lack of food in the digestive tracts of Baltic chaetognaths may originate from either the fact that the animals expel food from their systems when caught or that they do not feed.

The first of these hypothesis can be verified easily. Rakusa-Suszczewski (1967, 1969), Różańska (1971), Kuhlmann (1977), Maciejewska (1992) all detected food in the guts of chaetognaths in net hauls. Thus, only the second hypothesis can be valid. Sporadic feeding or the lack thereof for 3 to 9 months, from the time of inflow to the moment the animal is caught, may result from their occurrence in an atypical water layer. Chaetognaths are epipelagic animals, but in the Baltic they occur in inflow waters which are near the bottom waters where illumination and feeding conditions are different. The gradual decrease in the amount of natural food brought in with the inflow waters or its lack may lead to chaetognath starvation. The often-described morphological changes in the animals (Różańska 1971, Maciejewska 1992, Conway personal communication) may also indicate pathological changes among Baltic chaetognaths due to starvation.

Based on the analyses of chaetognaths occurrence and the range of saline water inflows from Kattegat and the vertical distribution, size and age structures of the population as well as feeding patterns of *Sagitta elegans* and *Sagitta setosa* in the Baltic Sea the following scenario is plausible:

Plankton, including chaetognaths, is brought into the Baltic with winter and spring inflows of saline waters. The more saline surface waters from Kattegat submerge under the less saline warmer Baltic waters. The inflow waters which bring in the fauna reach the Gdańsk Deep through the Bornholm Deep and the Słupsk Furrow.

As the inflow water masses move along the Baltic bottom, the environmental (oxygen, salinity and temperature) and trophic conditions (food) gradually worsen. The allochthonous chaetognaths do not develop normally due to adverse environmental and trophic conditions: growth and maturation are halted at the moment of the animal's advection from their natural environment into the Baltic Sea. Since the animals do not feed, grow, mature or reproduce they comprise a pseudo-population in the Baltic Sea with altered body morphology. This pseudo-population becomes extinct, but the subsequent inflow supplements the chaetognaths fauna and thus they are regarded as a stable, and even endemic, element of Baltic fauna.

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Isolation and some properties of malic enzyme from the abdomen muscle of Antarctic krill *Euphausia superba*

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Abstract. Malic enzyme (EC 1.1.1.40) was purified about 1800-fold from the abdomen muscle of *Euphausia superba* to a specific activity of 20.3 μmol · min^{-1} per mg protein. The molecular weight of the native malic enzyme was determined to be 270,000. The K_m values determined at pH 7.2 for decarboxylation reaction for malate and $NADP^+$ were 0.229 mM and 10.6 μM, respectively. The K_m values for carboxylation reaction for pyruvate, NADPH and bicarbonate were 5 mM, 25.8 μM and 12 mM, respectively. The effect of temperature on apparent K_m for malate was studied. The minimum K_m appeared at 0°C, the ambient temperature of the species. The optimum pH for the decarboxylation reaction was between 7.0 and 8.0 and varied with the malate concentration. The enzyme showed substrate inhibition at a high malate concentration for the oxidative decarboxylation reaction at pH 7.0. The optimum pH for the carboxylation reaction was between 6.5 and 7.0 and varied with the pyruvate concentration. The heat stability of the purified malic enzyme of Antarctic krill *E. superba* was determined and compared with heat stability of the purified malic enzyme from the Baltic shrimp *Crangon crangon* abdomen muscle. The enzymes lost their activities at about 34°C and 65°C, respectively.

Key words: malic enzyme, kinetic properties, thermostability, abdomen muscles, *Euphausia superba*

INTRODUCTION

Malic enzymes have been investigated in several animals, microorganisms and plants (for a review, see Frenkel 1975). Malic enzyme [L-Malate: NADP oxidoreductase (decarboxylating) EC 1.1.1.40] catalyzes the reversible decarboxylation of malate to pyruvate in the presence of the coenzyme and a divalent cation (Mn^{2+} or Mg^{2+}). Malate is the central compound of intermediary metabolism participating in the bioenergetics of aquatic organisms; malic enzyme occurs in cells of more metabolically active tissues and may be present as three different molecular forms: two in the mitochondria and one in the cytosol (Skorkowski 1988a). In the mussel *Mytilus edulis*, an equal distribution of malic enzyme activity was found in the cytosol and mitochondrial compartment of the adductor muscle. Only the cytosolic enzyme was observed in the mantle and hepatopancreas (de Zwaan and van Marrewijk 1973). It was shown that the cytosolic and mitochondrial forms of malic enzyme in abdominal muscle of the shrimp *Crangon*

crangon (Biegniewska and Skorkowski 1983) and the crayfish *Orconectes limosus* (Świerczyński *et al.* 1980a) differed in their kinetic properties. In crustacean and bivalves, malic enzyme may play an important role in pyruvate and Krebs cycle intermediate metabolism (Skorkowski 1988b). It is suggested that extramitochondrial malic enzyme in crustacean abdomen muscle might be one of the enzymes involved in the anaplerotic supply of Krebs cycle intermediates in skeletal muscle (Biegniewska and Skorkowski 1983).

Studies on enzymes from polar organisms can provide indications on the physiology and biochemistry of the organism, on the molecular mechanisms of cold adaptation or on the temperature effects on metabolism. Stenothermal *Euphausia superba*, living constantly at temperatures close to 0°C, is characterized by high enzyme activities, e.g. proteases and lipases (Osnes and Mohr 1985).

The present paper reports the purification and some properties of Antarctic krill *Euphausia superba* abdomen muscle cytosolic NADP-dependent malic enzyme. We have also attempted to compare the heat stability properties of purified malic enzyme obtained from *E. superba* and the Southern Baltic shrimp *Crangon crangon*, two crustaceans that live in different marine ecosystems.

MATERIALS AND METHODS

Animals

The krill *E. superba* (Dana, 1852) was collected from Admiralty Bay, South Shetland Islands. The shrimp *C. crangon* (Linnaeus, 1758) were caught in summer in the Gdańsk Bay. The abdomen muscles of the both species were immediately dissected free of the cuticule and frozen at –70°C until the analyses were carried out. The studies were conducted in 1997 and 1998.

Preparation of tissue homogenates

The abdomen muscles were washed in cold 0.15 M KCl and homogenized at 4°C for 30 s with 3 vols of 10 mM Tris-HCl + 2 mM EDTA, pH 7.8 (Buffer A). The homogenate was centrifuged at 5000 g at 4°C for 30 minutes. Surface lipids were then removed by filtering the supernatant through cotton gauze. The final supernatant was used for further purification of the NADP-dependent malic enzyme.

Purification of malic enzyme

All the purification steps were conducted in the cold (4°C). In each case, the chromatographic column materials were pre-equilibrated and washed with buffer A.

$(NH_4)_2SO_4$ fractionation: The supernatant was adjusted to 40% saturation of $(NH_4)_2SO_4$ by the gradual addition of solid $(NH_4)_2SO_4$. After stirring for 60 minutes, the suspension was centrifuged at 5000 g for 30 minutes. The resulting supernatant was brought to 70% saturation of $(NH_4)_2SO_4$ by the gradual addition of solid $(NH_4)_2SO_4$. After stirring for 60 minutes, the suspension was centrifuged at 5000 g for 30 minutes. The precipitate was dissolved in a minimum volume of buffer A and dialyzed against 100 vols of the same buffer for 18 h with two changes of buffer. Insoluble material was removed by centrifugation at 20 000 g for 20 minutes.

DEAE-Sepharose chromatography: The dialyzed enzyme solution was applied to a column (2.5 x 35 cm) packed with DEAE Sepharose. After the application, the column was washed with about 2 vols of buffer A. The flow rate was 30 ml/hr and 7.5 ml fractions were collected. Malic enzyme activity was eluted as a single symmetrical peak by a linear gradient of KCl concentration prepared by mixing 250 ml of buffer A with 250 ml 0.5 M KCl in buffer A. The active fractions were pooled and made up to 2 mM malate and 2 mM manganese sulfate by additions from concentrated stock solutions.

2'5'ADP-Sepharose 4B chromatography: Fractions from the DEAE- Sepharose containing 2 mM malate and 2 mM $MnSO_4$ were applied to a 2',5'-ADP-Sepharose 4B column (1.5 x 5 cm) previously equilibrated with buffer A containing 2 mM malate and 2 mM manganese sulphate (Skorkowski and Storey 1987). After the protein had entered the column, washing was continued with buffer A + 2 mM malate and 2 mM $MnSO_4$ to remove any weakly adsorbed protein. The flow rate was 8 ml/hr and 4 ml fractions were collected. Malic enzyme was then eluted by a pulse of buffer A without any additions. The active fractions were pooled and concentrated with a Centriprep-30 concentrator (Amicon, USA).

Sepharose 6B gel filtration and molecular weight determination: Concentrated malic enzyme from ADP-Sepharose was applied to a column of Sepharose 6B (3 x 40 cm). Elution was performed with buffer A at a rate of 12 ml/hr. Three ml fractions were collected. Fractions containing NADP-dependent malic enzyme were pooled and concentrated with a collodion bag apparatus (Shleicher and Schull GmbH, FRG) and then in 40% glycerol in buffer A and stored at –20°C. The estimation of molecular weight by gel filtration was carried out according to the instruction by Pharmacia Fine Chemicals.

Enzyme and protein assays

Malic enzyme activity at all purification steps was followed spectrophotometrically with a UV-1601 UV-Visible spectrophotometer (Shimadzu Europe GMBH) by observing the appearance of NADPH (decarboxylation) or disappearance of NADPH (carboxylation) at 340 nm and 30°C. The standard reaction mixture contained: 50 mM Tris-HCl, pH 7.5, 0.5 mM NADP, 10 mM L-malate and 1 mM $MnSO_4$. Enzyme activities were calculated using $E_{mM/340} = 6.22$ for NADPH in 1 cm light path quartz cell. Protein concentration was determined using the Coomassie Blue method (Spector 1978).

Polyacrylamide gel electrophoresis

Polyacrylamide gels [5% (w/v) total acrylamide, 3.2% of which was bisacrylamide] were used to monitor malic enzyme activity by native electrophoresis. The sample of the final purified enzyme (25 μg) was applied on polyacrylamide gel prepared in a buffer containing 0.1 M Tris-HCl (pH 8.5). Electrophoresis was carried out in glass tubes (0.5 x 8 cm) at 2.5 mA per tube for 90 min in the cold (2°C). 0.1 M Tris glycine (pH 8.5) was used as the electrode buffer. Malic enzyme activity was monitored by incubating gels in the dark at 37°C in a medium consisting of 50 mM Tris-HCl, 10 mM L-malate, 0.5 mM NADP, 2 mM $MnSO_4$, 0.1 mg/ml

phenazine-methosulphate and 0.1 mg/ml nitro blue tetrazolium, at the final pH 7.5. Formation of the formazan precipitate corresponding to the location of the enzyme in the gel occurred within 30 minutes. Yellow gels were distained in distilled water and stored in 7% (v/v) acetic acid.

Sodium dodecyl sulphate-polyacrylamide gel electrophoresis (SDS-PAGE) was performed after all the purification steps according to the procedure of Laemmli (1970) using 10% gels. The following molecular weight protein standards were used: Phosphorylase b- 94 kDa, Albumin- 67 kDa, Ovalbumin- 43 kDa, Carbonic anhydrase- 30 kDa, Tripsin inhibitor- 20 kDa and α-Lactalbumin- 14.4 kDa.

Kinetic constants (K_m) determination

Reaction rates for decarboxylation were measured at pH 7.2 at 30ºC in a medium containing: 50 mM Tris-HCl, 20 mM imidazole-HCl, 10 mM L-malate, 0.5 mM $NADP^+$, 1mM $MnSO_4$, 1.5 μg enzyme. The rates of reductive carboxylation were measured at pH 7.2 at 30ºC in a medium containing: 50 mM Tris-HCl, 20 mM imidazole-HCl, 50 mM $NaHCO_3$, 20 mM pyruvate, 0.2 mM NADPH, 1 mM $MnSO_4$, 1.5 μg enzyme. For estimation of the K_m, all components required were present at the concentrations mentioned above, with a varied concentration of the component tested.

Reversibility of the reaction catalyzed by malic enzyme from the abdomen muscle of *E. superba*

The rate of oxidative decarboxylation and reductive carboxylation was measured at 30º C. The medium (final volume 1 ml) for decarboxylation contained : 10 mM L-malate, 0.5 mM $NADP^+$, 1 mM $MnSO_4$ and 1.5 μg malic enzyme in 50 mM Tris-HCl + 20 mM imidazole-HCl, pH 6.0-8.0. The rate of reductive carboxylation was measured in the medium (final volume 1ml) containing: 20 mM pyruvate, 0.2 mM NADPH, 1mM $MnSO_4$, 1.5 μg enzyme, 50 mM Tris-HCl + 20 mM imidazole-HCl + 50 mM $NaHCO_3$, pH 6.0-8.0.

Heat stability

Heat stability was determined using the method of Sensabaugh and Kaplan (1972), modified as follows. Pure enzyme diluted in buffer A was added to the standard reaction mixture in amounts that resulted in an increase of absorbency within the range 0.1-0.2 per minute. The enzyme dilution was divided into two parts. Samples of the first part were heated for 20 minutes at various temperatures, rapidly cooled in an ice bath and assayed for malic enzyme activity. Bovine albumin was then added to the samples of the second part to a final concentration of 0.1%, and the enzyme dilutions were treated as above.

Chemicals

DEAE-Sepharose, 2',5'-ADP-Sepharose 4B, Sepharose 6B and protein standards were obtained from Pharmacia Fine Chemicals; L-malate, NADP, $MnSO_4$ and Brilliant Blue G were from Sigma Chemicals Co.; Tris was from Ubichem and imidazol was from Fluka AG, Buchs SG. All other chemicals were of the highest purity commercially available.

RESULTS

Enzyme purification

Table 1 summarizes the results of a typical purification of extramitochondrial malic enzyme from krill abdomen muscle carried out as described under Materials and Methods. Estimation of the malic enzyme activity before $(NH_4)_2SO_4$ fractionation was difficult due to interference from some proteins present in the abdomen muscle extract. The purification procedure involved ion-exchange chromatography on DEAE-Sepharose (Fig. 1a), affinity chromatography on 2',5'-ADP-Sepharose 4B (Fig. 1b) and gel filtration on Sepharose 6B (Fig. 1c). The NADP-dependent malic enzyme from krill abdomen muscle was purified about 1835-fold with a recovery rate of 33%. The specific activity of purified enzyme measured in the decarboxylation direction was 20.3 μmoles $min^{-1} \cdot mg^{-1}$ protein.

Homogeneity and molecular weight

As seen in Fig. 1a, krill malic enzyme activity was eluted from DEAE-Sepharose at a continuous KCl gradient concentration as a single symmetrical peak activity. The enzyme did bind to 2', 5'ADP-Sepharose 4B and chromatography on this column (Fig. 1b) plus gel filtration on Sepharose 6B (Fig. 1c) removed residual proteins. The pooled and concentrated active fractions from Sepharose 6B column were used in all the studies of krill malic enzyme reported here.

The homogeneity of purified malic enzyme from abdomen muscle of *E. superba* was demonstrated by polyacrylamide gel electrophoresis. As can be seen in Fig. 2, the purified native enzyme migrated as a distinct single band when stained for malic enzyme activity (Fig. 2, line 7). When electrophoresis was performed in the presence of SDS, only one protein band was obtained after several purification steps (Fig. 2, line 5).

The molecular weight of the native malic enzyme from the abdomen muscle of *E. superba* estimated by gel filtration through a calibrated Sepharose 6B column was about 270,000 (ranging between 260,000-280,000 in three experiments). Aldolase, catalase, ferritin and thyroglobulin were used as marker proteins. The molecular weight of the SDS-treated malic enzyme of *E. superba* was estimated to be about 65,000 (Fig. 2, line 5).

Table 1. Purification of NADP-dependent malic enzyme from krill abdomen muscle

Step	Total protein (mg)	Specific activity (nmol/min/mg)	Total activity (μmol/min)	Yield (%)	Purification (fold)
Cytosol	5,069	11.1	56.2	100	1
$(NH_4)_2SO_4$ fractionation (40-70%)	2,352	36.5	81.6	145	3.3
DEAE-Sepharose chromatography	248	331.4	80.8	144	29.9
2'5'ADP-Sepharose chromatography	1.8	17,778	32	57	1,605
Sepharose 6B gel filtration	0.9	20,333	18.3	33	1,835

Enzyme was isolated from 275 g abdomen muscle. The enzyme activity was measured as described under Materials and Methods.

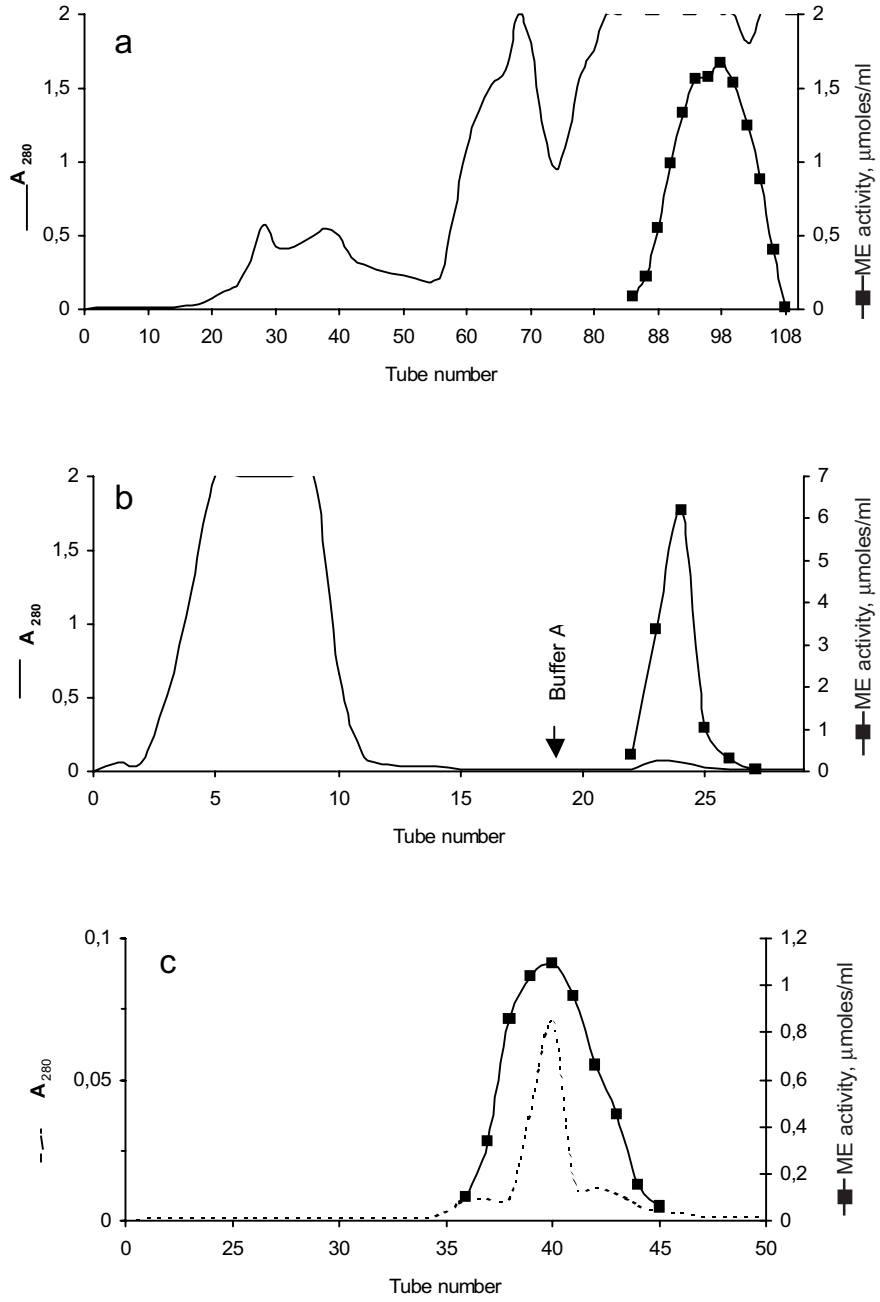

Fig. 1. Purification of malic enzyme (ME) from krill abdomen muscle involving chromatography on a) DEAE-Sepharose, b) 2'5'ADP-Sepharose 4B, c) Sepharose 6B. The protein concentration (—) was monitored by measuring the absorption at 280 nm. The enzyme activity was measured as described under Materials and Methods

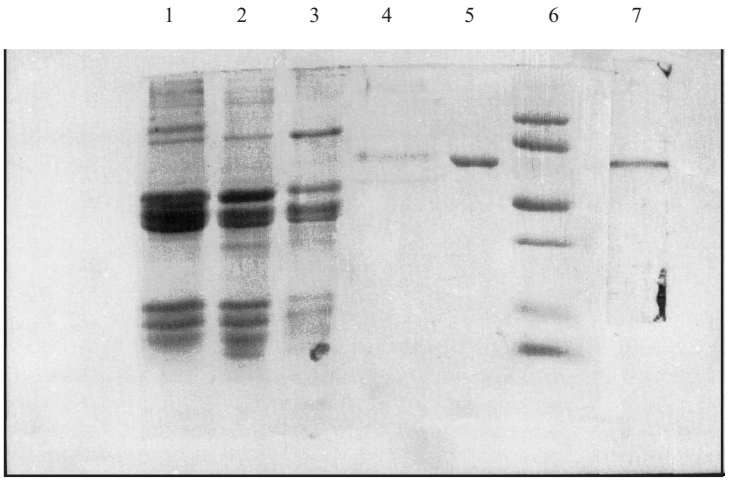

Fig. 2. Polyacrylamide gel electrophoresis of SDS-treated (lines 1-6) and native krill abdomen muscle malic enzyme (line 7). 1 – muscle extract; 2 – after $(NH_4)_2SO_4$ fractionation; 3 – after DEAE-Sepharose chromatography; 4 – after 2'5'ADP-Sepharose 4B chromatography; 5 – after Sepharose 6B gel filtration; 6 – molecular weight protein standards; 1-6 – stained for protein with Coomassie blue. 7 – stained for enzyme activity with tetrazolium blue.

