# Summer phytoplankton successions close to the shore in three brackish water bays on the East coast of Sweden (Gulf of Bothnia)

ROMAN A. DANILOV\* & NILS G. A. EKELUND

Department of Applied Science, Mid Sweden University, 871 88 Härnösand, Sweden; tel: +46 611 86292; fax: +46 611 86160; email: roman.danilov@tnv.mh.se

DANILOV R. A. & EKELUND N. G. A. (2000): Summer phytoplankton successions close to the shore in three brackish water bays on the East coast of Sweden (Gulf of Bothnia). – Thaiszia – J. Bot. 9(1999): 131-142. – ISSN 1210-0420.

ABSTRACT: Three brackish water bays between Härnösand and Sundsvall on the East coast of Sweden (Gulf of Bothnia) were investigated between June and August 1998 in order to reveal summer phytoplankton dynamics close to the coast. All samples were collected at depth of 0,5 m. The results obtained show patterns in phytoplankton dynamics. In the spring Bacillariophyceae dominated, followed by an increase in Dinophyceae and small flagellates of Prasinophyceae and Cryptophyceae. Chlorophyceae were represented during the whole period of investigation especially with species of Monoraphidium, which often dominated or subdominated. In total 84 phytoplankton species were identified. Cluster analyses based on similarities in species' diversity and their abundance made it easy to distinguish between the bays close to Härnösand and the Bay of Sundsvall. However, no clear differences were found between the sampling stations within the Bay of Sundsvall.

KEYWORDS: phytoplankton, summer successions, brackish water, Gulf of Bothnia

corresponding author

#### Introduction

The Gulf of Bothnia is a large reservoir of brackish water with dynamic environmental conditions. Chemical and physical variables vary from north to south (GRANÉLI & al. 1990). In recent decades intensive studies of the phytoplankton communities in the Gulf of Bothnia were performed (e. g. HAJDU & WILLEN 1985, HUTTUNEN & al. 1986, KANGAS & al. 1993, WILLEN 1995, ANDERSSON & al. 1996). In all investigations the samples were taken far away from the coast. However, it is well known that shallow coastal ecosystems and especially estuaries play an important role in the sea life as transition zones at the land-sea interface (CLOERN 1996). Coastal ecosystems which are influenced by rivers have different physical conditions compared with the open sea. They are nutrient-rich as a result of influence from different human activities (MALONÉ & al. 1988, JUSTIC & al. 1995, NIXON 1995). Recently changes in the shallow coastal ecosystems increased due to human activity. Most of these changes begin with the successions in the species composition, abundance or production rate on the phytoplankton level. Thus a better understanding of the mechanisms and trends of phytoplankton successions, "blooms" and their interaction with human activities in the shallow coastal ecosystems could play a key-role in monitoring eutrophication processes in the seas (CLOERN 1996). In this context it is clear that the investigation of the seasonal phytoplankton successions is increasingly important in the monitoring of coastal ecosystems (TAYLOR & Howes 1994, Andersson & al. 1996, Nogueira & al. 1997, Casas & al. 1997).

The present study is an attempt to detect patterns in phytoplankton successions during the most productive period from June to the end of August close to the shore (50 cm depth) in the Gulf of Bothnia (Sundsvall and Härnösand, Sweden). The secondary task was to reveal if the sampling at especially low depths along the coast would provide with reliable results to make comparisons sensitive enough between stations of different environmental conditions. All sampling areas are estuaries greatly influenced by rivers and human activities.

# **Material and Methods**

Eight different sampling areas were chosen, six close to the city of Sundsvall (Bay of Sundsvall, sampling sites 1-6), and two close to the city of Härnösand in Gånsvik (sampling site 7) and Smitingen (sampling site 8). The locations of the eight sampling stations are shown in Figure 1. All investigated estuaries are situated on the East coast of Sweden and are greatly influenced by the rivers Ångermanälven (Härnösand) and Navarn, Indalsälven and Mjällån (Sundsvall). In the period from June to the end of August salinity varied at the sampling sites 1-6 in the range from 1.7 to 5.3, at 7 and 8 - from 3.7 to 5.8. No significant differences in the water temperature between sampling sites were observed. Chlorophyll a varied from 1-2 mg m<sup>-3</sup> at station 1 and from 2-4 mg m<sup>-3</sup> at other stations (County Administration, Härnösand, personal communication).

