

# Mass occurrence of unattached *Enteromorpha intestinalis* on the Finnish Baltic Sea coast

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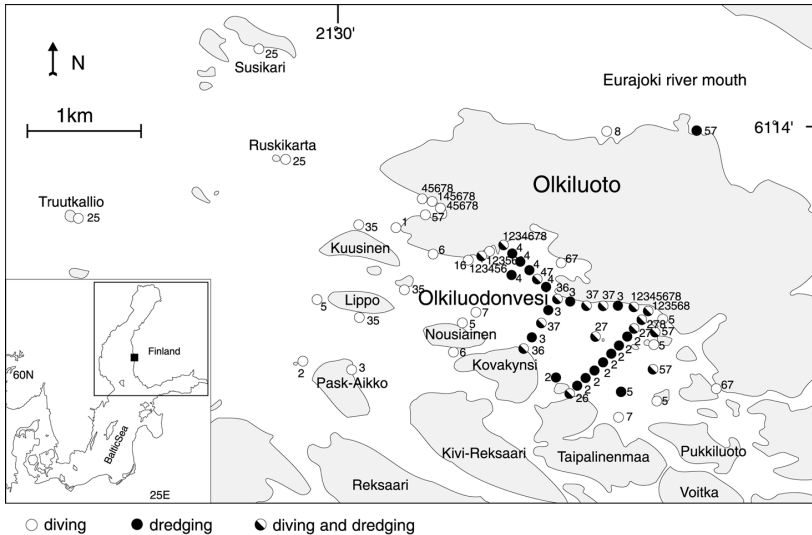
The occurrence and summer biomass of an unattached *Enteromorpha intestinalis* mat was studied in Olkiluodonvesi on the Finnish Baltic Sea W coast between 1993 and 1997. *Enteromorpha intestinalis* thalli had lost their tubular shape, spread, and formed unattached monostromatic sheets. The mats were found in areas of soft sediment and sandy substrates where water depth was one to six metres. Optimum growth was at one to two metres. The mats were 5–15 cm thick with biomass maximum of 97 tn in an area of 3.7 km<sup>2</sup> in 1993. Even during severe winter conditions, monostromatic *E. intestinalis* appeared in healthy state. In early spring, just after the ice melt, small amounts of *E. intestinalis* were found floating on the surface. Massive floating were observed after sunny and calm weather periods with low water level. On both occasions, *E. intestinalis* was moving within the water column.

Keywords: Baltic, green tide, macroalgal mats

## INTRODUCTION

Macroalgal mass occurrences are recognised world-wide as a response to elevated levels of sea-water nutrients in coastal areas (Fletcher 1992, 1996, Bonsdorff *et al.* 1997). On the west coast of Sweden as much as 30%–40% of the total shallow bottom area, in depth less than 1 m, is covered by free-lying green algae (Isaksson & Pihl 1992, Moksnes & Pihl 1995, Pihl *et al.* 1996).

The phenomenon of thick green algal mats occurring regularly on seabed is known as “green tide”. In the affected areas, typically one or a few unattached green algae species, such as *Cladophora* spp., *Enteromorpha* spp. (Vadas & Beal 1987, Fletcher 1996) and *Ulva lactuca* (Thorne-Miller *et al.* 1983, Soulsby *et al.* 1985), are responsible for the large biomasses that cover the bottoms of sheltered areas. The accumulations are observed especially at low tide when the seabed is exposed.



**Fig. 1.** Study area off the W coast of Finland and study points investigated during the intensive vegetation mapping in 1993. Sampling dates: 1 = 1–2 Dec. 1992; 2 = 1–2 Feb. 1993; 3 = 18–19 Feb. 1993; 4 = 10–11 Mar. 1993; 5 = 31 Mar.–1 Apr. 1993; 6 = 19–20 Mar. 1993.

By creating a shortage of oxygen algal mats increase the production of hydrogen sulphide in the sediment, which has negative effects on the fauna and flora (Bonsdorff 1992).