The dependence of activity on pH

The effect of pH variation on the malate decarboxylase activity (Fig. 3) and pyruvate carboxylase activity (Fig. 4) of krill abdomen muscle malic enzyme was examined. The sensitivity of the krill malic enzyme activity to changes of pH in the case of decarboxylation direction varied with the L-malate concentration (Fig. 3). With a malate concentration of 0.1, 1 and 10 mM the respective optima were about pH 7, 7.5 and 8. The optimum pH for the carboxylation reaction was 6.5 in the presence of 2.5 mM and 5 mM pyruvate, and 7.0 in the presence of 10 mM and 20 mM pyruvate (Fig. 4).

Kinetic parameters

Table 2 summarizes apparent K_m values for different substrates in the decarboxylation and carboxylation reaction. The effect of temperature on apparent K_m for malate was also studied. As shown in Fig. 5, the K_m for malate of malic enzyme from krill muscle reaches its minimum at 0° C.

Reversibility of the reaction catalyzed by extramitochondrial malic enzyme from the abdomen muscle of *E. superba*

The results of experiments designed to show the rate of decarboxylation and carboxylation reaction catalyzed by the krill abdomen muscle malic enzyme at different pH are shown in Table 3. It is evident that the enzyme readily catalyzed carboxylation of pyruvate. The reverse reaction was found to proceed at about two and a half times the velocity of the forward rate at pH 6.5 (Table 3). The rate of pyruvate carboxylation at pH 7.0 was about the same as that of the forward reaction.

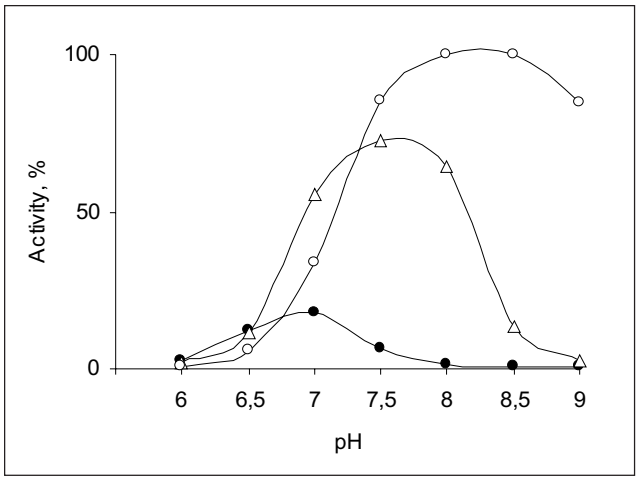

Fig. 3. The effect of pH on oxidative decarboxylation of malate catalyzed by krill malic enzyme. Reaction was carried out at 30°C in the medium containing: 50 mM Tris-HCl, 20 mM imidazole-HCl, 0.5 mM $NADP^+$, 1 mM $MnSO_4$, 0.1 mM malate (●), 1 mM malate (Δ), 10 mM malate (o).

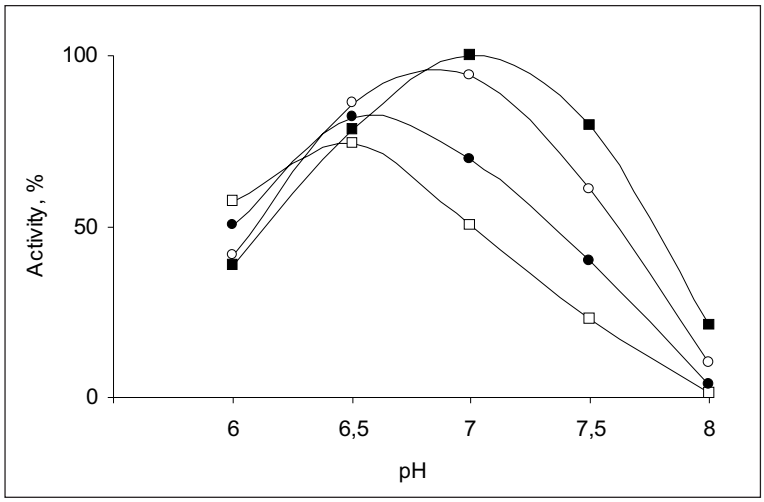

Fig. 4. The effect of pH on reductive carboxylation of pyruvate catalyzed by krill malic enzyme. Reaction was carried out at 30°C in the medium containing: 50 mM Tris-HCl, 20 mM imidazole-HCl, 50 mM $NaHCO_3$, 0.2 mM NADPH, 1 mM $MnSO_4$, 2.5 mM pyruvate (□), 5 mM pyruvate (●), 10 mM pyruvate (o), 20 mM pyruvate (■)

Table 2. Kinetic constants for the malic enzyme from Antarctic krill abdomen muscle

Decarboxylation		Carboxylation	
K_m (malate)	0.228 mM	K_m (pyruvate)	5.01 mM
K_m ($NADP^+$)	10.65 μM.	K_m (NADPH)	25.78 μM
		K_m ($NaHCO_3$)	12.01 mM

For experiment conditions see Materials and Methods.

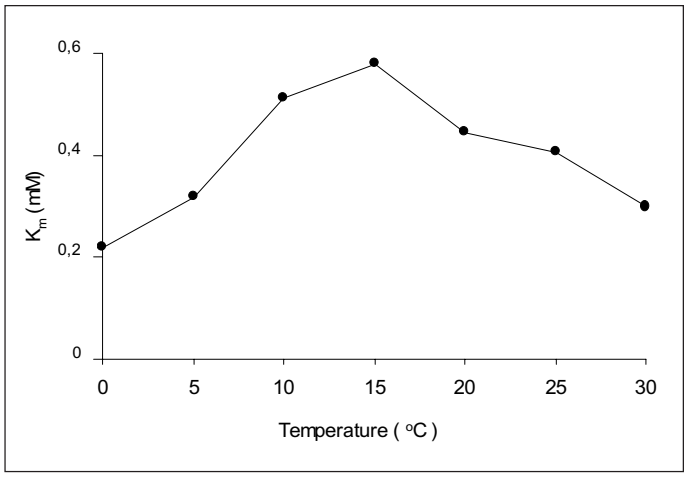

Fig. 5. The effect of the temperature assay on apparent K_m for malate of malic enzyme from krill abdomen muscle. Reaction rates for decarboxylation were measured at pH 7.2 in a medium containing: 50 mM Tris-HCl, 20 mM imidazole-HCl, 0.5 mM $NADP^+$, 1mM $MnSO_4$, 1.5 mg enzyme and a varied concentration of the L-malate.

Table 3. Reversibility of the reaction catalyzed by krill abdomen muscle malic enzyme

pH	Decarboxylation (μmol/min/mg)	Carboxylation (μmol/min/mg)	% of forward reaction
6.0	0.41	3.41	831
6.5	1.83	4.71	257
7.0	7.66	6.68	87
7.5	17.98	6.43	35
8.0	21.68	2.25	10

For experiment conditions see Materials and Methods.

Heat stability

The heat inactivation profile of NADP-dependent malic enzyme from krill abdomen muscle is shown in Fig. 6. The pure malic enzyme was stable up to about 20°C and then the activity systematically decreased, both without the bovine albumin and in the presence of 0.1% bovine albumin. At a temperature of 34°C the krill malic enzyme lost its activity. The heat stability of the pure shrimp *C. crangon* abdomen muscle malic enzyme was also determined (Fig. 6). It was observed that extramitochondrial malic enzyme of *C. crangon* was stable up to about 40°C and the activity slowly decreased to about 60°C. At a temperature of 65°C the enzyme reaction did not appear, both without the bovine albumin and in the presence of 0.1% bovine albumin.

DISCUSSION

The malic enzymes isolated from crustaceans are relatively little known. Keller (1965) showed the presence of this enzyme in selected tissues of the crayfish *Cambarus affinis*. Only the extramitochondrial NADP-dependent malic enzyme was observed in the shrimp *Crangon crangon* abdomen muscle (Biegniewska and Skorkowski 1983). It was shown that NADP-

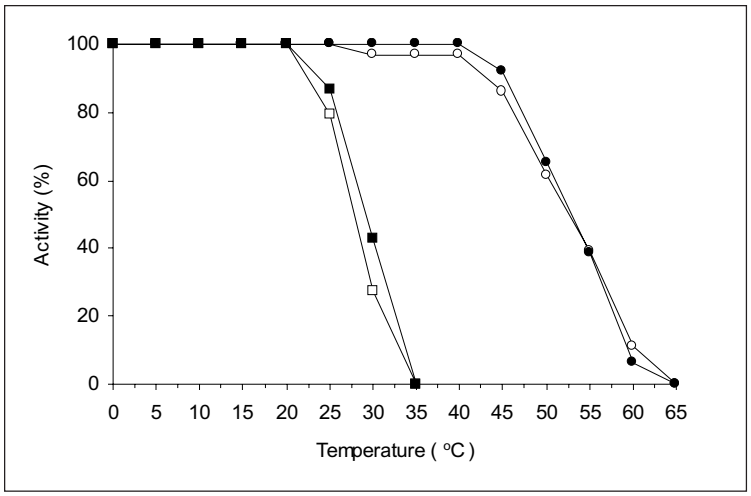

Fig. 6. Heat inactivation profiles of krill malic enzyme and shrimp malic enzyme.
(□), pure krill malic enzyme, (■), the enzyme plus the bovine albumin (final concentration 0.1%);
(o), pure shrimp malic enzyme, (●), the enzyme plus the bovine albumin (final concentration 0.1%).
Experimental conditions as described under Materials and Methods.

dependent mitochondrial form from the abdomen muscle of crayfish *Orconectes limosus* is the only molecular form of malic enzyme present in this tissue (Skorkowski *et al.* 1977; Świerczyński *et al.* 1980a). Rouleau *et al.* (1991) isolated and studied some properties of NADP-dependent malic enzyme from the abdomen muscle of the shrimp *Pandalus borealis*.

During these studies, the malic enzyme was isolated from the abdominal muscle of Antarctic krill *Euphausia superba* (Crustacea, Euphausiacea). The specific activity of purified enzyme was about 20 μmoles $min^{-1} \cdot mg^{-1}$ protein. It was higher than the specific activity for partly purified NADP-dependent malic enzyme from the shrimp *C. crangon* abdomen muscle (Biegniewska and Skorkowski 1983) and was very close to the specific activity reported by Świerczyński (1980) for extramitochondrial malic enzyme from rat skeletal muscle.

The homogeneity of purified malic enzyme from abdomen muscle of *E. superba* was demonstrated by polyacrylamide gel electrophoresis – one band stained for enzyme activity was obtained. These electrophoretic data correspond well with genetic studies of *E. superba* which found that malic enzyme locus is monomorphic (Kühl and Schneppenheim 1986). The molecular weight of the native malic enzyme from the abdomen muscle of krill was estimated to be about 270,000. The molecular weight of the krill malic enzyme was similar to the reported values of molecular weights of malic enzyme derived from other sources, e.g. shrimp *C. crangon* abdomen muscle 260,000 (Biegniewska and Skorkowski 1983), extramitochondrial rat skeletal muscle 264,000 (Świerczyński 1980) and Drosophila 266,000 (Geer *et al.* 1980). The molecular weight of SDS-treated malic enzyme of *E. superba* was estimated to be about 65,000. These results demonstrated that the native malic enzyme, similarly to enzyme isolated from pigeon liver (Hsu and Lardy 1967), was a tetramer composed of identical molecular weight subunits.

Variation of pH has a great influence on malate decarboxylase and pyruvate carboxylase activity. The optimum pH for the carboxylation reaction was 7.0 in the presence of 10 mM and 20 mM pyruvate, and 6.5 in the presence of 2.5 mM and 5 mM pyruvate (more "physiological"

concentrations). It was reported that the activity of extramitochondrial malic enzyme from the shrimp *C. crangon* abdomen muscle (Biegniewska and Skorkowski 1983) and rat skeletal muscle (Świerczyński 1980) did not vary with the pyruvate concentration. The sensitivity of the krill malic enzyme activity to the changes of pH in the case of decarboxylation direction varied with the L-malate concentration. With malate concentration of 0.1, 1 and 10 mM the respective optima were about pH 7, 7.5 and 8. It was observed that the pH optimum of the malate decarboxylase activity of shrimp abdomen muscle malic enzyme varied with the concentration of L-malate (Biegniewska and Skorkowski 1983). Upon changing the L-malate concentration from 0.1 to 10 mM, the pH optimum of the shrimp muscle malic enzyme activity shifted from 7.0 to 8.5 (Biegniewska and Skorkowski 1983). The results obtained for the malate decarboxylase activity of krill muscle malic enzyme were close to that presented for the extramitochondrial malic enzyme from rat skeletal muscle (Świerczyński 1980).

As shown previously, crustacean abdomen muscle mitochondrial malic enzyme (Świerczyński *et al.* 1980a) and the mitochondrial malic enzyme from rat skeletal muscle (Świerczyński *et al.* 1980b) showed a sigmoid-shaped substrate saturation curve and this characteristic was accentuated at higher pH values. In the case of krill malic enzyme no evidence of sigmoidicity at any pH was observed. At pH value 7.0 and lower than 7.0, the enzyme was inhibited by high (greater than 1.5 mM) malate concentrations (data not shown). A similar effect was observed with the extramitochondrial malic enzyme from rat skeletal muscle (Świerczyński 1980). Pry and Hsu (1980) described the existence of strong negative cooperativity between subunits of pigeon liver cytosol NADP-dependent malic enzyme. They showed a tentative catalytic mechanism which depicts the enzyme as a functional dimer with two of the four potentially available sites undergoing catalysis; the two remaining sites bind malate only weakly, at high malate concentration and in a non-catalytic manner, inhibiting turnover at the adjacent catalytic sites (Pry and Hsu 1980). Malate inhibition of the oxidative decarboxylation of malate at pH 7.0 suggests the possible modulation of the krill muscle cytosol NADP-dependent malic enzyme by its own substrates.

To further characterization of NADP-dependent malic enzyme from abdomen muscle of *E. superba* some kinetic measurements were performed at pH 7.2, both for the carboxylation and decarboxylation directions. The K_m values presented did not differ essentially from the K_m values reported for decarboxylation direction by extramitochondrial malic enzyme from other sources. The K_m values for carboxylation were a little lower than that of shrimp *C. crangon* (Biegniewska and Skorkowski 1983) but not very different from K_m values reported for other vertebrates.

The ability of malic enzyme to perform carboxylation/decarboxylation reactions may give the malic enzyme an important role in the control of intracellular pH in the cell to provide a buffering mechanism by regulating the levels of dissolved CO_2. It was shown that NADP-linked malic enzyme from crayfish abdomen muscle mitochondria (Świerczyński *et al.* 1980a) and rat skeletal muscle mitochondria (Świerczyński *et al.* 1980b) catalyzed the reductive carboxylation of pyruvate at a relatively low rate as compared to the forward reaction. The NADP-dependent malic enzyme from krill abdomen muscle readily catalyzed carboxylation of pyruvate. The rate of pyruvate carboxylation at pH 7.0 was about the same as that of the forward reaction. At pH between 6.0 and 6.5, the malic enzyme from krill abdomen muscle catalyzed the reductive carboxylation of pyruvate at a relatively high rate as compared to the forward reaction. The results obtained for krill abdomen muscle malic enzyme resembled the shrimp abdomen muscle malic enzyme. In the case of extramitochondrial malic enzyme from abdomen muscle of *C. crangon*, the rate of pyruvate carboxylation at a pH ranging between 6.5 and

7.0 was the same as that of malate decarboxylation (Biegniewska and Skorkowski 1983). In crustacean and bivalves, malic enzyme may play an important role in pyruvate and Krebs cycle intermediate metabolism (Skorkowski *et al.* 1977, de Zwaan *et al.* 1981, Paynter *et al.* 1985, Brodey and Bishop 1992 a, b). As the carboxylation of pyruvate to malate could be catalyzed by malic enzyme there is a possibility that the enzyme is involved in the anaplerotic maintenance of Krebs cycle intermediates. This function of the extramitochondrial malic enzyme from rat skeletal muscle (Świerczyński 1980) and shrimp abdomen muscle (Biegniewska and Skorkowski 1983) was suggested earlier.

The possible modification of the substrate binding site of malic enzyme, in the range of temperatures between 0° and 30°C, was indirectly analysed by measuring the apparent K_m which inversely approximates the binding ability ("affinity") of an enzyme for its substrate. In several fish species the K_m of different enzymes have a minimum which matches normal environmental temperatures (for a review see Hochachka and Somero 1984). Comparable results are reported for amylase (Van Wormhoudt 1980) and lactate dehydrogenase (Thébault 1984) in the shrimp *Palaemon serratus*, and for *N*-acetyl-β-D-glucosaminidase in the Antarctic krill *E. superba* (Bucholz and Vetter 1993). The K_m for malate of malic enzyme from krill muscle reached its minimum at 0°C. This value is closest to the environmental temperature of *E. superba*. However, K_m value at 30°C was not much higher than that at 0°C. The assay temperature of more than 10°C does not correspond to the ambient temperatures normally experienced by *E. superba*. As can be seen on the heat inactivation profile (Fig. 6), at the temperature of 34°C the krill malic enzyme lost its activity. In the heat stability tests enzyme was incubated at the temperatures given in Fig. 6 for 20 minutes. During the kinetic measurements the enzyme was incubated at the temperatures given in Fig. 5 for 1 minute.