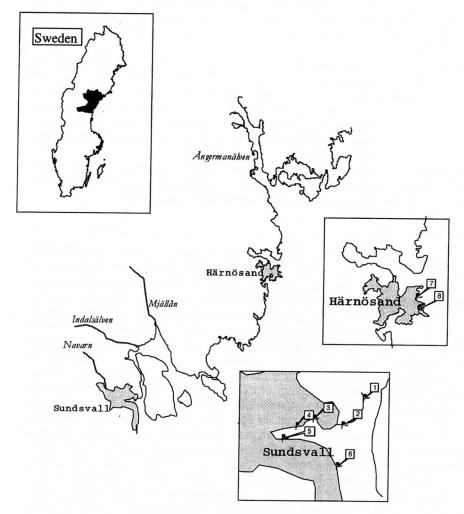


Figure 1. Location map of sampling stations in Härnösand and Sundsvall (East coast of Sweden, Bay of Bothnia). Rivers names are styled italic.

Samples were taken twice in June, once in July and twice in August near the shore at the depth of 50 cm. Sampling was done with the help of 500 ml PVC flasks. From each sampling station two flasks (for qualitative and quantitative analyses) were taken. The samples for quantitative analyses were fixed in 1% Lugol's solution immediately after collecting. Later in the laboratory the preserved samples were left for 24 h in order to achieve sedimentation of algal cells. After sedimentation the samples were concentrated in the first step until 50 ml by

careful sucking off 450 ml using plankton nets with 3 µm mesh size. Then the rest was centrifugated for 20 sec at 4000 rpm, the liquid phase was immediately removed and the pellet was resuspended in approx. 10 drops (sample water)

with a Pasteur pipette.

Phytoplankton species were identified with the aid of a wide range of literature, the most important being PANKOW (1990) and TIKKANEN & WILLEN (1992). When the exact identification of species was not possible from the fixed samples, unfixed samples were used for assistance. A rather traditional algal system was used for the classification of the taxa found. Frequency of each present species in the fixed samples was determined according to relative units: 1 - occasional, 2 - rare, 3 - frequent, 4 - dominant.

The cluster analyses were performed by using the average linkage distance algorithm in the computer package Minitab 11. Sampling stations were clustered according to similarities in species diversity and their abundance.

#### Results

During summer 1998 a total of 84 phytoplankton species were identified. Most of the phytoplankton belonged to Bacillariophyceae, Chlorophyceae and Cyanophyceae with 20, 20 and 15 species, respectively. Dinophyceae, Chrysophyceae, Euglenophyceae, Cryptophyceae and Prasinophyceae were present with 8, 7, 6, 4 and 4 species, respectively (Table I). Differences in phytoplankton assemblages were revealed both in space and time. No phytoplankton blooms occurred during the period of investigation. During the whole studied period Diatoma vulgare, D. elongatum, Fragilaria ulna (Bacillariophyceae), Monoraphidium contortum (Chlorophyceae) and Kephyrion spp. (Chrysophyceae) were present at all sampling stations most of the time and often dominated. Occasionally other species were found dominating at different time: Thalassiosira lacustris, Navicula spp. (Bacillariophyceae), Monoraphidium minutum (Chlorophyceae), Cryptomonas marssonii, Rhodomonas lacustris (Cryptophyceae), Euglena spp. (Euglenophyceae), Nephroselmis pyriformis and Pyramimonas sp. (Prasinophyceae, Table II). Though some Dinophyceae species were abundant during June, they never became dominant. At the beginning of June Diatoma vulgare, D. elongatum and Monoraphidium contortum were highly abundant at almost all stations, Prasinophyceae were present in huge numbers, too. At the end of June Bacillariophyceae became less abundant Cryptophyceae belonged to species dominant and Prasinophyceae, an increase in the presence of Euglenophyceae at the stations 1, 3, 4, 5 and 6 was also detected. In the middle of July a general decrease in the phytoplankton abundance was observed. This time dominant species belonged, depending on the sampling station, to Bacilariophyceae (stations 1, 5, 6, 7, 8), Chlorophyceae (station 8) and Cryptophyceae (station 5). In August Chlorophyceae and Cryptophyceae became dominant (Table III).