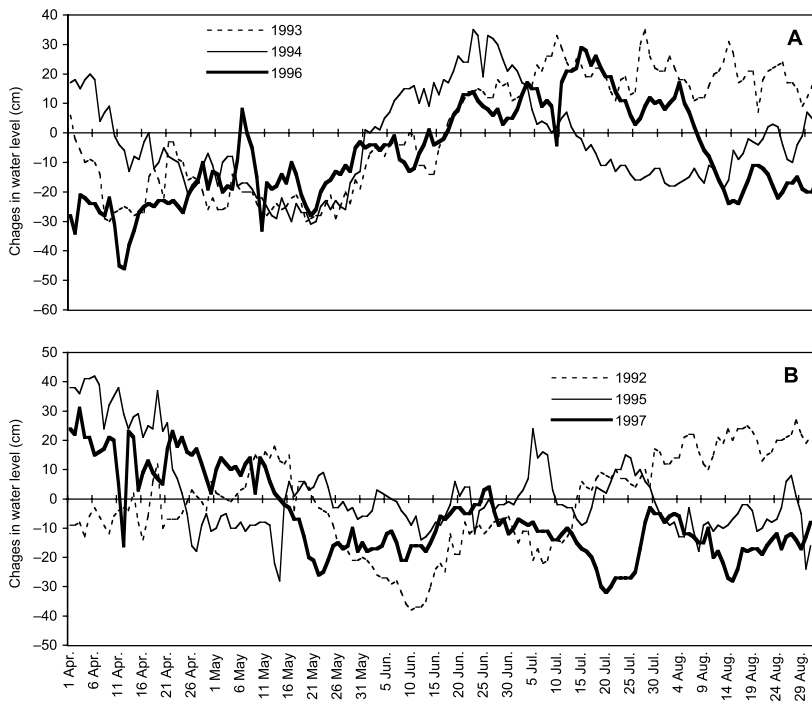
Phenomenons similar to “green tide” have been reported in the northern Baltic but the algal masses are polytypic and sometimes deposited on shores in the absence of tide. *Cladophora glomerata* has been found growing vigorously on sandy beaches of the northern and south-western coasts of the Neva Bay, seriously impairing recreational use of the coast (Alimov *et al.* 1994). Unattached filamentous algae, such as *Pilayella littoralis*, *Sphacelaria* sp., *Dictyosiphon tortilis*, *Ectocarpus siliculosus* and *Enteromorpha* spp., have been identified in large biomasses covering sediment bottoms at water depths of 3–15 metres in parts of the South-eastern Gulf of Bothnia (Bonsdorff 1992, Mäkinen *et al.* 1994, Norkko & Bonsdorff 1996). Wallentinus (1979) reported free-lying filamentous and unusually broad *Enteromorpha* sp. and *Monostroma grevillei* in the Askö area of Sweden. Extensive mats of a single species of *Enteromorpha*, with high biomass, have also been reported to cover large sheltered areas e.g. Hanko peninsula, Tammisaari and Uusikaupunki archipelagos along the Finnish coast (Kautsky 1982, Koistinen 1989, Bäck *et al.* 1993b, Lampolahti 1997). We found large *Enteromorpha* in 1992 on the West Coast of Finland, near the mouth of the Eurajoki. The species was identified as *Enteromorpha intestinalis* by molecular systematic meth-

ods (J. Blomster unpubl.).

The aim of the present investigation was to provide information on the occurrence of the ephemeral monostromatic sheet form of *Enteromorpha intestinalis* on the Finnish West Coast. The seasonality and summer biomasses of the algal mat were followed during a five-year period.

## MATERIAL AND METHODS

The study was carried out on the W coast of Finland near the mouth of the Eurajoki (Fig. 1). A mosaic of islands and skerries of various size dominate the area. The principal sampling site, Olkiluodonvesi, is a fairly sheltered water body, characterised by mainly with sandy and soft sediment bottoms. On the shores of the several islands the underwater rock does not extend to great depth but forms only a narrow zone where algae can attach and grow. The annual seawater temperature varies between 0 and 20 °C. During the winter, ice up to one meter thick may cover the area for up to four months. The salinity of the water varies between 4 and 5 ppt seasonally. Records were kept of the winds and rainy and sunny days in the study area. There is no tide in the Baltic Sea and the seawater level varies only in response to barometric conditions. In general, the pattern is low water level in spring (March–April), rising gradually to highest levels in autumn. This pat-



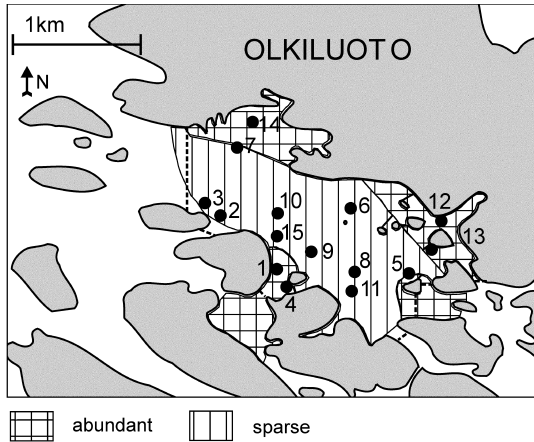
**Fig. 2.** Water level in the Rauma area. — A: General pattern of changes in water level, which is lowest in spring and rises during the summer months (years 1993, 1994, and 1996). — B: Water level is high in spring and decreases temporarily during the summer months (1995 and 1997). Extra data from 1992 have been added to demonstrate the pattern.

tern characterised the years 1993, 1994 and 1996 (Fig. 2a). In 1995 and 1997, water level is high in spring and but dropped for a short period of time in summer before rising again later in the autumn (Fig. 2b).