For further characterization of the NADP-dependent malic enzyme from krill abdomen muscle, the heat stability was determined and compared with the heat stability of the pure shrimp *C. crangon* abdomen muscle malic enzyme (Fig. 6). It was observed that the extramitochondrial malic enzyme of *C. crangon* was a much more stable one.

The results presented above indicate that the kinetic properties of the cytoplasmic malic enzyme from krill abdomen muscle and shrimp abdomen muscle (Biegniewska and Skorkowski 1983) showed similarities. Since substantial differences in heat stability profiles for the malic enzyme from both species has been observed, malic enzyme protein stability appears to change due to the ambient temperature regimes of the species investigated. However, further research is required in order to discover more about the mechanism of malic enzyme temperature adaptation.

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Fish distribution on the shelves of the Atlantic Ocean Antarctic Area with respect to stock density

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Abstract. Only a few species of Antarctic fishes, most of which inhabit near-bottom waters, occur on a wide-spread scale.

From the investigations that were carried out in 1975-89 from the R/V PROFESOR SIEDLECKI, it was determined that 14 species of fish are widespread, all of them belong to two families (*Channichthyidae* and *Nototheniidae*). This paper presents the results of investigations of the distribution of these fish species with respect to the density of their occurrence and identifying sets in particular regions.

Key words: Antarctica, Atlantic Ocean Antarctic Area, zoogeographic zones, fish, Channichthyidae, Nototheniidae, distribution, density

INTRODUCTION

Antarctica is surrounded by the Southern Ocean. The area of this ocean between the Antarctica above the Antarctic Polar Front line is called the Antarctic Zoogeographic Region (Eastman 1993) and it is inhabited by 275 fish species from 49 families (Kulesz 1998).

One of the most widely-investigated areas in this region in terms of ichthyofauna is the Atlantic Ocean Antarctic Area (AOAA). Specific climatic conditions and the sea bottom configuration influence the distribution of ichthyofauna, and are jointly responsible for the creation of separate zoogeographic regions. The AOAA, according to the Andriashev division, belongs to the Glacial Subregion and consists of two provinces, South Georgia and West Antarctica (Eastman 1993). The AOAA is divided into three areas with various degrees of ice-cover (Kock 1992), and it is inhabited by 168 of 275 Antarctic fish species (Kulesz 1998). Only a few of them occur widely. They are, however, significant for the ecosystems and they play an important role in the trophic chain. The majority of them are commercially exploited.

The aim of this paper is to analyze the distribution of major fish species (in terms of biomass) which inhabit benthic areas on the shelves of the AOAA. The analysis was carried out using the fish density data which were collected during research cruises of the R/V PROFESOR SIEDLECKI.

MATERIALS AND METHODS

The investigations covered the shelves of the AOAA, according to the FAO-CCAMLR statistical Antarctic division 48.1, 48.2, 48.3(Anon. 1990), located south of the Antarctic Polar Front. The shelves spread around islands and the southwestern part of the Antarctic Peninsula, which form the Scotia Ridge (Fig. 1).

They are inhabited by benthic fish species which form concentrations. The investigations did not cover the shelves of the islands which form the South Sandwich archipelago due to the relatively narrow strip of shelf that surrounds them making it impossible to carry out benthic catches (Romer and Andrzejak 1979). The shelf areas and the percentage of particular depth layers, as used in this work, were calculated using Everson's [1984] data.

The investigations were carried out during the principally summer research-reconnaissance cruises of the R/V PROFESOR SIEDLECKI in 1975-89 (Table 1). The selection of haul sites

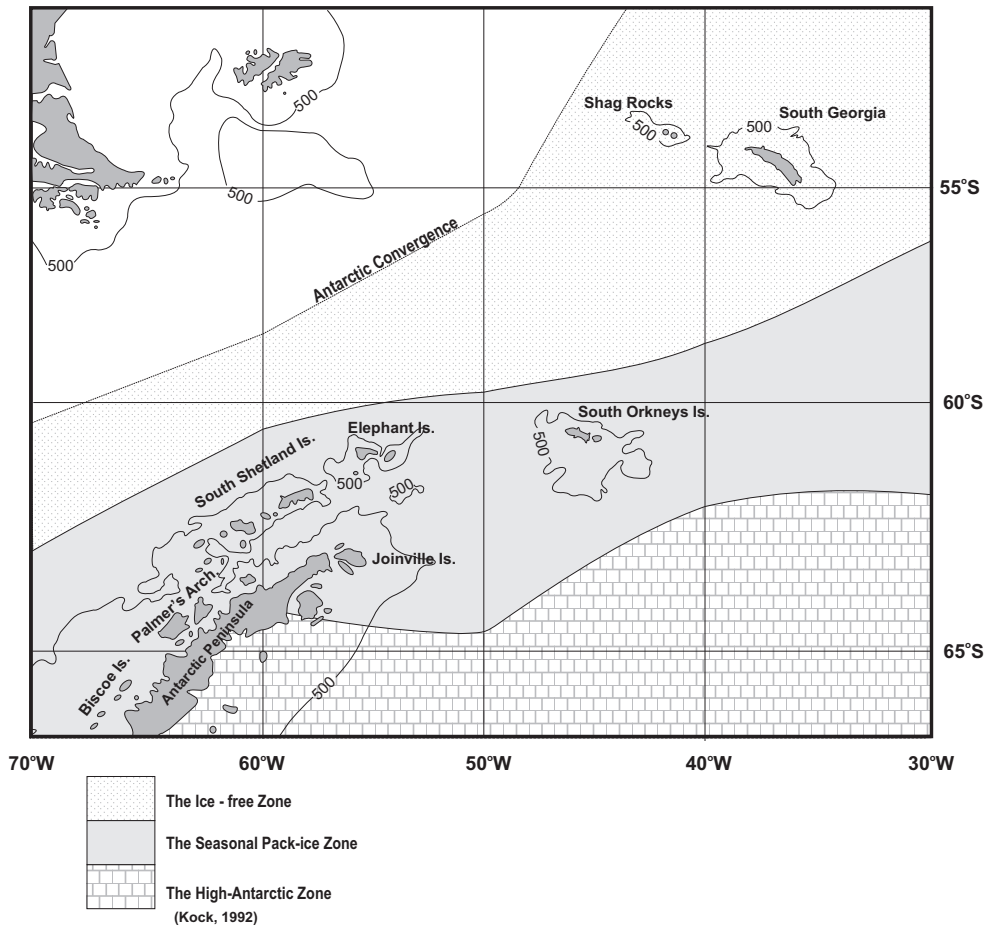

Fig. 1. Atlantic Ocean Antarctic Area

Table 1. Number of research hauls made by the R/V PROFESOR SIEDLECKI

Region	Season	Months							∑
		10	11	12	01	02	03	04	
	1978/79				3		3		6
	1980/81							5	5
Shag Rocks	1986/87		11	2					13
	1987/88				4				4
	∑		**11**	**2**	**7**		**3**	**5**	**28**
	1975/76						17		17
	1978/79			17	11		15		43
South Georgia Is.	1986/87			111					111
	1987/88			79	51				130
	1988/89					52			52
	∑			**207**	**62**	**52**	**32**		**353**
	1978/79			7			4		11
South Orkneys Is.	1983/84			15					15
	∑			**22**			**4**		**26**
	1978/79				6	4	1		11
	1980/81						3		3
	1983/84			6					6
Elephant Is.	1986/87	11	6	5					22
	1987/88					7			7
	1988/89				4				4
	∑	**11**	**6**	**11**	**10**	**11**	**4**		**53**
	1978/79				7	1	1		9
	1980/81						3		3
Joinville Is.	1983/84			5					5
	1986/87		6						6
	∑		**6**	**5**	**7**	**1**	**4**		**23**
	1978/79				5	13	3		21
	1980/81						7		7
South Shetlands Is.	1986/87					2			2
	1987/88					8			8
	∑				**5**	**23**	**10**		**38**
Palmer Arch.	1978/79					6			**6**
Biscoe Is.	1978/79					9			**9**
Total		**11**	**23**	**247**	**91**	**102**	**57**	**5**	**536**

usually depended on the sea bottom configuration; preference was given to sites that did not pose potential problems for the realization of the investigations. Only in 1986/87, 1987/88 and 1988/89 near South Georgia were the hauls carried out according to a fixed network of positions that also included the proportions for the depth zone occurrence. A detailed list of the number of hauls in particular regions is presented in Table 2.

The investigations were carried out with a bottom trawl with a horizontal opening of 18 m, and a vertical opening of 4.5 m. The trawling speed was 3.5 knots. The trawl codend mesh size was 80mm and the insert had a 20 mm mesh bar length.

Table 2. Number of hauls according to squares and depth zones

Region	Square[1)]	Depth layers (m)					
	°S - °W	0-100	101-200	201-300	301-400	401-500	Σ
1	2	3	4	5	6	7	8
	53.0-41		3				3
Shag	53.0-42		2	2	2		6
Rocks	53.5-41		12	2		1	15
	53.5-42		4				4
	4	**0**	**21**	**4**	**2**	**1**	**28**
	53.5-35		1	9	2		12
	53.5-36		9	18	3		30
	53.5-37		17	8	2		27
	53.5-38	1	15	6	1		23
	53.5-39			1	3	2	6
	54.0-35	1	6	20	4		31
	54.0-36		9	13			22
	54.0-37		13	3			16
	54.0-38		6	24			30
	54.0-39			5			5
South	54.5-34		6	6	1	1	14
Georgia	54.5-35	7	14	20	12		53
Is.	54.5-36		5	2			7
	54.5-37		7	7	1		15
	54.5-38		7	4	3		14
	54.5-39			1			1
	55.0-34		4	3			7
	55.0-35		25	8	1		34
	55.0-36		2	3			5
	55.0-37			1			1
	20	**9**	**146**	**162**	**33**	**3**	**353**
	60.0-45			1		1	2
	60.0-46					1	1
	60.0-47			2	1		3
	60.5-43			1	1		2
South	60.5-44			1			1
Orkneys	60.5-46			7			7
Is.	60.5-47			4	2		6
	61.0-44				1		1
	61.0-45			1	1		2
	61.0-46			1			1
	10	**0**	**0**	**18**	**6**	**2**	**26**
	60.5-55	1	5	6	1		13
Elephant	61.0-55		6	8	1	1	16
Is.	61.0-56		6	8	4	6	24
	3	**1**	**17**	**22**	**6**	**7**	**53**

Table 2 (cont.)

1	2	3	4	5	6	7	8
	62.0-54			1	3		4
	62.0-55			10	1		11
	62.5-54		1	1	1		3
Joinville	62.5-55			1	1		2
Is.	63.0-53			2			2
	63.0-54			1			1
	6	**0**	**1**	**16**	**6**	**0**	**23**
	61.5-57			1			1
	61.5-58		1	20	1		22
	61.5-59			1	5		6
South	61.5-60				1		1
Shetlands	62.0-58		1				1
Is.	62.0-59	2	1				3
	62.5-60		2				2
	62.5-61			1			1
	63.0-58		1				1
	9	**2**	**6**	**23**	**7**	**0**	**38**
	63.5-62				2		2
Palmer	63.5-63					1	1
Arch.	63.5-64			1	2		3
	3	**0**	**0**	**1**	**4**	**1**	**6**
	64.5-67				1		1
	65.0-67					3	3
Biscoe	65.0-68					1	1
Is.	65.5-68				2		2
	66.0-69					2	2
	5	**0**	**0**	**0**	**3**	**6**	**9**
Total	**60**	**12**	**191**	**246**	**67**	**20**	**536**

[1)]Geographic coordinates refer to the northeast edge of the square.

Density was investigated using the swept area method (Anon 1977, Mucha 1984), and it is expressed in kg per 1 km^2 of sea bottom area. The gear effectiveness [s] was assumed to be 1.

Of the fish species that were identified during the cruises (Skóra and Sosiński 1983, Sosiński and Szlakowski 1992, Sosiński 1990, 1994, 1999), those which constituted a minimum of 1% of the mass of caught fish during the investigations in one of the seasons were chosen for density investigations. There were 14 such species, 5 from the family Channichthyidae and 9 from the family Nototheniidae. They were marked according to the list of fish from the region within the scope of Commission for the Conservation of Antarctic Marine Living Resources [CCAMLR] (Fischer and Hureau 1985). The fish names were taken from Gon and Heemstra (1990) and in accordance with the verified list of the most numerous fish group, Notothenioidei, which was published by Eastman and Eakin (2000). The work also presents *Lepidonotothen kempi*, which is currently regarded as synonymous to *Lepidonotothen squamifrons*.

RESULTS

Control catches were carried out on the shelves of the following islands: Shag Rocks, South Georgia, the South Orkneys, Elephant, Joinville, South Shetlands, Palmer and Biscoe. The areas of their shelves, up to the 500 m isobath, and the percentage of depth zones are found in Table 3.

Among the fish species identified during the investigations, 14 were noted as having significant density, 5 were from the family Channichthyidae and 9 from the Nototheniidae.

The species were as follows:

Family Channichthyidae:

Champsocephalus gunnari Lönnberg, 1905,
Chaenocephalus aceratus Lönnberg, 1906,
Pseudochaenichthys georgianus Norman, 1937,
Chionodraco rastrospinosus De Witt & Hureau, 1979,
Chaenodraco wilsoni Regan, 1914,

Family Nototheniidae:

Notothenia rossii Richardson, 1844,
Notothenia coriiceps Richardson, 1844,
Gobionotothen gibberifrons Lönnberg, 1905,
Lepidonotothen squamifrons Günther, 1880,
Lepidonotothen kempi Norman, 1937,
Dissostichus eleginoides Smitt, 1898,
Dissostichus mawsoni Norman, 1937,
Patagonotothen guntheri Norman, 1937,
Pleuragramma antarcticum Boulenger, 1902.

The mean densities of particular fish species according to regions are given in appendices 1-13.

Of the white-blooded fish from the family Channichthyidae three species, *Champsocephalus gunnari*, *Chaenocephalus aceratus* and *Pseudochaenichthys georgianus,* appeared throughout the AOAA (appendices 1, 2 and 3).

Table 3. Areas of shelves and percentage of depth zones in particular regions of the Atlantic Ocean Antarctic Area

Region	Percentage of depth layers (m) [in %]					Total shelf area (0-500 m) [in km^2]
	0-100	101-200	201-300	301-400	401-500	
Shag Rocks	14	39	30	9	8	11,368
South Georgia Is.	14	35	29	11	11	40,332
South Orkneys Is.	5	11	22	31	31	29,308
Elephant Is.	12	19	19	25	25	10,067
Joinville Is.	3	8	22	34	33	40,468
South Shetlands Is.	24	32	15	15	14	25,505
Palmer Arch.	11	19	20	25	25	39,872
Biscoe Is.	8	16	22	27	27	49,686
Sandwich Is.			100			1,294

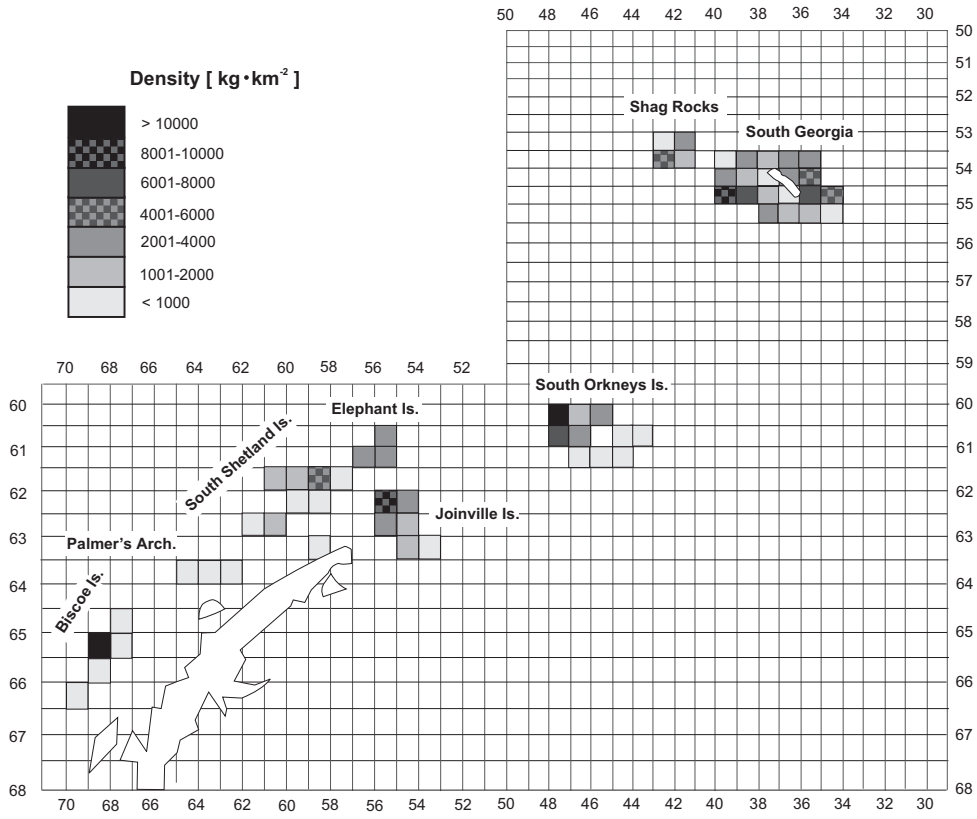

Fig. 2. Fish density on the shelves of the Atlantic Ocean Antarctic Area

Two species from the family Channichthyidae, *Chionodraco rastrospinosus* and *Chaenodraco wilsoni*, occurred only in areas located farther to the south (appendices 4 and 5). However, the densities of these two species varied in particular regions. *Chionodraco rastrospinosus* inhabited (average density) the majority of southern regions, while *Chaenodraco wilsoni* only occurred widely near Joinville Is. However, its density in this area was high.

Three groups of fish species from the family *Nototheniidae* which had a higher density in the AOAA are distinguishable.

One group consists of species which inhabited all regions of the AOAA, they are *Notothenia rossii*, *Gobionotothen gibberifrons* and *Lepidonotothen squamifrons* (appendices 6, 7 and 8).

The second group of widely occurring species from the family Nototheniidae are *Dissostichus eleginoides* and *Patagonotothen guntheri*, they only inhabit the northern regions, i.e. Shag Rocks and South Georgia (appendices 9 and 10).

The third group from the family Nototheniidae include species which were only observed in the southern regions. They are *Notothenia coriiceps*, *Dissostichus mawsoni*, *Lepidonotothen kempi* and *Pleuragramma antarcticum* (appendices 11, 9, 12 and 13).

The density of all fish which inhabit the AOAA shelves, including those which are described as *pisces nei* in the tables, are presented in Figure 2. The greatest density of fish

occurred on the South Georgia and South Orkneys shelf, while relatively lower densities were observed in the southern part of the Antarctic Peninsula. The high concentration of *Pleuragramma antarcticum*, which was confirmed in February 1979 on the Biscoe shelf, was exceptional.

This work also presents fish distribution according to depth zones. Table 4 presents the densities in depth zones in particular regions, while Table 5 and Figure 3 present the averages for the entire area.