# Table 1. List of taxa found at all sampling stations in the period June - August

#### BACILLARIOPHYCEAE

Asterionella formosa HASS.
Chaetoceros holsaticum SCHÜTT
Chaetoceros wighamii BRIGHTW.
Chaetoceros spp.
Cyclotella caspia GRUNOW in SCHNE

Cyclotella caspia Grunow in Schneider Diatoma elongatum (LYNGB.) C. A. AG.

Diatoma vulgare BORY

Fragilaria crotonensis KITTON

Fragilaria ulna (= Synedra ulna) (NITZSCH) LANGE-BERTALOT

Fragilaria sp.

Melosira arctica (Ehrenberg) Dickie Melosira islandica ssp. helvetica O. Müller

Melosira lineata (DILLW.) C. A. AG.

Melosira sp.

Navicula spp.

Rhizosolenia spp.

Skeletonema costatum (GREV.) CLEVE Tabellaria fenestrata (LYNGB.) KÜTZ. Tabellaria flocculosa (ROTH) KÜTZ. Thalassiosirá lacustris HASLE

#### **CHLOROPHYCEAE**

Carteria sp.

Chlamydocapsa sp. (=Gloeocystis sp.) Chlamydomonas spp.

Chlorella sp.

Coelastrum microporum Näg. Dictyosphaerium pulchellum WOOD Didymocystis bicellularis (CHOD.)KOMAREK Lobomonas sp.

Monoraphidium contortum (THURET in BREB.) KOM.-LEGN.

Monoraphidium griffithii (BERK.) Kom.-LEGN.

Monoraphidium minutum (NÄG.) KOM.-LEGN.

Oocystis borgei Snow

Oocystis lacustris CHODAT

Oocystis marssonii LEMM.

Oocystis submarina LAGERH.

Oocystis sp.

Planctonema sp.

Scenedesmus longispina CHODAT

Scenedesmus quadricauda (TURPIN)
BREBISSON
Scenedesmus sp.

#### **CHRYSOPHYCEAE**

Chrysococcus minutus (FRITSCH) NYG. Dinobryon cylindricum IMHOF Dinobryon suecicum LEMM. Dinobryon sp. Kephyrion spp. Monas sp. Pseudopedinella pyriforme CARTER

#### CRYPTOPHYCEAE

Cryptomonas erosa Ehrenberg Cryptomonas marssonii Skuja Cryptomonas ovata Ehrenberg Rhodomonas lacustris Pasher & Ruttner

#### **CYANOPHYCEAE**

Anabaena constricta (SZAFER) GEITLER Anabaena spiroides KLEBAHN Anabaena sp.

Aphanizomenon flos-aquae (L.) RALFS ex BORNET & FLAH.

Aphanothece clathrata W. & G. S. WEST Coelosphaerium kuetzingianum Näg. Coelosphaerium minutissimum LEMM. Gomphosphaeria pusilla (VAN GOOR) KOMAREK

Merismopedia punctata Meyen Microcystis reinboldii (RICHTER) FORTI Oscillatoria laetevirens CROUAN & CROUAN ex GOMONT

Oscillatoria limnetica LEMM.

Oscillatoria limosa C. A. Ag ex GOMONT Oscillatoria sp.