An intensive study on the distribution of *Enteromorpha intestinalis* was conducted in 1993. Altogether 77 sites were visited in order to plot the overall distribution of the *E. intestinalis* mat (Fig. 1). To estimate the distribution and thickness of individual mats, investigations at sites with *E. intestinalis* were carried out by SCUBA divers. During winter only the distribution was surveyed by dredging through holes drilled through the ice. Monitoring of the area for floating *E. intestinalis* was done daily from a motor boat.

Further documentation of the distribution of the sheet form of *Enteromorpha intestinalis* was carried out in Olkiluodonvesi in spring and summer 1994–1997. During this period the number of sampling points was reduced and only sites 1, 4–7, 10 and 14 were observed (Fig. 3). The thickness of the mat was examined by diving and the distribution either by diving and or by dredging from a boat. The distribution was scored as absent, sparse or abundant.

The summer biomass of *Enteromorpha intestinalis* was estimated on the basis of 15 sampling points randomly selected (Fig. 3). The study area was divided into squares of  $100 \times 100$  m and squares to be investigated were chosen randomly. Biomass samples were taken once a year from 1993 to 1997 in the middle of June. A plastic frame (size of  $0.12 \text{ m}^2$ ) was thrown into the water from the anchored boat and a diver placed it on the bottom. All the loose material within the frame was collected into a sieve net. Two samples ( $0.12 \text{ m}^2$  each) from the same square were collected in the same way, were combined for a coverage of  $0.24 \text{ m}^2$ . The visibility in the water was extremely poor on the soft sediment bottom and the use of a small frame made it easier for the diver to collect all the material within the frame. In the laboratory, *E. intestinalis* was washed clean from the mud and bottom fauna. Excess water in the samples was removed by gently soaking it into a tissue paper. The same person did the work each year. The fresh weight of the sample was used for biomass estimation of *E. intestinalis*. The total biomass of *E. intestinalis* in the area was calculated as fresh weight per  $\text{m}^2$  with the mean value for each of the 15 squares in the calculation.



**Fig. 3.** Randomly located sampling points for study of biomass and distribution of *Enteromorpha intestinalis* in 1993–1997, with indication of abundant and sparse occurrences.

## RESULTS

The distribution of *Enteromorpha intestinalis* mat in Olkiluodonvesi varied only slightly over the five years of the study. In 1993, *E. intestinalis* occurred in greatest abundance close to the shoreline where the water was 1–2 m deep. Likewise in 1994–1997, it favoured the sheltered coastal areas and was not found at open shore locations (Fig. 3). The mat occurred mostly in small shallow (0–3 m) bays where it formed a fairly uniform community over a wide area. The distribution was patchy in deeper parts (3–5 m) where soft silt formed the bottom. The thickness of the *E. intestinalis* mat was uneven, varying from less than five up to 20 centimetres. Occasionally, black sediments smelling of sulphide were found beneath the mat. There were no major differences during the study in the survival of *E. intestinalis* over the winter months. The algae remained alive under the ice. *Enteromorpha intestinalis* sheets were deeper in colour and smaller in size in winter than in summer.

*Enteromorpha intestinalis* mats were found floating once and sometimes twice each year. The first period occurred in March–April, just after ice melt normally was short and not intensive. At that time the seawater temperature was still close to zero. In some years a second episode of floating occurred, after a period of calm and sunny

weather and abnormally low water. The second episode occurred only in years when the water level was high in spring and dropped in early summer, e.g. in 1995 and 1997. In 1997 floating did not occur until July, when the water level declined abnormally. Normally, this massive floating lasted from two to three days and large amounts of decaying *E. intestinalis* were deposited on the shore. Abundant gas bubbles were observed underneath the *E. intestinalis* mat. The plants were lifted up and buoyed up and moved with the waves and water currents.