The results obtained indicate that particular species inhabit the shelf in a large depth range, however, the distribution curves are of the one peak type indicating a preferred depth. Of the fish from the family *Channichthyidae* (Fig. 3A), three species inhabit the shelf in a large depth range (*Champsocephalus gunnari*, *Chaenocephalus aceratus* and *Pseudochaenichthys georgianus*). They are observed in both the shallow (up to 100 m) and deep areas of the shelf. However, the majority of them occur at depths of 100-200 m. *Chionodraco rastrospinosus* and *Chaenodraco wilsoni* occur in the southern regions inhabiting mainly deeper shelf areas. They were not observed at all at depths to 100 m.

Fish from the family *Nototheniidae* (Fig. 3B) also exhibit various depth preferences among species. The wide-spread *Gobionotothen gibberifrons* is present at all shelf depths, but its greatest concentrations were observed at 100-200 m. Similar depths are preferred by *Notothenia coriiceps,* while the greatest densities of *Lepidonotothen squamifrons*, *Lepidonotothen kempi* and *Notothenia rossii* were found in the deeper parts of the shelf (300-400 m).

Two fish species which occur in very limited and distant regions also preferred different depths. *Patagonotothen guntheri*, which occurs near Shag Rocks, inhabits a relatively shallow shelf, 100-200 m (Table 4). *Pleuragramma antarcticum,* which inhabits the shelf of the southern part of the Antarctic Peninsula (Biscoe Is.), was caught at depths of 400-500 m and deeper (Table 4).

Fish that inhabit the shelves of the islands located within the AOAA form groups which vary in terms of species composition, shelf density and distribution according to depth zones.

This paper presents the analysis of fish species that occurred in significantly higher numbers. The investigations indicated that the shelf density varied with region and season (Table 6). The highest fish density was observed in 1975-76 near South Georgia (16,000 kg · km^{-2}), while the lowest density, below 1,000 kg · km^{-2} was observed in 1978-79 (Palmer Arch.), 1980-81 (Elephant Is., Joinville Is.) and in 1987-88 (Shag Rocks and South Shetlands Is.). Relatively high sea bottom density of approximately 6,000-8,000 kg · km^{-2} was confirmed in 1978-79 (South Orkneys Is., Joinville Is., Biscoe Is.), 1983-84 (Elephant Is.) and 1986-87 (South Shetlands Is.). Throughout the investigation period, the greatest settlement density on average, approximately 4,000-5,000 kg · km^{-2}, was observed in the areas of South Georgia and the South Orkneys. The average settlement in other regions (including Palmer Arch. and Biscoe Is.) was from 2,200 kg · km^{-2} to 3,500 kg · km^{-2} (Elephant) (Table 6, Fig. 4).

Low density of fish on the shelf of Palmer Arch. and high density in the region of Biscoe Island were confirmed once in February 1979.

By considering the areas of shelves in particular regions and their predominant densities (Table 3), the density of fish and the percentage of fish species in the groups and the predominant depth of their occurrence (Tables 4 and 6, Figure 4), the regions can be characterized as follows:

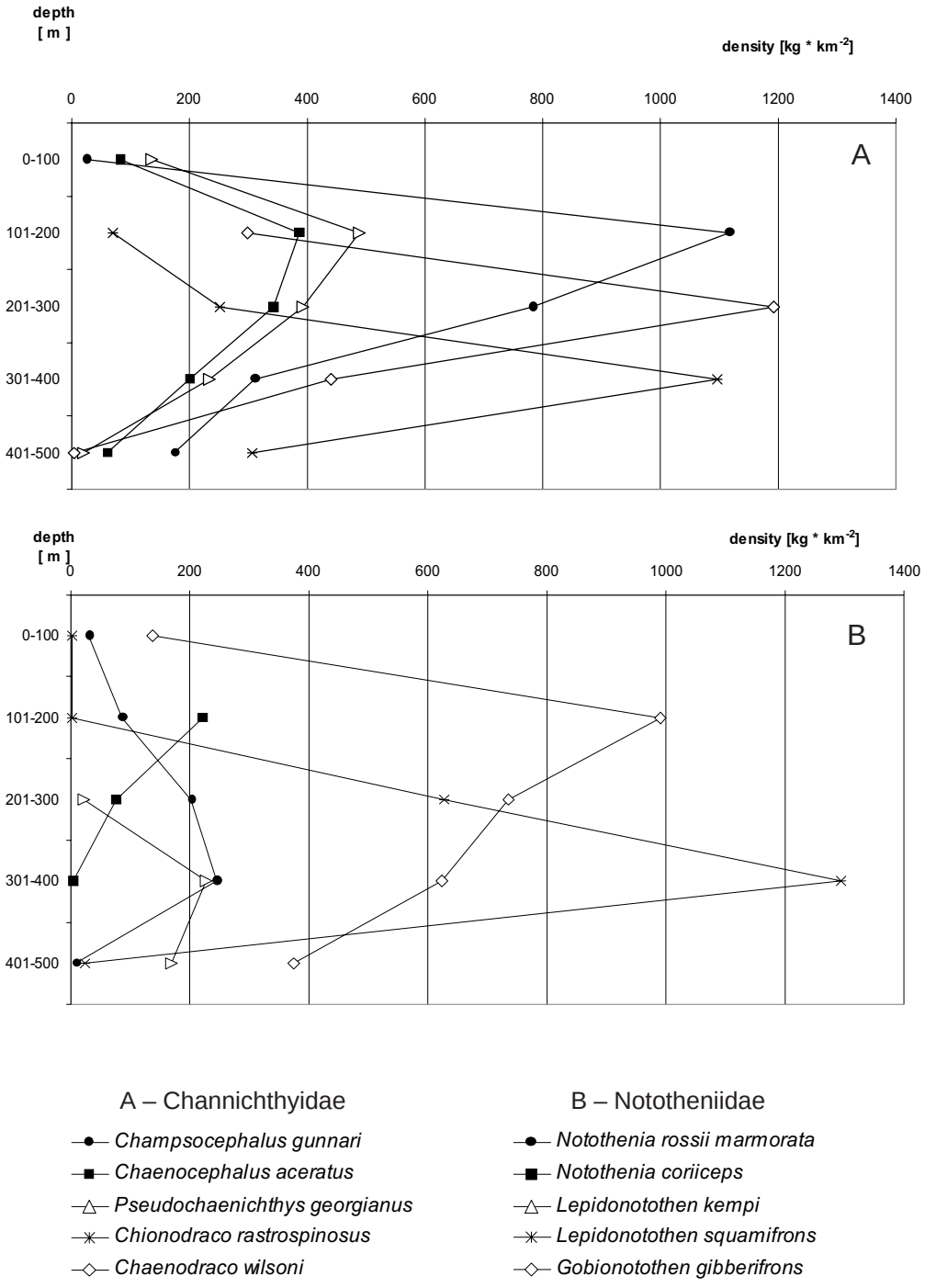

Fig. 3. Density of fish from the families Channichthyidae (A) and Nototheniidae (B)

Table 4. Mean fish density (kg · km^{-2}) in the regions of the Atlantic Ocean Antarctic Area

Region	Depth layer	Species[1)]															Total
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Shag Rocks	2	892	27	0	0	0	0	0	138	0	0	1,215	0	654	0	125	3,051
	3	388	0	0	0	0	0	0	31	17	0	18	0	0	0	75	529
	4	0	0	0	0	0	0	0	0	0	0	35	0	0	0	23	58
	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	106	1,06
South Georgia Is.	1	31	102	149	0	0	32	0	188	2	0	4	0	0	0	96	604
	2	1,284	320	640	0	0	108	0	481	1	0	6	0	0	0	119	2,959
	3	872	375	538	0	0	272	0	509	696	0	64	0	0	0	649	3,975
	4	328	187	235	0	0	351	0	337	1,437	0	653	0	0	0	346	3874
	5	6	6	0	0	0	0	0	0	23	0	30	0	0	0	560	625
South Orkneys Is.	3	1,868	331	174	221	8	12	10	1,708	0	2	0	0	0	0	73	4,407
	4	320	505	582	3,858	438	108	0	2,140	0	16	0	0	0	0	779	8,746
	5	39	148	75	383	0	0	0	417	0	0	0	0	0	0	423	1,485
Elephant Is.	1	0	45	0	0	0	0	0	0	0	0	0	0	0	0	60	105
	2	1,172	812	31	12	0	18	296	4,084	0	0	0	4	0	0	48	6,477
	3	473	414	14	100	2	58	99	1,743	0	72	0	7	0	0	88	3,070
	4	877	253	0	305	0	14	0	957	9	104	0	20	0	0	53	2,592
	5	452	102	6	502	0	26	0	953	0	384	0	0	0	0	481	2,906
Joinville Is.	2	0	0	0	106	787	0	0	106	0	0	0	0	0	0	35	1,034
	3	21	2	0	264	3,446	0	120	153	0	2	0	0	0	0	218	4,226
	4	16	0	0	350	1,171	9	12	385	0	75	0	49	0	0	492	2,559
South Shetlands Is.	1	9	18	0	0	0	22	0	4	0	0	0	0	0	0	9	62
	2	190	243	15	179	508	9	221	264	3	4	0	8	0	0	176	1,820
	3	248	299	71	579	8	9	72	970	4	14	0	13	0	0	120	2,407
	4	30	90	50	206	4	0	4	423	0	0	0	49	0	0	710	1,566
Palmer Arch.	3	44	119	97	106	4	0	0	84	0	123	0	24	0	0	66	667
	4	21	134	34	285	12	0	0	70	0	137	0	0	0	0	42	735
	5	0	0	0	44	26	0	0	18	0	35	0	0	0	0	26	149
Biscoe Is.	4	0	100	0	69	13	0	0	39	0	1,310	0	29	0	0	56	1,616
	5	0	0	0	21	1	0	0	4	0	70	0	0	0	8,391	39	8,526

[1)]list of species:

1 – *Champsocephalus gunnari*
2 – *Chaenocephalus aceratus*
3 – *Pseudochaenichthys georgianus*
4 – *Chionodraco rastrospinosus*
5 – *Chaenodraco wilsoni*
6 – *Notothenia rossii*
7 – *Notothenia coriiceps*
8 – *Gobionotothen gibberifrons*
9 – *Lepidonotothen squamifrons*
10 – *Lepidonotothen kempi*
11 – *Dissostichus eleginoides*
12 – *Dissostichus mawsoni*
13 – *Patagonotothen guntheri*
14 – *Pleuragramma antarcticum*
15 – *Pisces nei*

Table 5. Average concentrations of fish inhabitance by depth zones

Species	Depth layer [m]									
	0-100		101-200		201-300		301-400		401-500	
	mean	δ^2	mean	δ^2	mean	δ^2	mean	δ^2	mean	δ^2
Champsocephalus gunnari	24	18.3	1,117	2,254.2	782	1,856.4	312	848,9	173	405.1
Chaenocephalus aceratus	82	64.9	387	428.0	343	379.0	199	477.4	59	125.1
Pseudochaenichthys georgianus	136	179.6	489	1,660.4	393	1,202.0	233	782.6	20	49.0
Chionodraco rastrospinosus	0		70	170.5	252	479.8	1,097	4,266.6	308	508.6
Chaenodraco wilsoni	0		301	466.4	1,192	5,876.7	441	1,053.6	3	8.6
Notothenia rossii marmorata	30	23.5	87	380.3	202	1,255.1	246	1,233.9	8	20.0
Notothenia coriiceps	0		222	364.4	76	133.2	4	12.4	0	
Lepidonotothen kempi	0		0		22	61.0	228	623.6	169	197.5
Lepidonotothen squamifrons	2	4.5	1	3.2	628	4,343.2	1,294	5,665.2	23	17.5
Gobionotothen gibberifrons	137	220.3	990	1,865.1	736	1,225.2	623	1,441.7	375	834.9

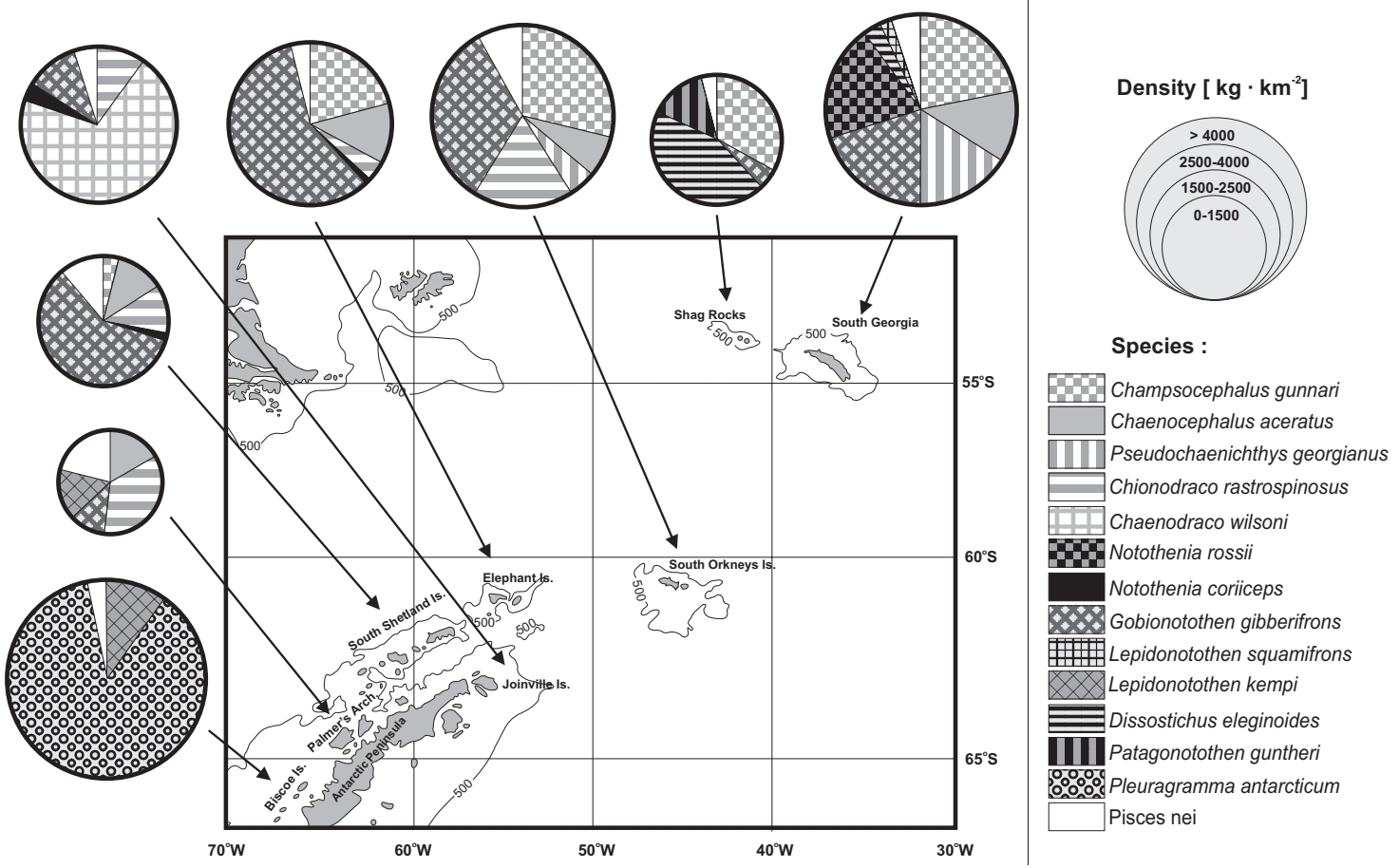

Fig. 4. Density and distribution of massively occuring fish in particular regions of the Atlantic Ocean Antarctic Area

Table 6. Mean fish density (kg · km^{-2}) and species composition (% of biomass) on the shelf of the Atlantic Ocean Antarctic Area

Region	Season	Density		Species[1)]													
		mean	δ^2	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Shag Rocks	1978/79	4,168	847.0	9	1						3			68		18		1
	1980/81	1,806	10.6	18							7			46		28		1
	1986/87	2,214	2,753.9	86							3			5				6
	1987/88	616	644.2	38							17	3		11				31
	total	2,204	1.476.2	33	+						5	+		44		14		4
South Georgia Is.	1975/76	16,472	6,745.1	14	12	16			30		22			2				3
	1978/79	1,822	873.4	13	21	20			4		25			5				8
	1986/87	4,010	4,361.6	47	8	4			3		12	21		1				4
	1987/88	1,880	1,430.1	28	10	24			3		15	1		12				7
	1988/89	2,257	2,591.7	43	10	8			3		16	1		1				8
	total	5,287	6,315.3	22	12	16			20		20	3		2				5
South Orkneys Is.	1978/79	8,125	8,004.1	32	6	4	20	2			30							6
	1983/84	1,225	1,645.0	11	14	10	5	1		1	54		1					3
	total	4,705	4,879.0	29	7	5	18	2	1	+	33		+					5
Elephant Is.	1978/79	3,462	2,613.3	46	8	1	12				28							3
	1980/81	487	485.8		1		2	1		3	76							17
	1983/84	8.185	0.0	24	7		4		1	1	61							1
	1986/87	3,833	1,281.1	5	15						79							1
	1987/88	2.049	1,989.7	3	24		2		2	10	57	1						2
	1988/89	2,899	645.2	17	18	1			1		62							1
	total	3,486	2,592.5	21	12	+	4	+	1	1	58	+	1					2
Joinville Is.	1978/79	8,361	13,942.1				5	87			5							3
	1980/81	831	0.0				15	5		49	26							5
	1983/84	1.400	596.3				33	14		4	28		1					20
	1986/87	1,425	1,083.7				9	57			24							10
	total	3,004	3,581.7				9	70		4	11		+					6
South Shetlands Is.	1978/79	2,647	3,283.9	12	7	3	27	6		1	35				1			8
	1980/81	1,303			1		4			3	47							45
	1986/87	6,789			15		9				73							3
	1987/88	760		7	20	1	4		1	21	43				1			2
	total	2,875	2,727.4	4	12	1	12	1	+	2	59				+			9
Palmer Arch.	1978/79	519	324.0	4	17	6	35	3			11		16		1			7
Biscoe Is.	1978/79	5,866	10,589.8		1		1						10				87	1

[1)]Species numbers as in Table 4.

The Shag Rocks shelf**,** with an area of 11,000 km^2, has a predominant depth of between 100 and 300 m. The group of fish with higher density includes the following species (beginning with the highest percentage):

Dissostichus eleginoides,
Champsocephalus gunnari,
Patagonotothen guntheri,
Gobionotothen gibberifrons.

The greatest density was confirmed in the 100-200 m depth zone.

The South Georgia shelf**,** with an area of 40,000 km^2, has predominant depths of between 100 and 300 m. The high density fish are as follows:

Champsocephalus gunnari,
Gobionotothen gibberifrons,
Notothenia rossii marmorata,
Pseudochaenichthys georgianus,
Chaenocephalus aceratus,
Dissostichus eleginoides,
Lepidonotothen squamifrons.

The greatest density was observed in the 200 to 400 m layer. However, the 100-200 m layer also had relatively high density (Table 4). In this region, in addition to the above fish, *Trematomus hansoni* and *Bathyraja sp*. were also relatively abundant (Table 4, pisces nei column).

The South Orkneys shelf**,** with an area of 30,000 km^2, has a relatively large area that has deeper waters with depths from 200 to 500 m. The fish group consists of:

C*hampsocephalus gunnari,*
Gobionotothen gibberifrons,
Chionodraco rastrospinosus,
Chaenocephalus aceratus,
Pseudochaenichthys georgianus.

In comparison with the regions described above, the greatest density was observed much deeper at 300-400 m.