Spirulina major Kütz. ex Gomont

#### DINOPHYCEAE

Ebria tripartita (SCHUMANN) LEMM.
Glenodinium foliaceum STEIN
Glenodinium sp.
Gymnodinium spp.
Protoperidinium brevipes (PAULSEN)
BALECH

#### Table 1. continued

Protoperidinium granii (OSTENFELD)
BALECH
Protoperidinium pallidum (OSTENFELD)
BALECH
Protoperidinium pellucidum BERGH

#### **EUGLENOPHYCEAE**

Euglena spp.
Phacus pleuronectes (O. F. Müller) Duj.

Phacus pseudonordstedtii Pochmann Phacus suecicum LEMM. Trachelomonas volvocina EHRENBERG Trachelomonas volvocinopsis SWIRENKO

#### **PRASINOPHYCEAE**

Nephroselmis pyriformis (N. CARTER) ETTL Nephroselmis sp. Pyramimonas sp. Tetraselmis sp.

# Table 2. List of species dominating in the period June - August.

## BACILLARIOPHYCEAE

Diatoma elongatum (Lyngb.) C. A. AG. Diatoma vulgare BORY Fragilaria ulna (= Synedra ulna) (NITZSCH) LANGE-BERTALOT Navicula spp. Thalassiosira lacustris HASLE

#### **CHLOROPHYCEAE**

Monoraphidium contortum (THURET in BREB.) KOM.-LEGN. Monoraphidium minutum (NÄG.) KOM.-LEGN.

#### CHRYSOPHYCEAE

Kephyrion spp.

### CRYPTOPHYCEAE

Cryptomonas marssonii Skuja Rhodomonas lacustris Pasher & Ruttner

#### **EUGLENOPHYCEAE**

Euglena spp.

#### **PRASINOPHYCEAE**

Nephroselmis pyriformis (N. CARTER) ETTL Pyramimonas sp.

Beside phytoplankton 16 typical benthic species were occasionally found in the samples. Fifteen of them represented Bacillariophyceae (Achnantes taeniata, Cocconeis sp., Cymbella sp., Entomoneis paludosa, Epithemia sp., Eunotia sp., Gomphonema sp., Gyrosigma sp., G. scalproides, Licmophora sp., Nitzschia sp., N. longissima, N. sigma, Rhoicosphaenia abbreviata, Surirella sp.) and one (Oscillatoria laetevirens) belonged to Cyanophyceae. All identified benthic species were never frequent in the samples with exception of the station 7, where due to high turbulence Licmophora sp. was abundant.

The stations 7 and 8 were grouped together by the cluster analysis and represented separate clusters towards stations 2-6 (Figure 2). During June and July (Figure 2a-c) stations 5 and 6 showed high similarity to each other and were

grouped together. Station 1 showed in August (d, e) high differences to all other stations. The presented diagrams show in general the existence of three clusters: stations 7 and 8, stations 2, 3, 4, 5 and 6, and station 1. While the cluster built by stations 7 and 8 were detectable all the time, station 1 was grouped during June and July together with stations 2-6. At the end of August stations 7 and 8 showed higher similarity in species content than ever before compared to other stations (except station 1).

## Discussion

The present study clearly indicates that phytoplankton populations at the investigated stations close to the coast are not static and undergo changes in time and space. As pointed out by many authors, phytoplankton dynamics in estuaries depend on the interactions of abiotic and biotic factors (e. g. CLOERN & al. 1992, CLOERN 1996, CASAS & al. 1997). The patterns obtained in phytoplankton dynamics during summer close to Härnösand and in the Bay of Sundsvall agree in general with those reported earlier (SMETACEK & POLLEHNE 1986, TETT & al. 1986, MALLIN & al. 1991): spring dominance of Bacillariophyceae followed by an increase in Dinophyceae and small flagellates (Prasinophyceae and Cryptophyceae). Chlorophyceae were represented during the whole investigated period especially with species of Monoraphidium, which often dominated or subdominated. Blooms could be expected according to the increased level of eutrophication in the investigated region (County Administration, personal communication, NEHRING 1992, CLOERN 1996). The fact that no blooms were obtained could be explained by unusually cold weather during the summer of 1998 in the area studied.