The total summer biomass of *Enteromorpha intestinalis* in the area (3.7 km<sup>2</sup>) gradually diminished from 97 to 32 tonnes during the study period (Table 1). The greatest biomasses were measured near the shore at 1–2 metres depth, and the smallest at a depth of 6 metres (Fig. 3).

## DISCUSSION

The identity of the monostromatic, unattached sheet like *Enteromorpha* in the Baltic Sea has caused some controversy. Kautsky (1982) identified sheet like green alga as *E. compressa* and found it to form massive mats in SW Finland. Wallentinus (1979) mentioned torn parts of *Monostroma grevillei*, unattached and drifting about in spring but absent in summer. The identification of *Enteromorpha* (Blomster *et al.* 1999) and other green algal species (Coat *et al.* 1998) has become more reliable with the use of molecular biological methods. This non-morphological approach also enabled the identification of the monostromatic form of *E. intestinalis* (J. Blomster unpubl.).

Monostromatic sheet-like *Enteromorpha intestinalis* occupies an unusual niche for macroalgae. It grows successfully unattached in shallow water with on a sediment bottoms and can tolerate the harsh winter conditions of the Baltic Sea. *Vaucheria* spp. and *Chara* spp. and seed plants, such as *Potamogeton* spp., *Myriophyllum* spp. and *Callitriche* sp. are the usual occupants of sand or silt bottoms in the Baltic Sea. These plants die out in late autumn and they do not begin to grow again until the water temperature has risen (Luther 1951, Ulvinen 1955, Hällfors *et al.* 1987). Large *E. intestinalis* mats on sediment substrates may be much more common on the Finnish shoreline

than thought. The extensive length of the shoreline and the complex mosaic structure of the Finnish archipelagos, together with the growth depth of these mats, make observations laborious. There may also be some confusion with *Monostroma balticum*. In many cases drifting sheet-like green alga identified as *M. balticum* could be *E. intestinalis*.

Free-lying *Enteromorpha* has been recorded in 1990s in the archipelago of Uusikaupunki (Lampolahti 1997). In the late 1970s and early 1980s, a sheet-like alga identified as *Enteromorpha compressa* occupied a large area of sandy bottoms on the northern side of the Hanko peninsula, Finland (Kautsky 1982, Koistinen 1989). The biomass values (440 dryweight g m<sup>-2</sup>) were much higher than the values measured in our study. With the decrease in ammonium sulphate load in the area, the biomass and the area covered by *Enteromorpha* mats were decreased. Some *Enteromorpha* sheets evidently still persist, though *Enteromorpha compressa* is not longer the dominant species in the area (A. Ruuskanen pers. comm.). A sheet-like *Enteromorpha* would be able to take up nutrients quickly and thus successfully compete with other benthic algae and higher plants

(Kautsky 1982). The cells of a sheet-like alga are optimally exposed to light and nutrients (Hein *et al.* 1995). Moreover, the anoxic conditions under an algal mat might cause a rapid release of nutrients from the sediment, making them available to the alga (Sfriso *et al.* 1992, McGlathery *et al.* 1997). Anoxic conditions were observed in our study area, and black foul-smelling decaying algae and sediment were found under the densest mats.

Algal mats interfere with the benthos by creating hypoxic or anoxic conditions with development of hydrogen sulphide in the sediment (Sundbäck *et al.* 1990, Bonsdorff 1992). The natural littoral vegetation and bottom fauna may suffer due to the algal mat covering the available substrata (Mäkinen *et al.* 1994, Norkko & Bonsdorff 1996). Norkko and Bonsdorff (1996) demonstrated very rapid structural changes in the zoobenthos community due to an algal mat. Bonsdorff (1992) reported that multi-species algal mats disappear and move with water currents. Compared with multi-species algal mats, an *Enteromorpha intestinalis* mat is extremely stable: during our five-year study, high values of *E. intestinalis* biomass were measured every summer at almost the

**Table 1.** The biomass of *Enteromorpha intestinalis* (fresh weight g/m<sup>2</sup>) in Olkiluodonvesi in 1993–1997. The sampling sites are shown in Fig. 3.