The Elephant Island shelf has a much smaller area (10,000 km^2), and the percentages from the five depth zones are more uniform than in the other regions. High density benthic fish include:

Gobionotothen gibberifrons,
Champsocephalus gunnari,
Chaenocephalus aceratus,
Chionodraco rastrospinosus,
Notothenia coriiceps neglecta.

The 100-200 m layer was inhabited most frequently. However, the deeper parts of the shelf were also characterized by high density. Relatively high concentrations of *Cryodraco antarcticus* and *Trematomus eulepidotus* (Table 4, pisces nei column) were observed in the area.

The Joinville Island shelf (40,000 km^2) has the highest percentage of deep areas (from 300 to 500 m). Widely occurring fish include:

Chaenodraco wilsoni,
Chionodraco rastrospinosus,
Gobionotothen gibberifrons,
Notothenia coriiceps neglecta.

The highest fish density was observed in the 200-300 m layer. Similarly to the Elephant area, higher numbers of *Trematomus eulepidotus* and *Cryodraco antarcticus* were observed. Their density in both regions ranged from 100 to 200 kg per km^2 of sea bottom.

The South Shetlands shelf (25,000 km^2) has a relatively large number of shallow areas, 0-100 and 101-200 m, which are inhabited by higher densities of fish:

Gobionotothen gibberifrons,
Chionodraco rastrospinosus,
Chaenocephalus aceratus,
Champsocephalus gunnari.

The greatest fish densities were observed in the 200-300 m layer, an area which constitutes only 15% of the shelf. Of the fish which are in the *pisces nei* column in Table 5, the bathypelagic species *Gymnoscopelus nicholsi* was relatively numerous, and in 1980-81 it appeared near the bottom at depths of 300-400 m. Its density was 650 kg · km^{-2}.

The shelves of the Palmer Arch. (40,000 km^2) and Biscoe Is. (50,000 km^2) archipelagos have a high percentage of deep areas, 300-500 m. The species composition of widely occurring fish was determined from a one-time investigation that was carried out in February 1979.

The multi-species composition of fish near Palmer Island was represented by the following:

Chionodraco rastrospinosus,
Lepidonotothen kempi,
Chaenocephalus aceratus,
Gobionotothen gibberifrons.

Near Biscoe Island, widely occurring fish were:

Pleuragramma antarcticum,
Lepidonotothen kempi.

In both regions, high densities of these fish were observed in the 300-400 m layer.

DISCUSSION

Characteristic features of Antarctic ichthyofauna include: a relatively low number of species - 272 according to Gon and Heemstra (1990), highly developed endemism – about 95% of the species are related to the Southern Ocean (Kulesz 1998), the largest number of species inhabit the benthic coastal areas (63.2%) (Eastman 1993). Only a few species occur in greater densities, however, their relatively small biomass constitutes an important element in the Antarctic marine trophic chain.

Based on the results of investigations which were carried out from the R/V PROFESOR SIEDLECKI in 1975-89, 14 fish species were identified that formed higher densities in the western Atlantic Ocean Antarctic Area of the western Antarctic. Additionally, their densities near the sea bottom were determined and expressed in the form of biomass per 1 km^2 of sea bottom.

Champsocephalus gunnari is a species endemic to the Antarctic. It appears around the islands in the Scotia Sea, in the northern part of the Antarctic Peninsula, and around the Bouvet, Kerguelen and Heard islands. It usually inhabits the bottom zone, however, it also feeds in the pelagic zone (Iwami and Kock 1990). The results of the investigations described above indicate that it is widely distributed throughout the AOAA, the highest densities were confirmed on the shelves of the South Georgia, Shag Rocks and South Orkneys and Elephant islands (appendix 1). In the other areas, this species was observed in amounts lower than 100 $kg \cdot km^{-2}$; it was not observed at all near Biscoe Island.

Chaenocephalus aceratus is a species endemic to the Antarctic which inhabits areas near Bouvet Island and the islands in the Scotia Sea as well as the shelves in the northern part of the Antarctic Peninsula (Iwami and Kock 1990). In the area investigated, it was observed in almost all regions, however, its density was lower than that of *Champsocephalus gunnari* (appendix 2). Only near the Palmer Archipelago was this species more abundant than *Champsocephalus gunnari.*

Pseudochaenichthys georgianus is also an endemic Antarctic species. It is observed only in this part of the Southern Ocean near the islands in the Scotia Sea and on the shelf of the northern part of the Antarctic Peninsula (Iwami and Kock 1990). In the area investigated, its density was higher only on the shelves of South Georgia and the South Orkneys (appendix 3).

Chionodraco rastrospinosus is an endemic Antarctic species whose occurrence was only observed near the South Orkneys and on the shelves of the islands in the northern part of the Antarctic Peninsula (Iwami and Kock 1990). The current research indicates that the greatest concentrations of these fish are observed on the west shelf of the South Orkneys and the shelves of the Joinville and South Shetlands islands (appendix 4).

Chaenodraco wilsoni inhabits areas around the Antarctica, near the continental shelf and more to the north, near the South Orkneys and the Antarctic Peninsula (Iwami and Kock 1990). The investigations in the AOAA revealed that significant concentrations of these fish were observed only on the shelf of Joinville Island (appendix 5).

Notothenia rossii is widely scattered throughout the Antarctica (De Witt *et. al.*, 1990). Two subspecies can be identified: *N. rossii rossii* Richardson, 1844 which inhabits Subantarctic islands in the Indian Ocean area, and *N. rossii marmorata* Fischer, 1985 which inhabits the region which is discussed in this paper (Fischer and Hureau 1985). During the investigations, greater densities of *N. rossii marmorata* were confirmed only on the southeast shelf of South Georgia (appendix 6). This species occurred sporadically near the South Orkneys and in the northern part of the Antarctic Peninsula.

Notothenia coriiceps occurs in the coastal area around Antarctica, on the shelves of the Antarctic Peninsula and the islands in the Scotia Sea (De Witt *et al*., 1990). The subspecies *N. coriiceps neglecta* Nybelin, 1951 is associated with the AOAA (Fischer and Hureau 1985). During the investigations, it did not form great concentrations. Only in the small areas of Joinville Island and the South Shetlands was it observed at a density of 100-200 kg per 1 km^2 of sea bottom area (appendix 11). This species was not observed near South Georgia or Shag Rocks.

Gobionotothen gibberifrons occurs only in the AOAA near the islands of the Scotia Ridge and on the shelf of the northern part of the Antarctic Peninsula (De Witt *et al.*, 1990). This species was the most common in the investigated area and it inhabited all the shelves with relatively high densities. Its greatest densities were observed on the eastern shelf of South Georgia, the northeastern shelf of the South Orkneys and on the shelf of Elephant Island (appendix 7).

Lepidonotothen squamifrons occurs in the Antarctica and on the shelves of the subantarctic islands (De Witt *et al.*, 1990). The populations which occur near South Georgia and the islands of the Scotia Ridge are regarded by some taxonomists as the subspecies *Notothenia squamifrons atlantica* Permitin and Sazanow, 1974 (Fischer and Hureau 1985). During the investigations, their density was rather low in comparison with that of other species. Only in the southern part of the South Georgia shelf was a concentration of significant density confirmed – over 5,000 kg per 1 km^2 of sea bottom area (appendix 8).

Lepidonotothen kempi, according to De Witt *et al*., (1990), occurs around the Antarctica. During the investigations, it was only observed on the shelves of the Antarctic Peninsula and the South Orkneys (appendix 12).

Dissostichus eleginoides is a species that occurs on a wider scale. It is fished in the southern waters of Chile, Patagonia, and the Falkland Islands and near Shag Rocks and South Georgia (De Witt *et al*., 1990). In the investigated area, concentrations of it were observed near Shag Rocks and South Georgia (appendix 9). The higher density of this species was observed on the shallow shelf of Shag Rocks. The region of South Georgia this species occurred in concentrated schools in various parts of the deeper waters.

Dissostichus mawsoni, unlike the similar species *Dissostichus eleginoides,* is an endemic form which occurs around the Antarctica up to 55°S (De Witt *et al*., 1990). During the investigations carried out from the R/V Profesor Siedlecki, only small concentrations of this species were observed and their densities were 100 kg per 1 km^2 of sea bottom on the shelves of the islands in the northern part of the Antarctic Peninsula (appendix 9), mainly in the deeper parts.

Patagonotothen guntheri inhabits the Atlantic slopes of the Patagonian regions the Falkland Islands, Burdwood Bank and the Shag Rocks shelf (De Witt *et al*., 1990). The population which inhabits the Shag Rocks shelf is regarded as a subspecies of *Patagonotothen guntheri shagensis* Baluskin and Permitin 1982 (Fischer and Hureau 1985). This species was observed during the investigations only on the Shag Rocks shelf, where it formed dense concentrations.

Pleuragramma antarcticum is an endemic species which occurs in the pelagic waters around Antarctica and on the shelves of the islands located near the Antarctic Peninsula and the South Orkneys (De Witt *et al*., 1990). Significant concentrations were observed during the investigations only in February 1979 near Biscoe Island (appendix 13).

The list of high density species represent only two of the 33 families reported in the analyzed area, namely Channichthyidae and Nototheniidae (Kulesz 1998).

The majority of the species which occur in the AOAA on a wide scale are endemic to this area. Only three species have wider range that exceeds the Antarctic Polar Front zone in the north, these are: *Dissostichus eleginoides, Lepidonotothen squamifrons* and *Patagonotothen guntheri*.

Of the endemic Antarctic species which occur widely in the AOAA, *Champsocephalus gunnari*, *Chaenodraco wilsoni*, *Lepidonotothen kempi*, *Dissostichus mawsoni* and *Pleuragramma antarcticum* also occur in other Antarctic areas. However, *Chaenocephalus*

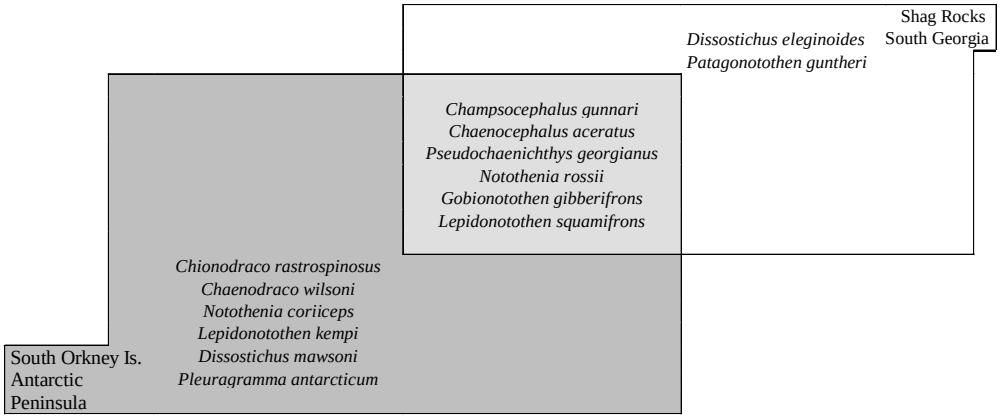

Fig. 5. Fish species which occur massively in the benthic zone in the Atlantic Ocean Antarctic Area

aceratus, *Pseudochaenichthys georgianus, Chionodraco rastrospinosus* and *Gobionotothen gibberifrons* were observed only in the AOAA.

The AOAA is divided into two sub-areas according to the Andriashev zoogeographic division of 1965 (Andriashev 1965), and updated by him in 1987 (Eastman 1993), and by Kock (1992). The first area includes the shelves of Shag Rocks and South Georgia, known as the South Georgia Province or the Ice-free Zone, where *Dissostichus eleginoides* and *Patagonotothen guntheri*, two species not found in other regions, occur abundantly. The second sub-area includes the shelves of the South Orkneys and the islands adjacent to the Antarctic Peninsula, known as the West Antarctic Province or the Seasonal Pack-ice Zone, where six fish species that are not found in the first sub-area occur massively. These are: *Chionodraco rastrospinosus*, *Chaenodraco wilsoni*, *Notothenia coriiceps*, *Lepidonotothen kempi*, *Dissstichus mawsoni* and *Pleuragramma antarcticum*.

The remaining six species of the 14 investigated, i.e. *Chamsocephalus gunnari*, *Caenocephalus aceratus*, *Pseudochenichthys georgianus*, *Notothenia rossii*, *Gobionotothen gibberifrons* and *Lepidonotothen squamifrons*, were observed in both sub-areas (Fig. 5).

Andriashev and De Witt (Eastman 1993) reported that the greatest number of fish species which inhabit the Antarctic shelf occurs at depths of 200-400 m. Their research also indicated that the shelves at these depths have the greatest density of massively occurring fish species.

The distribution and diversity of the densities of fish of particular species at particular shelves of the AOAA results in differentiated ichthyocenosis of major species (in terms of density). The percentage of particular species in groups of fish in various fishing grounds fluctuates temporally. However, over a longer period of time certain regularities are detectable and are presented in this paper.

In general, the shelves of particular islands of various areas have regions of lower or higher fish density (Fig. 2). The largest and most densely inhabited is the South Georgia shelf, followed by the South Orkneys shelf. The shelves of the islands located near the Antarctic Peninsula have a lower fish density. The tendency is southerly. The high density observed near Biscoe Island must have been a one-time event.

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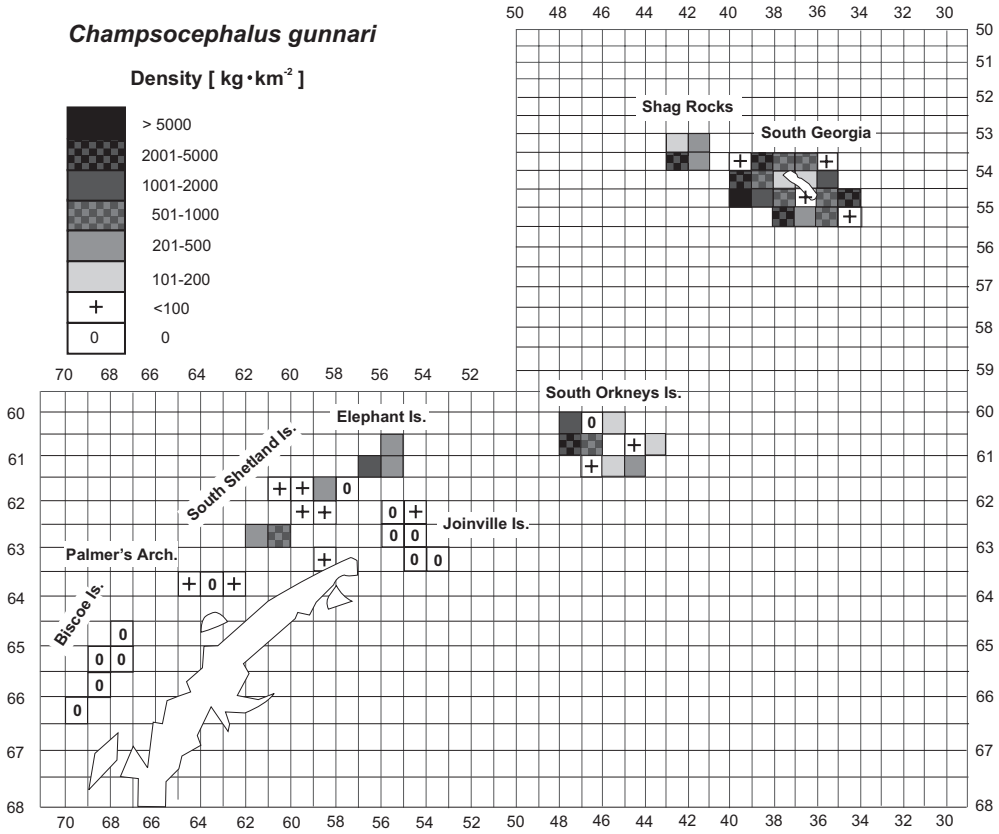
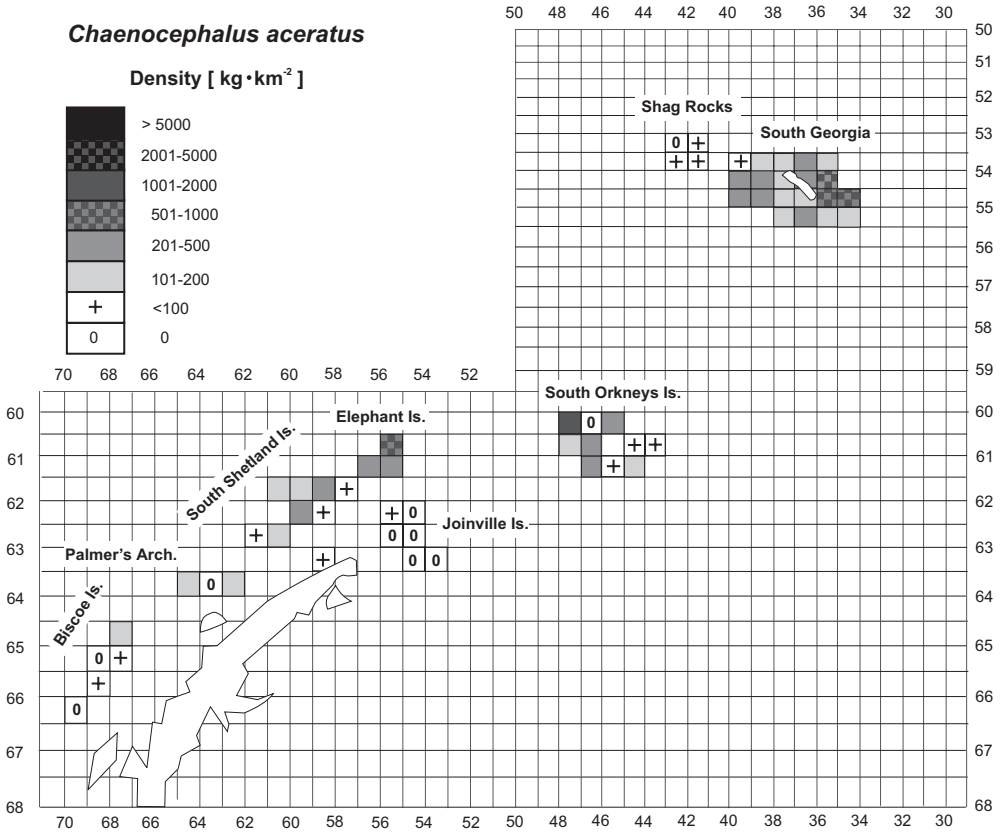
Appendix 1

Champsocephalus gunnari density
on the shelves of the Atlantic Ocean Antarctic Area



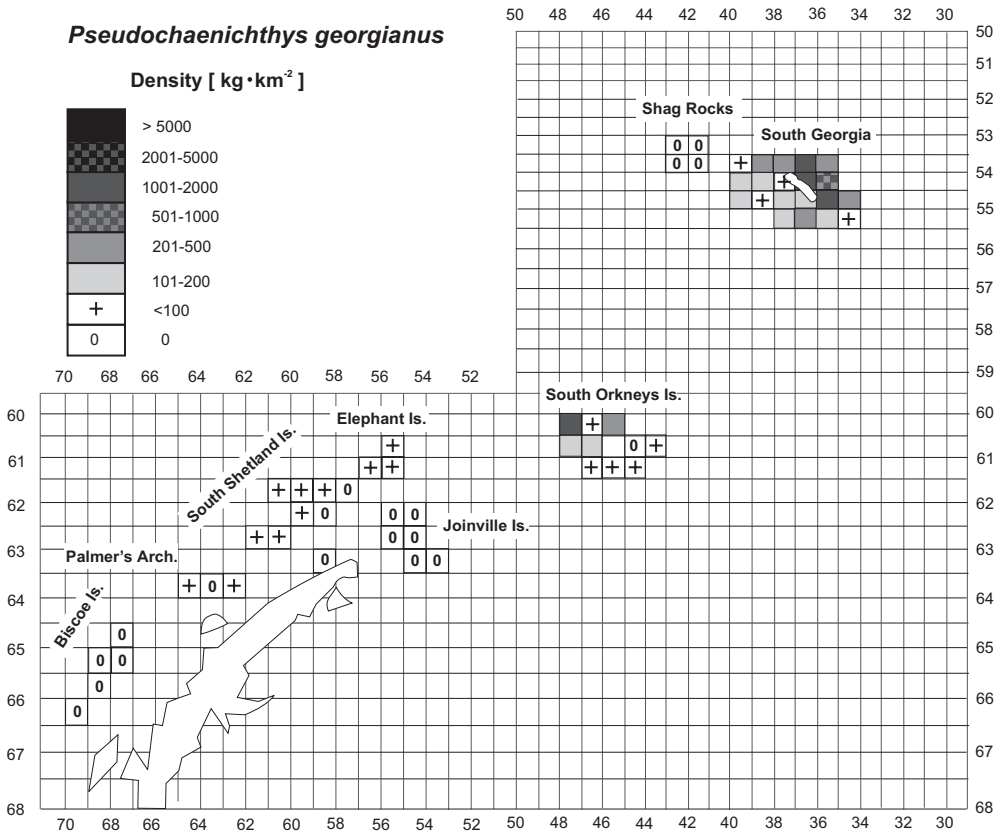
Appendix 2

Chaenocephalus aceratus density
on the shelves of the Atlantic Ocean Antarctic Area



Appendix 3

Pseuochaenichthys georgianus density
on the shelves of the Atlantic Ocean Antarctic Area



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Environmental factors controlling primary production in the Polish part of the Vistula Lagoon

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Abstract This work presents the characteristics of some environmental factors influencing primary production and chlorophyll *a* distribution of the Polish part of the Vistula Lagoon based on investigations that were carried out between April and November 1999. Due to the significant temporal and spatial variability of nutrient concentrations, the average values of particular parameters were derived in order to describe the hydrochemical conditions. The highest nutrient concentrations occurred near the outlets of the Nogat River and the Elbląg Canal. The highest N/P ratio, on average about 20, was also observed in these areas, whereas the average N/P ratio for the entire Polish part of the Vistula Lagoon is about 6. A significant decrease in nutrient concentration, especially of nitrates and ammonia nitrogen, was observed when the results of the current investigations were compared with those from 1975-1978. The transparency of the lagoon waters has also decreased. The average chlorophyll concentrations were estimated to be about 43.5 mg $\cdot$ m^{-3}. The chlorophyll distribution in the Vistula Lagoon was described, and the primary production rate was determined. Additionally, the monthly primary production was derived. The average annual production was estimated to be 303.8 gC $m^{-2} \cdot y^{-1}$. A dependence between the photosynthetic rate and the phosphate concentration was noted.