Great differences in the species composition at the stations 7 and 8 in relation to the other stations can be explained by different ecological conditions. Although in all cases sampling was performed in small bays, stations 1-6 are greatly influenced by river flows (Figure 1). However, stations 7 and 8 are much more influenced by the open sea. The fact that the salinity in the investigated estuaries was very low explains the presence of different species like the freshwater genera *Chlamydomonas*. The clustering of stations 5 and 6 together could be viewed as possible evidence of the influence from the river Navarn on the right coast in the Bay of Sundsvall in comparison to the left coast. The clustering of the station 1 in a separate group in August shows higher differences in the totality of especially biotic factors between the Bay of Sundsvall and station 1 after July. Otherwise the clustering of the stations 1 to 6 was often not unambiguously. It seems not to be possible to distinguish clearly between the stations 1 to 6 only with the help of phytoplankton presence-absence data.

According to our knowledge, the sampling strategy chosen in the present study has never been reported in the literature concerning earlier marine and

Tab. 3. Relative abundance of phytoplankton species groups in time and space. S.s. - sampling stations, Bac. - Bacillariophyceae, Chlor. - Chlorophyceae, Chrys. - Chrysophyceae, Crypt. - Cryptophyceae, Cyan. - Cyanophyceae, Din. - Dinophyceae, Eugl. - Euglenophyceae, Pras. - Prasinophyceae. Sampling periods: a) 9 June; b) 23 June; c) 15 July; d) 19 August; e) 28 August. Frequency of each species present in the fixed samples was determined according to relative units: 0 - absent, 1 - occasional, 2 - rare, 3 - frequent, 4 - dominant.

۵)	S.s.	Bac.	Chior.	Chrys.	Crypt	Cyan.	Din.	Eugl.	Pras.
۵).	1	4	2	2	0	2	0	1	2
	2	4	3	2	0	1	1	1	1
	3	4	2	2	0	1	0	1	1
	4	4	3	2	0	0	1	1	3
	5	4	3	1	0	0	1	1	2
	6	4	3	1	0	0	1	1	2
	7	4	3	2	0	1	1	2	3
	8	4	3	1	0	0	1	1	3
	•								
b)	S.s.	Bac.	Chlor.	Chrys.	Crypt.	Cyan.	Din.	Eugl.	Pras.
υ,	1	3	2	2	3	2	1	4	4
	2	3	2	2	2	1	1	1	4
	3	4	2	1	4	1	3	3	4
	4	3	2	2	4	1	2	2	4
	5	2	2	1	4	0	1	3	4
	6	2	2	2	4	1	2	2	4
	7	4	2	0	2	2	1	1	1
	8	4	2	1	2	1	1	1	1
C)	S.s.	Bac.	Chlor.	Chrys.	Crypt.	Cyan.	Din.	Eugl.	Pras.
0,	1	4	2	1	3	1	1	1	0
	2	2	2	2	3	1	0	0	1
	3	3	2	3	3	1	0	0	1
	4	3	3	3	3	1	1	0	0
	5	4	3	1	4	1	0	0	0
	6	4	3	3	3	0	1	1	0
	7	4	2	1	2	1	0	2	1
	8	4	4	3	1	1	0	1	0