Key words: nutrients, chlorophyll *a*, transparency of water, primary production, photosynthetic light curves, Vistula Lagoon

INTRODUCTION

The Vistula Lagoon plays an important role in many areas of the Polish economy; its most significant aspects are fisheries, natural and recreational resources. This is why hydrological, biological and ichthyological investigations have been carried out in this area for a number of years. The bibliography regarding the lagoon is extensive (Anon. 1978) and includes monographs (Łazarienko and Majewski 1975). However, almost no biological investigations of primary production and its environmental conditions have been carried out in this area. Many of the problems connected with the biological production of the Vistula Lagoon cannot be explained with the current state of knowledge. The lack of the data regarding primary production is especially disadvantageous when attempting to use mathematical models to describe and explain

the functioning of the Vistula Lagoon ecosystem. The aim of this work is to evaluate primary production and chlorophyll *a* distribution in the Vistula Lagoon and the impact of chemical and physical parameters on phytoplankton production.

THE AREA OF INVESTIGATION

The Vistula Lagoon is located in the south-eastern part of the Gdańsk Bay. It is separated from the Baltic Sea by a sandy spit 55 km long and about 400 m wide. The lagoon has an elongated shape, extending from the south-west to the north-east for 91 km and an average width of about 9 km. The area of the Vistula Lagoon is 838 km^2, of which 365 km^2 belongs to Poland. The volume of water in the lagoon is about 2.3 km^3, the mean depth is 2.7 m, and in the Polish part of the lagoon it is 2.4 m. The catchment area of the Vistula Lagoon is about 24,000 km^2. The rivers Pregel, Nogat, Pasłęka and the Elbląg Canal discharge about 17 km^3 of fresh water to the lagoon yearly. The lagoon is connected with the Baltic by a narrow strait. The temporal inflow of salt water from the Baltic influences the salinity of the lagoon water. The average salinity of the southern part of the lagoon is about 1.5 PSU, in the central part it is 3.3 PSU and in the part near the Baltic Strait it is 3.9-5.0 PSU. The investigation area and the location of 16 sampling stations in the Polish zone of the Vistula Lagoon is presented in Fig. 1.

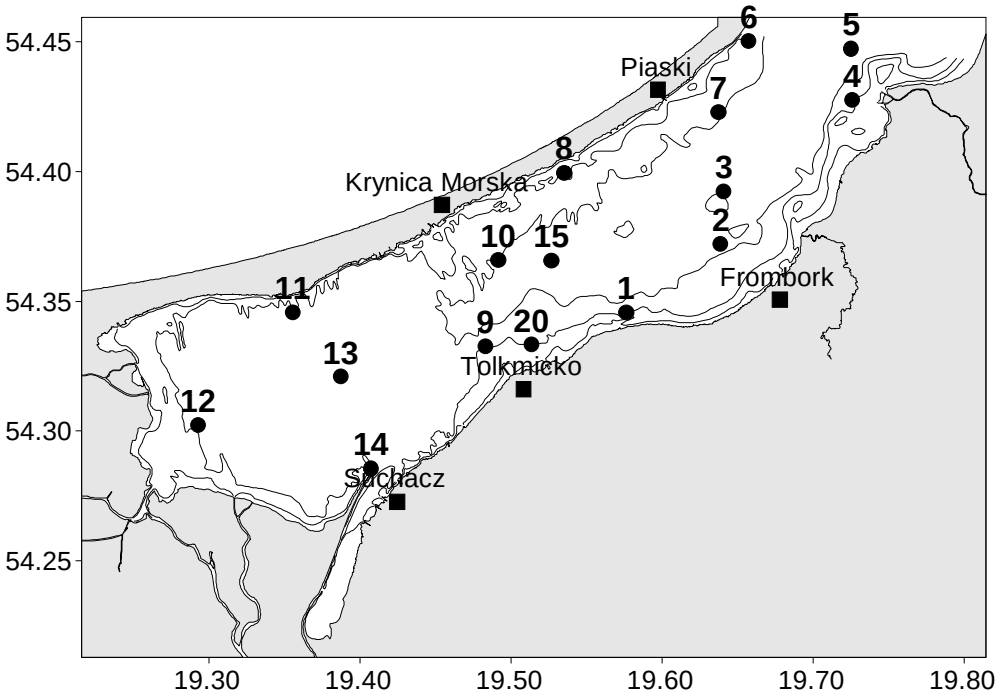

Fig. 1. Location of measurement stations in the Vistula Lagoon

MATERIALS AND METHODS

The investigations were carried out 14 times, between April and October in two week intervals and once in November. The following parameters were usually measured at all the stations: water temperature, salinity, chlorophyll *a* concentration and the Secchi depth. Nutrient concentrations (phosphates, nitrates, nitrites, ammonia, silicates), light attenuation coefficient, amount of solar radiation and photosynthetic light curves were determined each time at 3 to 5 stations. Measurements of *in situ* primary production were carried out at station 20.

All measurement procedures were carried out in accordance with those recommended for Baltic Sea investigations by the Helsinki Commission (Anon.1988), specifically, measurements of primary production by the radioisotope method using ^{14}C isotope (Steemann Nielsen 1952, Aertebjerg Nielsen, Bresta 1984) and those of chlorophyll by fluorimetric methods (Evans *et al.* 1987). Chlorophyll *a* concentrations were measured on the surface and at the depth of 1.5 m, and the results presented in this paper are the averages of these measurements. The measurements of *in situ* primary production were performed throughout the water column from 0.2 to 2.2 m every 0.25 m. The measurements of primary production for determining the photosynthetic light curves were carried out in an incubator for phytoplankton from the surface water. The light attenuation coefficient was derived from the results of scalar irradiance (in the visible light spectrum) measurements throughout the water column from the surface to 30 cm above the sea bottom.

The methodology for deriving the so-called photosynthetic light curves is described in Renk *et al.* 1999. Two types of curves were assigned to the experimentally derived dependence of the photosynthetic rate versus irradiance (Aalderink and Jovin 1997).

• The light curve proposed by Steele (1962) for the North Sea, which is also used for the Baltic Sea (Renk *et al.*1999), is as follows:

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

where:

P_h – photosynthetic rate described as the ratio of primary production over one hour to chlorophyll *a* concentration $\left[\frac{\text{mgC}}{\text{mgChl} \cdot \text{h}}\right]$,

E – irradiance $[\text{kJ} \cdot \text{m}^{-2} \cdot \text{h}^{-1}]$, AN – assimilation number $\left[\frac{\text{mgC}}{\text{mgChl} \cdot \text{h}}\right]$,

E_s – photosynthetic saturation irradiance $[\text{kJ} \cdot \text{m}^{-2}\ \text{h}^{-1}]$.

• The hyperbolic light curve was of the following type:

$$P_h = A \cdot \frac{E}{B + E} \qquad [2]$$

A – Asymptotic value of the photosynthetic rate $\left[\frac{\text{mgC}}{\text{mgChl} \cdot \text{h}}\right]$, (hypothetical maximum photosynthetic rate achieved at very high irradiance).

B – irradiance value at which $P_h = \frac{A}{2}$.

Primary production was determined either *in situ* or by using the parameters of the light curve in equation [1] and essential data from environmental investigations, including chlorophyll *a*, the light attenuation coefficient in the water and the daily dose of solar radiation. The following dependencies were used in the calculations:

– PAR (Photosynthetically available radiation) = 0.46 of total radiation (Sakshaug *et al.* 1997),

–water surface transmission in the Vistula Lagoon = 0.96 (Baker and Frouin 1987).

The procedure is described in detail in Renk and Ochocki (2000).

Other methodology details can be found in Głowińska *et al.* (1975), Grasshoff *et al.* (1983).

RESULTS

Hydrochemical conditions

The Vistula Lagoon is a brackish reservoir and its salinity varies significantly. The average salinity in the Polish area of the Vistula Lagoon during the investigations was about 2.40 PSU, although it was lower in the south-western lagoon and higher in the eastern part near the Russian border. Table 1 presents the salinity at three different stations in the lagoon. The lagoon is a shallow reservoir and intense mixing occurs resulting in water temperatures that are similar in its different parts. In order to characterize seasonal variations of water temperature in the lagoon, the average temperature from several stations was used. The seasonal variations of the water temperature in the Vistula Lagoon are presented in Fig. 2.

Nutrient concentrations in the lagoon varied significantly, both spatially and temporally. During the vegetative season, and especially during the spring phytoplankton bloom, the con-

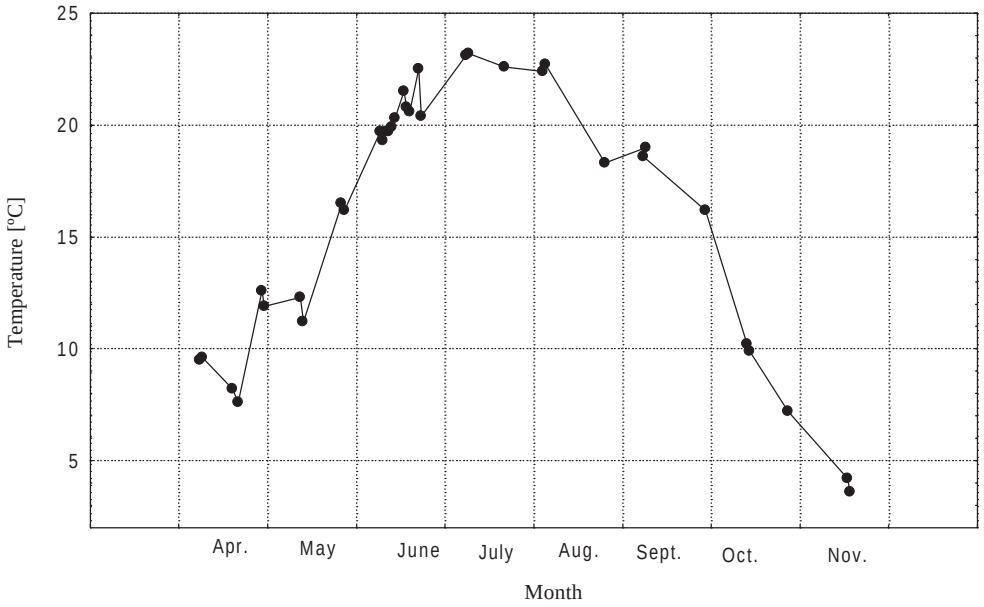

Fig. 2. Seasonal changes of water temperature in the Vistula Lagoon

Table 1. Average and extreme values of salinity [PSU] at three stations in the Vistula Lagoon in 1999

Station	Average sallinity	SD	Minimum (date)	Maximum (date)	*n*
12	1.52	0.92	0.90 (7. July)	2.41 (13. October)	10
15	2.40	0.58	1.50 (20. July, 3. August.)	3.35 (12. October)	15
5	3.30	0.86	2.15 (19. April)	4.89 (20. June)	11

Table 2. Average concentrations of nutrients for the entire investigated area during particular cruises

Cruise	Date	*n*	PO_4 $\left[\frac{mmolP}{m^3}\right]$	NO_2 $\left[\frac{mmolN}{m^3}\right]$	NO_3 $\left[\frac{mmolN}{m^3}\right]$	NH_4 $\left[\frac{mmolN}{m^3}\right]$	Si $\left[\frac{mmol}{m^3}\right]$	N/P
1	28. 04	6	0.25	0.16	1.74	0.17	81.2	26.83
2	11. 05	4	0.70	0	0.05	1.52	81.9	8.30
3	25. 05	5	1.33	0.56	0.56	0.78	77.0	0.53
4	8. 06	5	1.10	0.26	0.07	0.25	89.1	0.45
5	20. 06	5	0.99	0.07	0.16	0.27	84.2	0.67
6	7. 07	5	1.66	0.12	0.39	0.37	84.1	0.84
7	20. 07	5	0.91	0.07	0.28	0.57	86.0	1.81
8	24. 08	5	0.96	0.03	0.31	0.31	92.8	0.71
9	7. 09	5	0.46	0.06	0.22	0.05	124.8	0.81
10	28. 09	3	0.95	0.04	0.17	0.01	113.9	0.24
11	12. 10	5	1.55	0.19	0.77	2.87	112.9	3.23
12	26. 10	6	0.71	0.27	3.37	0.01	107.7	4.90
13	16. 11	3	0.82	0.25	2.65	0.09	104.6	3.60
14	30. 11	3	1.94	0.64	12.56	4.64	66.6	10.37
Average			0.98	0.11	0.75	0.58	93.4	6.34

centration of some nutrients fell below detectable limits. The average nutrient concentrations obtained at several stations during particular cruises are presented in Table 2.

The phosphate concentrations in the Vistula Lagoon were relatively high varying from 0.25 to 1.96 mmol · m^{-3}. Table 2 shows that, during the investigation period, the highest phosphate concentrations occurred in May-July and in fall, while the lowest were observed in April.

Concentrations of various forms of inorganic nitrogen in the vegetative season varied from zero to high values of approximately several mmol in 1 m^3, with the exception of station 12 where the highest nitrate concentrations occurred. Significant variations were observed at the different stations (Table 3). The distribution of particular forms of inorganic nitrogen clearly indicates that river waters are the main source of inorganic nitrogen in the Vistula Lagoon. Observations of temporal variations of different forms of inorganic nitrogen indicate that the highest levels occurred in October and April. During the vegetative season (from April to October) the average concentrations of various forms of inorganic nitrogen fluctuated around the following values: nitrites – 0.11 mmol · m^{-3}; nitrates – 0.75 mmol · m^{-3}; ammonia nitrogen – 0.58 mmol · m^{-3}. The average ratio of inorganic nitrogen to phosphorus in the Vistula Lagoon during the vegetative season is low. Only near Elbląg is the N:P ratio greater than 16:1 which is commonly regarded as the optimum for phytoplankton development (Redfield *et al.* 1963).

Table 3. Average concentrations of nutrients at particular stations for the period betwen April and October

Station	PO_4 $\left[\frac{mmolP}{m^3}\right]$	NO_2 $\left[\frac{mmolN}{m^3}\right]$	NO_3 $\left[\frac{mmolN}{m^3}\right]$	NH_4 $\left[\frac{mmolN}{m^3}\right]$	Si $\left[\frac{mmol}{m^3}\right]$	N/P	*n*
20	0.76	0.07	0.42	0.71	99.88	4.60	11
15	1.11	0.07	0.30	0.44	101.13	1.27	11
12	0.64	0.15	2.84	0.88	92.43	20.01	7
8	1.32	0.24	0.31	0.75	93.03	1.45	10
5	0.94	0.08	1.02	0.28	84.29	1.87	10
1	0.75	0.08	0.27	0.47	97.82	0.94	7
mean IV-X	0.94	0.11	0.75	0.58	94.95	6.34	56

n = number of data

Table 4. Average and extreme chlorophyll *a* concentrations,
Secchi depths and irradiance attenuation coefficients in particular months

Month	Average [mg · m^{-3}]	Max [mg · m^{-3}]	Min [mg · m^{-3}]	SD [mg · m^{-3}]	*n*	Secchi depth [m]	*k* [m^{-1}]
May 1998	34.5	64.7	16.7	11.0	24	0.39	
June 1998	39.1	70.6	20.3	13.2	29	0.35	
July1998	42.8	150.9	22.4	22.4	45	0.48	
August1998	44.3	68.9	20.3	13.4	28	0.33	
September1998	36.3	66.5	23.5	14.0	9	0.38	
October 1998	51.9	56.8	45.4	5.1	4	0.42	
Average in 1998	41.2			16.6	139	0.40	
April1999	35.9	93.9	1.9	15.6	32	0.75	2.32
May 1999	30.6	151.4	4.1	25.3	58	0.37	4.78
June 1999	26.9	72.2	8.7	14.4	63	0.37	3.79
July 1999	54.3	174.5	20.8	31.8	38	0.49	2.43
August 1999	86.3	215.6	38.1	40.9	44	0.41	3.54
September 1999	36.0	62.4	13.0	11.2	44	0.47	3.03
October 1999	49.0	80.8	23.6	17.3	32	0.33	4.67
November 1999	37.6	48.7	26.8	6.0	18	0.40	4.86
Average in.1999	43.5			30.2	329	0.43	

The silicate concentrations in the Vistula Lagoon are also high (Table 2 and 3). The average value for the Polish part of the Vistula Lagoon was 93.4 mmol · m^{-3}. Deviations of individual values did not generally exceed 20% of the average value. These deviations do not allow for the characterization of the regional differences. Table 2 reveals clear tendencies of time variations. Silicate concentrations oscillate around the average value of 84.5 mmol · m^{-3} from April to August, while from September to November the average silicate concentration was 107.6 mmol · dm^{-3}.

Table 5. Average and extreme values of chlorophyll *a* concentrations and Secchi depths at particular stations in 1999

Station	Chlorophyll *a* [mg · m^{-3}]					Secchi depth [m]			
	Average	SD	Min	Max	n	Average	SD	Min	Max
1	47.7	27.2	19.5	133.5	27	0.39	0.11	0.25	0.55
2	38.5	30.7	13.0	112.9	14	0.39	0.11	0.20	0.55
3	34.9	18.1	12.6	72.2	15	0.41	0.10	0.20	0.55
4	31.8	14.7	10.8	64.9	15	0.39	0.11	0.20	0.55
5	33.1	14.5	16.4	79.6	31	0.45	0.11	0.25	0.70
6	29.1	9.9	15.1	47.9	14	0.36	0.08	0.20	0.50
7	29.5	13.5	16.2	56.8	13	0.39	0.11	0.20	0.60
8	47.5	22.6	14.9	93.9	25	0.36	0.12	0.20	0.60
9	53.1	37.9	22.7	159.1	17	0.40	0.14	0.20	0.55
10	36.8	18.3	4.1	62.4	17	0.44	0.11	0.20	0.55
11	38.0	12.0	18.2	60.0	15	0.47	0.11	0.20	0.65
12	45.2	42.2	1.9	154.0	21	0.61	0.44	0.20	2.00
13	47.0	27.4	20.3	107.8	15	0.46	0.14	0.20	0.65
14	84.0	55.2	24.3	215.6	17	0.53	0.14	0.20	0.90
15	47.1	35.7	15.9	174.5	38	0.40	0.13	0.20	0.60
20	42.2	25.1	11.0	118.1	34	0.40	0.10	0.20	0.55
	43.0	26.3			329	0.43	0.18		

Chlorophyll *a* concentrations

Chlorophyll *a* concentration is used as the phytoplankton measure in this paper. Chlorophyll concentrations (average values for the 0-1.5 m layer) in the Vistula Lagoon were high during the vegetative season in both 1998 and 1999. The seasonal variability of average chlorophyll *a* concentrations (average values from all stations in a given month) are illustrated in Table 4, which also includes extreme values and the standard deviation of the arithmetic average. The maps in Figs. 3-4 illustrate the chlorophyll-a concentrations in the lagoon, and the average chlorophyll concentrations derived for particular stations are presented in Table 5. During the period in question, the highest chlorophyll concentrations occurred at station 14, which is located near the Elbląg River mouth, and is impacted by large amounts of pollution from the city of Elbląg and partially from the agricultural area of Żuławy. Statistical analysis of chlorophyll *a* determinations reveals that the average chlorophyll concentrations at the stations located west of the Krynica Morska - Tolkmicko line are 47.8 mg · m^{-3}, while for stations located east of this line the average chlorophyll concentrations are 37.9 mg · m^{-3}. It must also be noted that the chlorophyll concentrations along the peninsula were lower than those along the mainland coast. The greatest diversity of chlorophyll concentrations between different stations was observed in July and August.

Water transparency

Primary production distribution in the water column mainly depends on the distribution of the light field. The high concentration of both organic and inorganic suspensions in the waters of the Vistula Lagoon results in strong light attenuation in the water column. The Secchi depth in the lagoon is low ranging from 0.2 m to 2 m, with an average of 0.43 m (Tables 4 and 5). In the southwestern part of the lagoon the average Secchi depth was 0.40 m, and in the northeast it

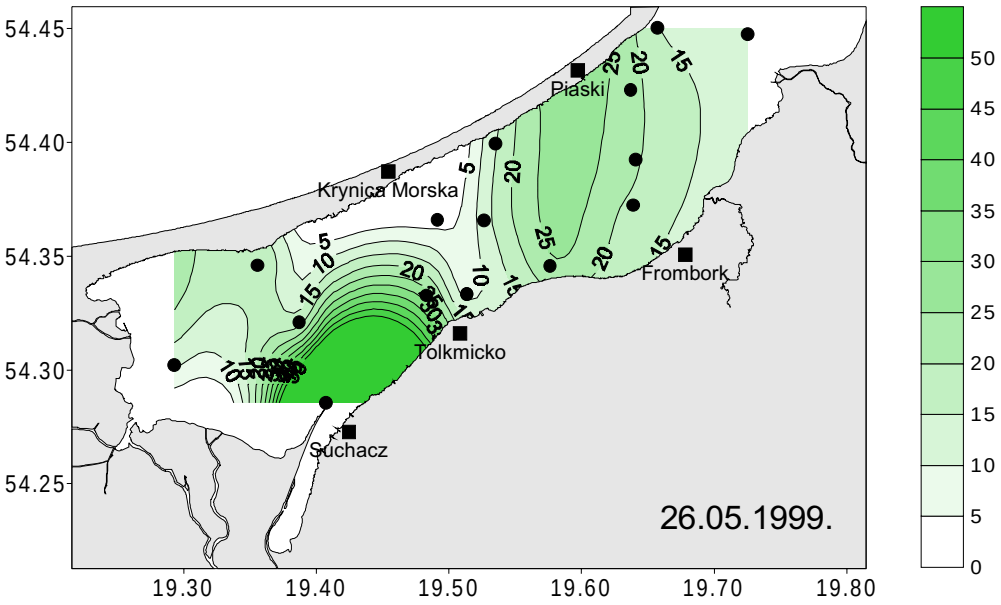

Fig. 3 . Chlorophyll *a* distribution [mgChl · m^{-3}] in Vistula Lagoon on 1999.05.26

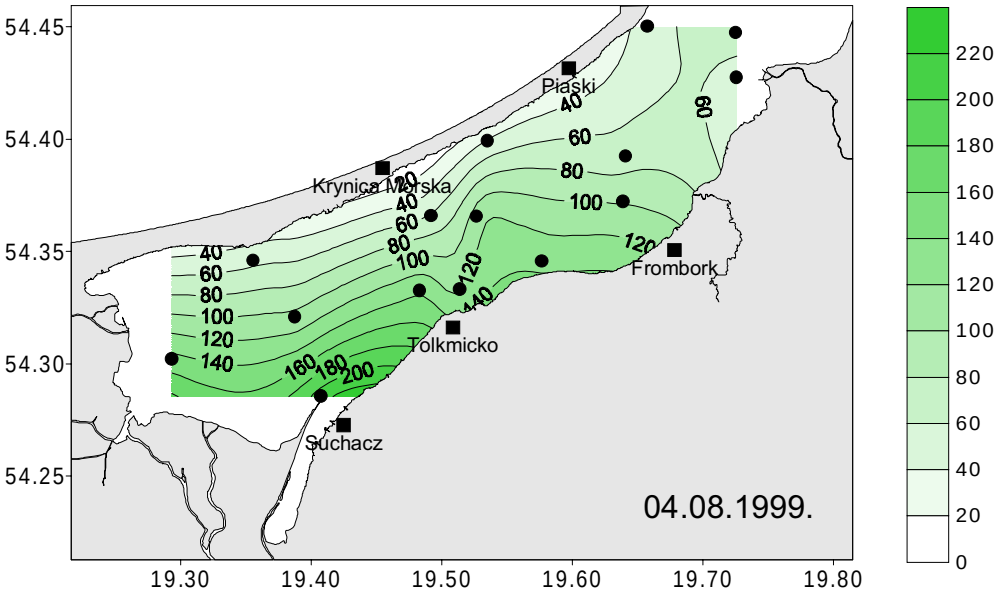

Fig. 4. Chlorophyl *a* distribution [mgChl · m^{-3}] in Vistula Lagoon on 1999.08.04

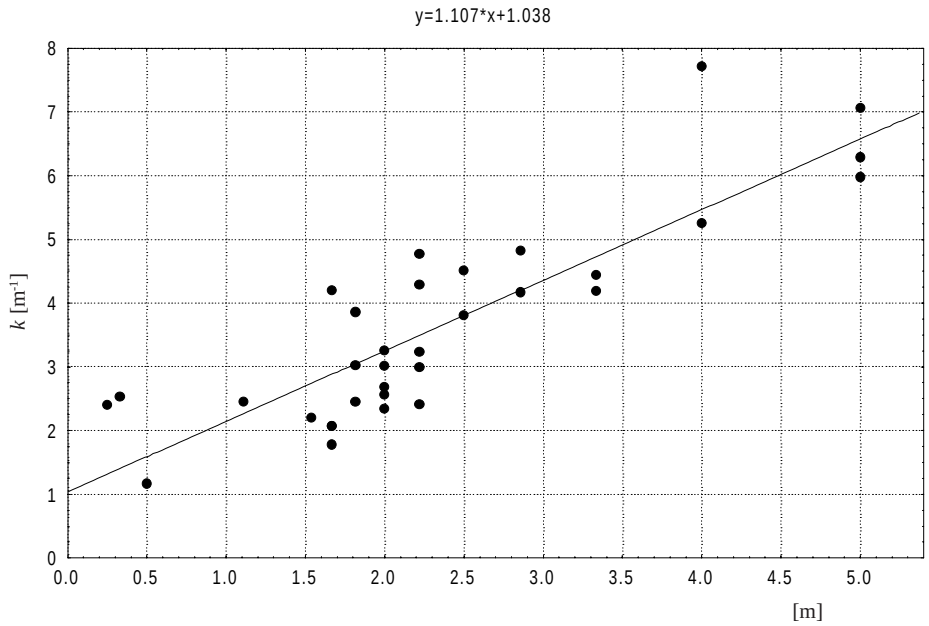

Fig. 5. Relationship between the of diffuse light attenuation coefficient and Secchi depth

was 0.47 m. The light attenuation coefficients in the Vistula Lagoon vary significantly from 1.5 m^{-1} to 7 m^{-1}. The average downward irradiance attenuation coefficients in various months are presented in Table 4. The greatest standard deviations of Secchi depth were observed at station 12 (Table 5); this indicates the greatest variations of this parameter. Fig. 5 illustrates the dependence between the light attenuation coefficient and the reciprocal of the Secchi depth. The straight line in the figure represents the following equation:

$$k = \frac{1.107}{S} + 1.038 \qquad [3]$$

where :

k = diffuse attenuation coefficient of downward irradiance PAR

S = Secchi depth.

Photosynthetic light curves

Empirical examples of photosynthetic rate-irradiance dependence for the phytoplankton of the Vistula Lagoon are presented in Fig. 6. The equation coefficients [1] and [2], which are used to describe the dependence of the photosynthetic rate on irradiance, have been derived using the least squares method based on measurements of the photosynthetic rate under various irradiance conditions. The calculated coefficients of these equations are presented in Table 6. The type [1] curve, which shows the characteristic maxima of the photosynthetic rate at optimum irradiance and a decrease in the photosynthetic rate at very high irradiance, is the most typical photosynthetic rate-irradiance dependence observed in the Vistula Lagoon. The type [2] curve for high irradiance runs toward the asymptotic value A, without considering the photosynthetic inhibition phenomenon, which occurs in the near surface layer (0-0.5 m) of this basin. The correlation

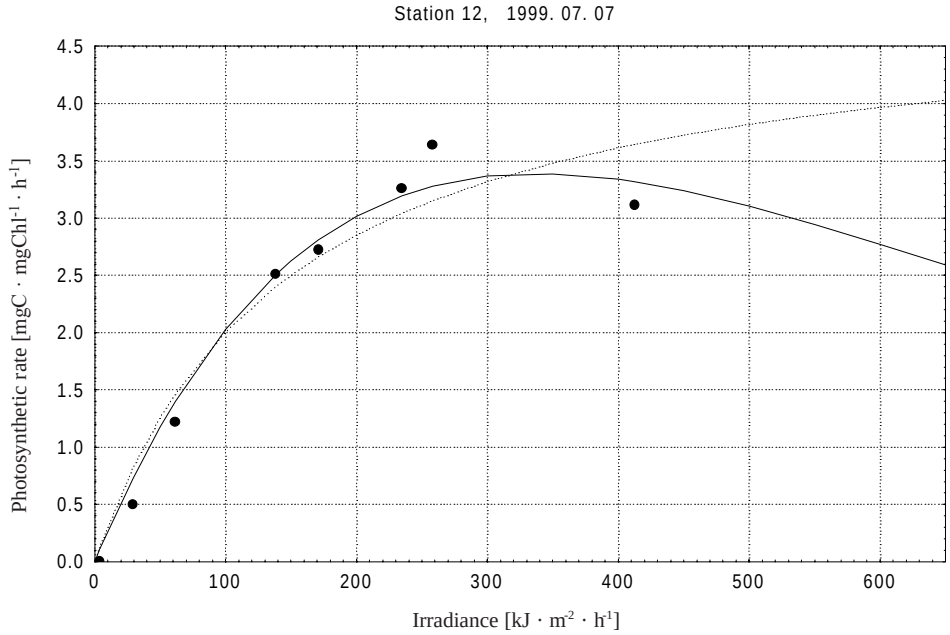

Fig. 6. Light curves of photosynthesis. Continous line – equ. [1], doted line – equ. [2]

coefficients (Table 6) between the results of measurements and particular values expected from equations [1] and [2] for the type [1] curve are usually higher than for the type [2] curve. This means that in the Vistula Lagoon the type [1] curve better describes the dependence of the photosynthetic rate on irradiance than does the type [2] curve. Thus, in further calculations, especially in the case of primary production, the maxima of the photosynthetic rates *AN* and the saturated irradiance E_s obtained from equation [1] were applied.

The assimilation number, which is the maximum photosynthetic rate that occurs at optimum irradiance, varies seasonally. The assimilation numbers in the Vistula Lagoon during the investigation period varied from 1.72 to 7.94 mgC · mgChl^{-1} · h^{-1}. The average photosynthetic light curves in various seasons for phytoplankton in the Vistula Lagoon are presented in Fig. 7. The greatest values of assimilation numbers were observed in summer and much lower in spring and fall.

The seasonal variability of the assimilation numbers presented in the figure is related to temperature variations, among other factors. Fig. 8 presents the dependence of assimilation numbers on temperature. This dependence may be disturbed by the impact of other factors on the assimilation number, including variations of nutrient concentrations, phytoplankton species composition, and others. Correlations were confirmed between the assimilation numbers at *in situ* temperature and phosphate concentrations (Fig. 9). The curve in Fig. 9 was derived using the least squares method and in accordance with the Michaelis-Menten equation (with correlation coefficient $k = 0.64$) and is as follows:

$$AN = 5.36 \frac{x}{0.15 + x} \qquad [4]$$

where:

x = phosphate concentrations.

Table 6. Parameters of the photosynthetic light curves

Station	Date	k [m^{-1}]	Chl $\left[\frac{mg}{m^3}\right]$	$P_h = AN \cdot \frac{E}{E_s}\exp\left(1-\frac{E}{E_s}\right)$			$P_h = A \cdot \frac{E}{B+E}$		
				AN $\left[\frac{mgC}{mgChl \cdot h}\right]$	E_s $\left[\frac{kJ}{m^2 \cdot h}\right]$	r	A $\left[\frac{mgC}{mgChl \cdot h}\right]$	B $\left[\frac{kJ}{m^2 \cdot h}\right]$	r
20	04. 28	2.56	50.66	2.48	277.2	0.99	3.25	97.5	0.96
15	04. 28	1.77	24.30	1.72	323.7	1	2.42	135.6	0.98
12	04. 28	1.16	1.50	2.61	359.6	0.99	4.57	174.8	0.96
20	11. 05	5.97	41.38	2.25	390.7	0.99	3.29	181.9	0.98
15	11. 05	5.97	31.96	4.03	330.7	0.99	5.85	143.1	0.96
5	11. 05	4.18	38.93	5.98	571.2	0.99	10.58	336.8	0.99
20	25. 05	4.03	20.44	4.97	342.8	0.99	6.72	119.2	0.99
15	25. 05	5.33	15.91	7.35	344.5	0.97	10.79	151.0	0.95
12	25. 05	2.45	10.52	7.94	390.4	0.95	13.03	213.6	0.93
20	8. 06	3.65	21.65	4.09	406.6	0.99	6.30	190.7	0.98
15	8. 06	3.01	17.97	4.38	377.4	0.99	6.64	173.7	0.97
5	8. 06	3.85	16.43	5.70	377.5	0.99	8.76	182.7	0.98
20	21. 06	3.69	19.21	5.20	412.8	0.99	8.09	197.3	0.98
15	21. 06	4.77	19.38	4.87	387.0	0.95	5.82	86.8	0.97
12	21. 06	3.25	25.00	4.32	382.4	0.99	6.48	170.6	0.98
20	7. 07	2.68	36.50	4.86	695.7	1	10.08	509.5	1
15	7. 07	2.07	27.58	5.30	744.7	1	9.84	469.7	1
12	7. 07	2.07	27.58	3.39	338.4	0.99	4.93	145.6	0.97
20	20. 07	3.48	47.04	7.13	507.8	0.97	12.76	310.3	0.96
15	20. 07	2.41	174.53	3.37	453.4	0.98	5.83	266.1	0.97
5	20. 07	2.34	40.55	4.97	533.1	1	8.63	306.2	0.99
20	3. 08	4.20	118.70	5.20	426.1	0.99	8.54	227.3	0.97
15	3. 08	4.29	112.93	5.62	631.7	1	10.23	388.4	1
12	3. 08	4.19	154.00	6.15	597.0	0.99	11.84	407.3	0.98
20	24. 08		62.45	5.30	384.0	1	7.91	169.2	0.99
15	24. 08		44.51	4.44	361.6	1	6.37	146.7	0.98
5	24. 08		38.12	3.94	286.7	0.99	5.09	92.9	0.97
20	7. 09	2.31	38.93	3.84	435.0	0.99	5.84	196.0	0.99
15	7. 09	2.45	29.20	2.90	328.8	1	3.93	117.3	0.99
12	7. 09	2.20	31.63	2.79	412.9	1	4.24	186.6	1
20	28. 09	4.71	34.06	4.47	331.4	0.99	6.04	116.7	0.99
15	28. 09	4.16	47.04	3.46	271.1	0.99	4.36	83.6	0.97
5	28. 09	3.80	30.82	5.27	317.6	0.99	6.83	110.5	0.98
20	12. 10.	7.37	73.15	2.36	220.6	0.99	2.59	44.1	0.97
12	12. 10.	7.71	53.90	2.18	220.1	0.99	2.38	44.3	0.97
20	26. 10.	2.99	24.33	2.88	205.4	0.99	3.02	35.1	0.97
15	26. 10.	3.40	31.63	2.78	218.2	0.98	3.01	41.1	0.98
5	26. 10.	2.40	23.61	2.95	238.7	0.99	3.56	70.2	0.93
20	16. 11	7.81	36.5	3.04	203	0.96	3.15	33.5	0.91
15	16. 11	5.22	36.5	1.88	217	0.93	2.07	45.1	0.91
20	30. 11	3.67	27.6	1.89	177	0.98	1.63	22.8	0.94
15	30. 11	2.72	38.9	1.28	179	0.95	1.24	22.8	0.95

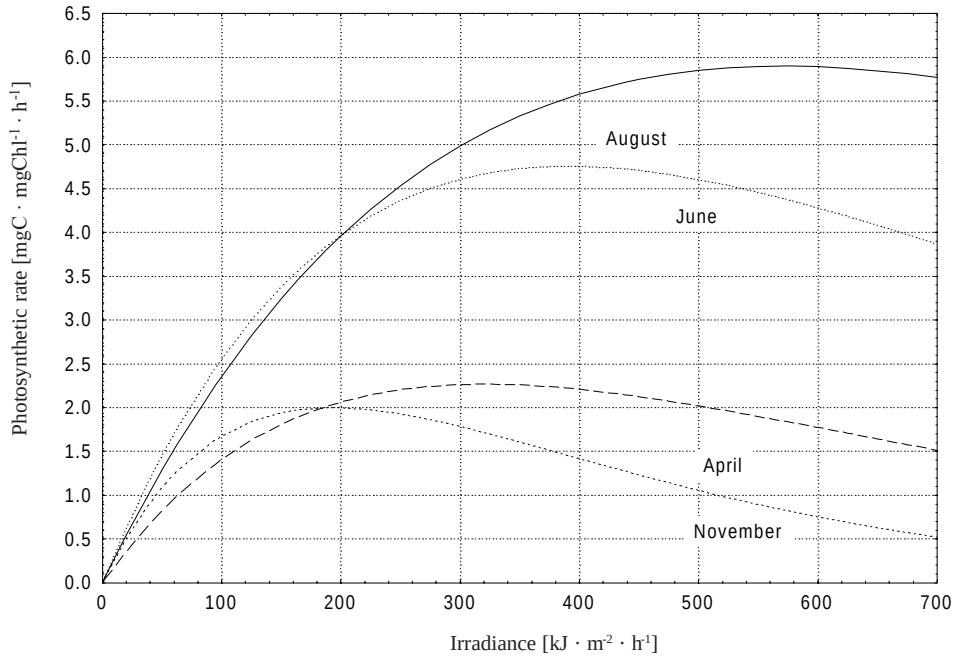

Fig. 7. Light curves of photosynthesis in phytoplankton of the Vistula Lagoon in different seasons. Parameters of the light curve equations – see table 9.