d)	S.s.	Bac.	Chlor.	Chrys.	Crypt.	Cyan.	Din.	Eugl.	Pras.
•	1	2	4	1	1	1	0		1 143.
	·	_	=	•		1	U	0	Ü
	2	1	2	1	4	1	1	0	1
	3	2	2	2	4	1	2	1	0
	4	1	3	1	4	1	1	0	1
	5	1	4	1	2	1	0	0	0
	6	2	3	2	4	1	0	3	2
	7	1	4	1	3	1	0	3	1
	8	1	3	1	4	2	0	0	4
e)	S.s.	Bac.	Chlor.	Chrys.	Crypt.	Cyan.	Din.	Eugl.	Pras.
e)	S.s.	Bac.	Chlor.	Chrys.	Crypt.	Cyan.	Din.	Eugl.	Pras.
e) <sub>.</sub>	S.s. 1 2							<b>Eugl.</b> 1 0	<b>Pras.</b> 0 1
e) <sub>.</sub>	1	2	3	0	4	0		1	Pras. 0 1
e) <sub>.</sub>	1 2	2 2	3	0	4	0	0	1 0	Pras. 0 1 1 0
e)	1 2 3	2 2	3	0 3 1	4 4 4	0	0 1 0	1 0 0	Pras.  0 1 1 0 0
e) <sub>.</sub>	1 2 3 4	2 2 2 1	3 3 4 1	0 3 1	4 4 4 4	0	0 1 0 0	1 0 0	Pras.  0 1 1 0 0 2
e) <u>.</u>	1 2 3 4 5	2 2 2 1 2	3 3 4 1 3	0 3 1	4 4 4 4	0	0 1 0 0	1 0 0 0 1	Pras.  0 1 1 0 0 2 1

estuary phytoplankton investigations. Commonly the samples are taken at greater depths and not close to the shore (e. g. HAJDU & WILLÉN 1985, BONALBERTI & al. 1992, KANGAS & al. 1993, ANDERSSON & al. 1996). We made an attempt to reveal if the sampling at especially low depths along the coast would provide us with reliable results to make comparisons sensitive enough between the different stations. This could allow in the perspective quick primary monitoring of changes in the environmental conditions close to the shore, e. g. as a result of pollution through industrial or human activities. In all cases except station 7 benthic species were scarcely represented in the water column independently of the upwelling activity. Although the use of phytoplankton presence-absence data allowed us to distinguish between clusters of the stations with high difference in the totality of environmental factors (7 and 8 in comparison to 1-6), fine comparison between similar sampling sites (1-5) was not possible. In this relation the suitability of other ecological indices should be tested.

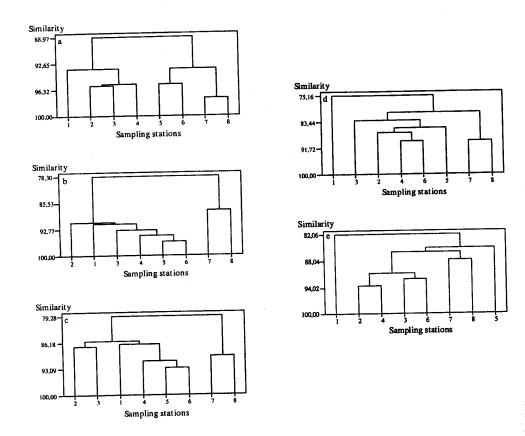


Figure 2. Clustering analysis of sampling stations based on similarities in species' diversity and their abundance. Sampling periods: a) 9 June; b) 23 June; c) 15 July; d) 19 August; e) 28 August.

# **Acknowledgements**

We wish to thank SEVED GRANBERG for good advice on cluster analyses and ANDERS LARSSON for help with the creation of the sampling stations map. We also thank MARIE ANDERSSON for her assistance in the laboratory.

#### References

- ANDERSSON A., HAJDU S., HAECKY P., KUPARINEN J. & WIKNER J. (1996): Succession and growth limitation of phytoplankton in the Gulf of Bothnia (Baltic Sea). Mar. Biol. 126: 791-801.
- BONALBERTI L., KUMER E., MAGGI G. & MILAN C. (1992): Marine coastal eutrophication south of the River Po, monitoring within 300 m of the coast. Sci. Total Envir., Suppl. 1992: 403-409.
- Casas B., Varela M., Gonzalez N. & Bode A. (1997): Seasonal variations of nutrients, seston and phytoplankton, and upwelling intensity of La Coruna (NW Spain). Estuar. Coast. Shelf Sci. 44: 767-778.
- CLOERN J. (1996): Phytoplankton bloom dynamics in coastal ecosystems, a review with some general lessons from sustained investigation of San Francisco Bay, California. Rev. Geoph. 34: 127-168.
- CLOERN J., ALPINE A., COLE B. & HELLER T. (1992): Seasonal changes in the spatial distribution of phytoplankton in small, temperate-zone lakes. J. Plankton Res. 14: 1017-1024.
- GRANÉLI E., WALLSTRÖM K., LARSSON U., GRANÉLI W. & ELMGREN R. (1990): Nutrient limitation of primary production in the Baltic Sea area. Ambio 19: 142-151.
- HAJDU S. & WILLEN T. (1985): Development of phytoplankton in the Gulf of Bothnia during May 1979-1984. The Swedish Marine Association, Annual Report. SMHI Press, Norrköping.
- HUTTUNEN M., KONONEN K., LEPPÄNEN J. & WILLÉN T. (1986): Phytoplankton of the open sea areas of the Gulf of Bothnia observations of the first stage of the Baltic Monitoring Programme in 1979-1983. In: Publ. No. 68 of the Water Research Institute, Helsinki, p. 139-144.
- JUSTIC D., RABALAIS N. & TURNER R. (1995): Stoichiometric nutrient balance and origin of coastal eutrophication. Mar. Pollut. Bull. 30: 41-46.
- KANGAS P., ALASAARELA E., LAX H., JOKELA S. & STORGARD-ENVALL C. (1993): Seasonal variation of primary production and nutrient concentrations in the coastal waters of the Bothnian Bay and the Quark. Aqua Fenn. 23: 165-176.
- MALLIN M., PAERL H. & RUDEK J. (1991): Seasonal phytoplankton composition, productivity and biomass in the Neuse River estuary, North Carolina. Estuar. Coast. Shelf Sci. 32: 609-623.
- MALONE T., CROCKER L., PIKE S. & WENDLER B. (1988): Influence of river flow on the dynamics of phytoplankton production in a partially stratified estuary. Mar. Ecol. Prog. Ser. 48: 235-249.
- NEHRING D. (1992): Eutrophication in the Baltic Sea. Sci. Total Envir., Suppl. 1992: 673-682.
- NIXON S. (1995): Coastal marine eutrophication, a definition, social causes, and future concerns. Ophelia 41: 199-219.
- NOGUEIRA E., PÉREZ F. & RIOS A. (1997): Seasonal patterns and long-term trends in an estuarine upwelling ecosystem (Ria de Vigo, NW Spain). Estuar. Coast. Shelf Sci. 44: 285-300.
- PANKOW H. (1990): Ostsee-Algenflora. Gustav Fischer Verlag, Jena.
- SMETACEK V. & POLLEHNE F. (1986): Nutrient cycling in pelagic systems, A reappraisal of the conceptual framework. Ophelia 26: 401-428.

TAYLOR C. & Howes B. (1994): Effect of sampling frequency on measurements of seasonal primary production and oxygen status in near-shore coastal ecosystems. – Mar. Ecol. Prog. Ser. 108: 193-203.

TETT P., GOWEN R., GRANTHAM B., JONES K. & MILLER B. (1986): The phytoplankton ecology of the Firth of Clyde sealochs Striven and Fyne. – Proc. R. Soc. Edinburgh, Sect. B, 90: 223-238.

TIKKANEN T. & WILLÉN T. (1992): Växtplanktonflora. Naturvårdsverket, Stockholm. WILLÉN T. (1995): Växtplankton i Östersjön 1979-1988. Naturvårdsverket, Stockholm.

Received: 13 September 1999 Accepted: 28 October 1999