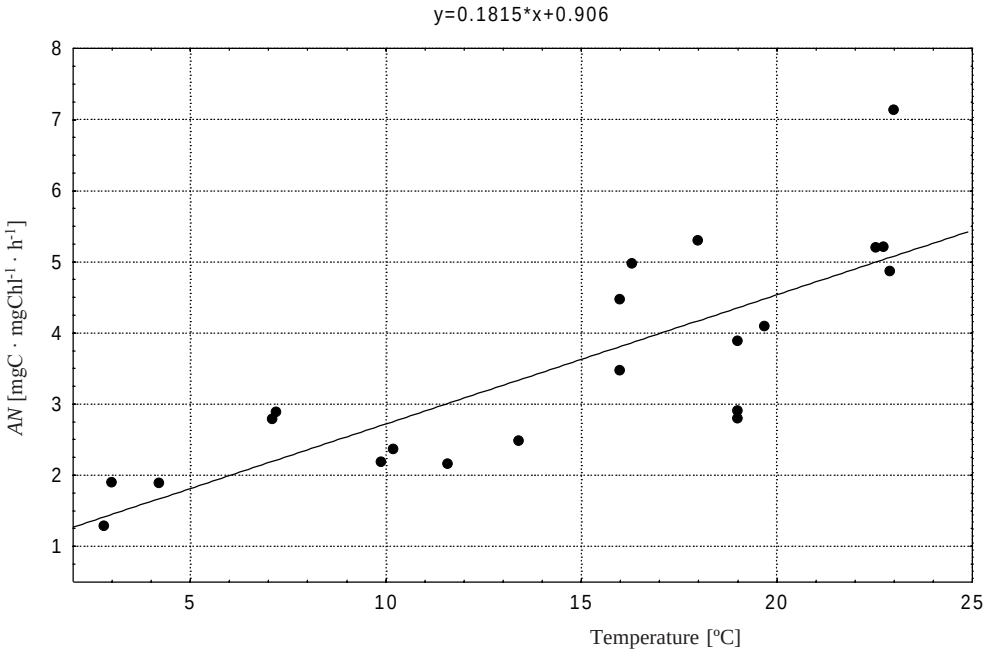

Fig. 8. Relationship between assimilation number and temperature

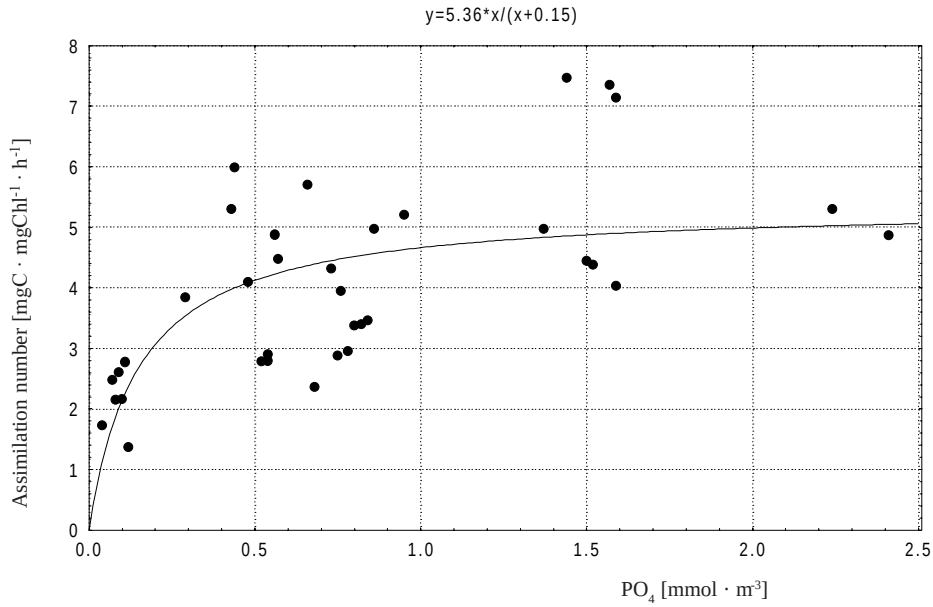

Fig. 9. Relationship between assimilation number and phosphate concentrations in the period from April to November

The above test reveals that at low phosphate concentrations, about 0.15 mmol · m^{-3}, the assimilation numbers are equal to the half of the maximum value (asymptotic), i.e. 2.68 mgC · $mgChl^{-1}$ · h^{-1}. This means that at phosphate concentrations of about 0.2 mmol · m^{-3} or lower, primary production limitation may occur as a consequence of phosphate deficiency. In 1999 no correlation was observed between the assimilation numbers and the concentrations of other nutrients, such as nitrates, nitrites, ammonia, or silicates.

Primary production

The vertical distribution of primary production in various seasons is illustrated in Fig. 10. The greatest rate of primary production usually occurs in the surface water layer, to a depth of about 0.4 m, or, in cases of low irradiance, directly at the surface. The values of the daily primary production in a 1 m^2 unit area, presented in Table 7, were derived in the following ways:

A – from *in situ* measurements at station 20 [Prod. $_{measur.}$]

B – based on the photosynthetic light curve and the necessary environmental parameters for particular stations: chlorophyll concentration, light attenuation coefficient, daily dose of solar radiation [Prod.$_{calcul.}$]

C – from the average values of all parameters, for particular days, i.e. photosynthetic light curve and the necessary environmental parameters for particular stations: chlorophyll concentration, light attenuation coefficient, daily dose of solar radiation [Prod.$_{average}$]. It is assumed that the latter value refers to the average value for a particular day for the entire Polish part of the Vistula Lagoon.

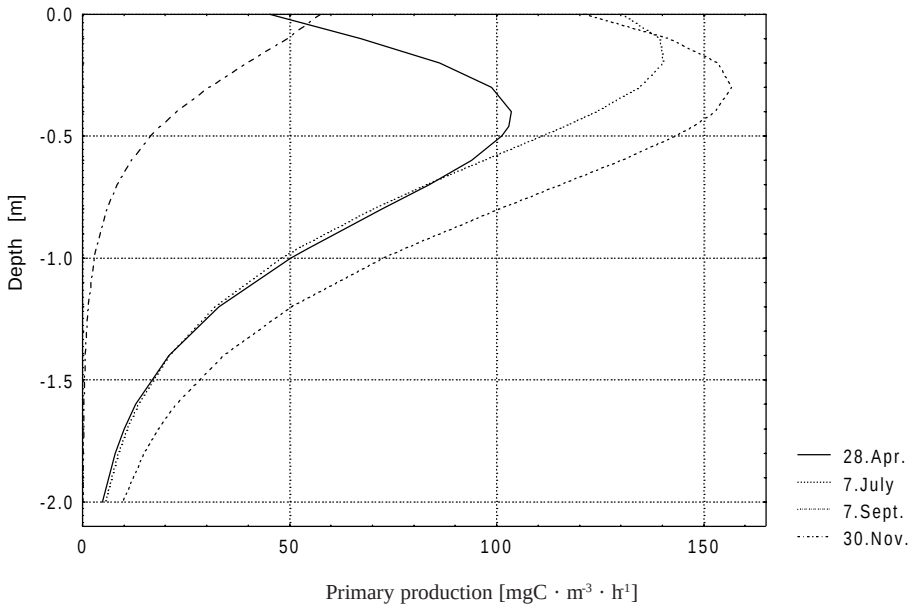

Fig. 10. Vertical distribution of primary production (at noon time) in different seasons

The daily primary production measured *in situ* shows rather significant variations that are mainly concerned with accidental irradiance variations. Clear seasonal primary production variability is also apparent. The greatest primary production in 1 m^2 unit area occurred in July and August.

DISCUSSION

The Vistula Lagoon waters are characterized by significant inputs of freshwater. In the western part of the lagoon the average salinity oscillates around 1.5 PSU and gradually increases towards the eastern Polish border, reaching a value of about 3.5 PSU. The salinity of the lagoon varies significantly with inflows of Baltic waters and the intensity of river water input. The comparison of the current investigation results with those from literature (Szarejko 1959, Różańska and Więcławski 1978) indicates that the state of the lagoon's salinity has not changed significantly over a period of several decades. The nutrient concentrations in this basin have, however. The average values presented by Trzosińska and Zurawleva (1975) as well as by Różańska and Więcławski (1981) vary significantly from the values measured in 1999. In 1975-1978 a significant increase in nitrate concentrations was observed (Różańska and Więcławski 1978, 1981) in comparison with 1954 (Stangenberg 1959). The results of the current research reveal a very high decrease in the concentrations of particular forms of nitrogen. In comparison with 1978, the nitrate and ammonia nitrogen concentrations during the vegetative season have decreased several ten-fold and nitrite concentrations have decreased approximately three to five-fold. Phosphate concentrations have also decreased two-fold. Similarly to previous investigations, the current research indicates that the Nogat and Elbląg rivers are the main

Table 7. Daily primary production measured and calculated

Station	Date	Irradiation PAR $\left[\frac{kJ}{m^2}\right]$	Prod. measur. $\left[\frac{mgC}{m^2 \cdot d}\right]$	Prod. calcul. $\left[\frac{mgC}{m^2 \cdot d}\right]$	Prod. average $\left[\frac{mgC}{m^2 \cdot d}\right]$
1	2	3	4	5	6
20	04. 28		1,488	1,373	
15	04. 28	8,700		634	645
12	04. 28			88	
20	11. 05		369	131	
15	11. 05	1,438		209	611
5	11. 05			339	
20	25. 05		701	545	
15	25. 05	4,723		474	674
12	25. 05			687	
20	8. 06		726	614	
15	8. 06	7,494		685	636
5	8. 06			636	
20	21. 06		825	587	
15	21. 06	5,527		444	678
12	21. 06			751	
20	7. 07		846	787	
15	7. 07	3,853		797	1,473
12	7. 07			1,149	
20	20. 07		1,480	1,902	
15	20. 07	9,823		6,496	3,925
5	20. 07			2,144	
20	3. 08		3,584	3,869	
15	3. 08	9,663		3,299	3,870
12	3. 08			5,052	
20	24. 08		2,667	2,297	
15	24. 08	6,458		1,405	1,566
5	24. 08			1,164	
20	7. 09		1,312	1,326	
15	7. 09	6,633		790	857
12	7. 09			841	
20	28. 09		324	565	
15	28. 09	4,064		747	606
5	28. 09			721	
20	12. 10.	2,581	383	383	303
12	12. 10.			250	
20	26. 10.		321	279	
15	26. 10.	1,422		297	329
5	26. 10.			314	
20	16. 11	1,257	184	215	146
15	16. 11			133	
20	30. 11	510	158	157	125
15	30. 11			86	

sources of nutrient input into the Polish part of the Vistula Lagoon. The river waters, and especially those of the Elbląg Canal, carry significant amounts of nutrients originating from municipal pollution and fertilizers that are washed off with rainwater. Nutrient concentrations are also higher at other stations that are located near the mouths of smaller rivers than in areas that are distant from the river mouths. This means that river waters are the main source of nutrients. The greatest nutrient concentrations in the Vistula Lagoon, as in the Gulf of Gdańsk, occur near river mouths (Renk *et al.* 1976, Pastuszak 1995).

The ratio of inorganic nitrogen to inorganic phosphorus in the water is a very important parameter in terms of biological production. It is common knowledge that the nitrogen to phosphorus ratio in organic matter is 16:1 (in mols) (Redfield *et al.* 1963). These elements are consumed in the same proportions during the biological production of organic matter. In the environment, i.e. water surrounding the cell, this ratio sometimes is very different from the optimum value (16:1) for biological production. During the vegetative season (April-October) the mean N:P ratio for all stations of the Vistula Lagoon except station 12 was 1.95:1, whereas at the station 12, the mean N:P.ratio was 20:1, that means it was higher than the optimal value for phytoplankton growth. In November, when the production processes slow down, the N:P ratio increased at all stations.

Using data concerning the river water inflow into the Gulf of Gdańsk and the Vistula Lagoon (Rybiński *et al.* 1992, Heybowicz *et al.* 1998), the average N/P ratio was determined in river waters. The relationship was 25:1 – 45:1 in the 1988-1996 period. This indicates that river waters enrich the Vistula Lagoon with inorganic nitrogen and are the cause of the high N/P values near river mouths.

According to calculations carried out using the results of Różańska and Więcławski (1978, 1981), the average ratio of inorganic nitrogen to phosphorus in the 1975-1978 period was 39.2:1 – 67.9:1, while in 1999 the average ratio for all stations was 6.34:1, and only at station 12 was it 20:1, on average. The decrease of nitrogen compound concentrations in comparison with 1970 levels may be connected with the varying intensity and means of agricultural fertilization.

Silicate concentrations in the Vistula Lagoon were about three to four times higher than the values presented by Trzosińska (1992) for the Gulf of Gdańsk.

During the investigation period, the greatest transparency was found at stations 12 and 14. These results are similar to those of Różańska and Więcławski (1978). Comparison reveals, however, that the water transparency in the Vistula Lagoon has decreased.

Investigations of chlorophyll distribution in the Vistula Lagoon have not been carried out for as long as hydrological investigations. The first rather wide-ranging description of the chlorophyll distribution in the Vistula Lagoon was presented by Latała (1978). The average chlorophyll concentrations in 1999 do not significantly vary from the comparative values given by Latała (1978) for 1975, with the exception that in August 1999 there was a clear chlorophyll maximum (about 200 $mg \cdot m^{-3}$) at station 12. The maximum values observed by Latała (1978) were 120 $mg \cdot m^{-3}$ and they occurred in April, during the spring phytoplankton bloom.

The photosynthetic light curves for the Vistula Lagoon waters can be described by a similar equation to that used for the Baltic Sea (Renk *et al.* 1999). Similarly to the Baltic Sea, the assimilation numbers in the Vistula Lagoon change seasonally. However, the spring increase and fall decrease of the assimilation numbers occur earlier in the Vistula Lagoon than in the Baltic Sea. Keeping in mind the dependence of the assimilation numbers on temperature that was presented earlier in the paper, this phenomenon can be explained by the fact that the lagoon's temperature rises in the spring and falls in the fall faster that it does in the sea.

A relationship between assimilation numbers and phosphate concentrations was observed. Similar relationships have been observed in the Gulf of Gdańsk and the Pomeranian Bay (Renk *et al.* 1999). No correlations were observed between the assimilation numbers and the concentrations of silicate or inorganic nitrogen compounds. This leads to the conclusion that concentrations of these compounds did not affect the primary production in the Vistula Lagoon in 1999.

The application of the parameters of the photosynthetic light curves to analytical calculations (Renk *et al.* 2000) of the primary production of the Vistula Lagoon yields results comparable with those obtained with *in situ* measurements. Fig. 10 shows that the maximum primary production occurs at a depth range of up to about 40 cm, and at depths exceeding 50 cm a strong decrease in primary production occurs that is caused mainly by decreased irradiance in the water column. The average thickness of the euphotic layer in the Vistula Lagoon is significantly thinner than that in the Gulf of Gdańsk. The primary production per unit water volume, similarly to chlorophyll concentrations in the lagoon, are much higher than in the Gulf of Gdańsk. As a result, primary production in a 1 m^2 unit area is almost two times higher than it is in the Gulf of Gdańsk. The productions calculated using the parameters of the photosynthetic light curves are presented in the last two columns of Table 7.

The average values of primary production by month are given in Table 8. To determine these values, the averages of the parameters necessary for the calculation of primary production, which are also given in the table, were used. The PAR irradiance [η_d] was determined from the model which describes the averaged irradiance for the entire year (Renk 1989). The average primary production which was derived in this way does not depend on accidental variations of irradiance caused by cloud coverage or weather conditions. It is also independent of accidental fluctuations or the patchiness of other parameters which determine the result of the evaluation of the primary production.

The average annual production in the Vistula Lagoon was estimated to be 303.8 gC · m^{-2} · $year^{-1}$. However, Niedoszytko and Wiktor (1978), based on measurements using the so-called oxygen method, obtained an annual Vistula Lagoon production in 1974-1975 of 461.3 gC · m^{-2} · $year^{-1}$. The question is if the decrease of primary production observed over a

Table 8. Average parameter for calculating the average primary production in particular months

Month	*AN* [mgC / mgChl·h]	*Es* [kJ / m² · h]	η_d PAR [kJ / m² · d]	*k* [m^{-1}]	Chl [mg / m³]	$Prod_d$ [mgC / m² · d]	$Prod_m$ [gC / m² month]	$Prod_q$ [gC / m² quart]
January	1.10	180	730	3.8	15	34	1.1	
February	1.20	196	1506	6.2	16	39	1.1	6.7
March	1.68	273	2965	3.4	18	146	4.5	
April	2.27	320	5138	2.3	36	766	23.0	
May	5.40	395	7333	4.6	31	896	27.8	87.9
June	4.76	391	8735	3.5	33	1238	37.1	
July	4.84	546	8550	2.4	54	2529	78.4	
August	5.11	448	6805	3.5	86	2723	84.4	188.5
September	3.79	350	4323	2.9	36	856	25.7	
October	2.63	239	2209	3.9	49	477	14.8	
November	2.46	210	938	6.2	37	126	3.8	20.7
December	1.59	178	512	3.6	25	67	2.1	

period of 25 years is only apparent because of a change in estimation method of if there has been a real decrease in the photosynthetic rate in the Vistula Lagoon resulting from a decrease in the nutrient concentration, among other reasons. The chlorophyll concentrations over this period of time have remained on a comparable level. The decrease of water transparency may explain the decrease of primary production in the Vistula Lagoon.

It can be stated that primary production in the Vistula Lagoon is about two times higher than in the southern Baltic Sea (Renk and Ochocki 2000), which was estimated as 161 $gC \cdot m^{-2} \cdot year^{-1}$ in the Gdańsk Deep, and 122 $gC \cdot m^{-2} \cdot year^{-1}$ in the Bornholm Deep. Indirectly, based on the chlorophyll *a* concentrations, it can be assumed that production in the Vistula Lagoon is comparable to that of the Kuroński Lagoon (Olenina and Kavolyte 1996). The primary production in the Vistula Lagoon is comparable with the phytoplankton production in the Szczecin Lagoon (Wiktor 1971) and some Rugia lagoons (Hübel 1968; Schiewer 1994).

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