Sampling site	Sampling depth (m)	Biomass freshweight g m <sup>-2</sup>				
		1993	1994	1995	1996	1997
1	5	5.9	25.4	25.6	6.1	39.8
2	5	0	1.1	3.3	0	28.1
3	3	10.1	1.6	0.3	0.1	0
4	2	27.3	27.3	4.3	10.4	12.8
5	3	1.3	0	0.5	0.1	0.3
6	3	0	0	31.6	16.2	1.2
7	4	0	8.8	1.3	0.1	0.6
8	3	25.6	1.4	4.6	2.2	0
9	5	2.1	1	0.2	0.5	0.1
10	6	0.8	0	0.3	0	0.2
11	3	1.3	2	0.2	2	0.1
12	1	64.3	9.9	0.4	63.6	0.1
13	2	255.5	157.9	10.5	8.5	1.5
14	2	3.4	53.7	94.2	69.9	47
15	6	0	2.2	0.9	0.8	1.5
Mean g m <sup>-2</sup>		26.5	19.5	11.9	12	8.9
Total biomass (3.7 km <sup>2</sup> )		96 720 kg	71 175 kg	43 358 kg	43 800 kg	32 930 kg



same locations. An *E. intestinalis* mat that stays in the same location can be assumed to have severe impact on the bottom fauna.

Ice cover affects the vegetation by reducing the amount of available light and in shallow areas abrasive action of the ice may cause additional harm (Kiirikki & Ruuskanen 1996). Unattached monostromatic *Enteromorpha intestinalis* is able to stay alive under the ice and exhibits extremely vigorous growth immediately after the ice has melted. A similar phenomenon has been noticed in *Ulva lactuca* on the Danish coast (Vermaat & Sand-Jensen 1987). A two months dark period and low temperatures did not influence the subsequent growth capacity of *U. lactuca*. In our study, *E. intestinalis* was found alive under the ice even after five months, demonstrating its ability to withstand prolonged darkness and temperatures close to zero. It is likely that *E. intestinalis* have a strong overwintering capacity as *U. lactuca* (Vermaat & Sand-Jensen 1987). In the inventory from December to April 1993, viable sheets were found in the study area at the depths from 1 to 6 metres. In the studies on the Swedish West Coast, Pihl *et al.* (1996) found algal mats of *Cladophora* spp. and *Enteromorpha* spp. to be present from June to August but they did not investigate the possible overwintering capacity of the mats. Overwintering capacity and the ability to grow from frond fragments are powerful tools for quick start and growth in spring. With this strategy, large areas can be colonised in spring, before higher plants begin their growth. Monostromatic *E. intestinalis* has a similar growth and survival pattern to that of *U. lactuca* (Vermaat & Sand-Jensen 1987), and after withstanding unfavourable winter conditions commences extremely vigorous growth in spring.

On the basis of our findings we believe that *Enteromorpha intestinalis* mats may have the potential to cause serious changes in the Baltic shallow water ecosystem. The mats are extremely persistent and tolerate well a variety of environmental conditions and seasonal changes. If the amount of macroalgal mats such as *E. intestinalis* mats are increasing in response to pollution as suggested by Fletcher (1992, 1996) and Bonsdorff *et al.* (1997), a significant threat to coastal ecosystems is indicated.

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## REFERENCES

- Alimov, A. F., Nikulina, V. N., Panov, V. E., Telesh, I. V. & Finogeva, N. P. 1994: Hydrobiology of the Neva Bay of the Gulf of Finland. — *Hydrobiol. J.* 30: 14–26.
- Blomster, J., Maggs, C. A. & Stanhope, M. J. 1999: Molecular and morphological analysis of *Enteromorpha intestinalis* and *E. compressa* (Chlorophyta) in the British Isles. — *J. Phycol.* 34: 319–340.
- Bäck, S., Mäkinen, A., Rissanen, J. & Rönnerberg, O. 1993a: Phytobenthos monitoring. Two case studies from the Finnish Baltic coast in summer 1993. — *Memorandum* 1993 1: 1–24. Min. Env., Helsinki, Finland.
- Bäck, S., Lehvo, A. & Kiirikki, M. 1993b: The occurrence of macroalgal mass blooms on the Finnish Baltic coast. — In: Rijsteinbil, J. W. & Haritonidis, S. (eds.), *Macroalgae, eutrophication and trace metals cycling in estuaries and lagoons*: 18–21. Proc. COST-48 Symp. Subgroup III, 24–26 Sep. 1993. Bridge. Comm. European Communities.
- Bonsdorff, E. 1992: Drifting algae and zoobenthos-effect on settling and community structure. — *Netherl. J. Sea Res.* 30: 57–62.
- Bonsdorff, E., Blomqvist, E. M., Mattila, J. & Norkko, A. 1997: Coastal eutrophication: cause, consequences and perspectives in the archipelago areas of the northern Baltic Sea. — *Estuar. Coast. Shelf Sci.* 44: 63–72.
- Coat, G., Dion, P., Noailles, M.-C., de Reviere, B., Fontaine, J.-M., Berger-Perrot, Y. & Loiseaux-de Goër, S. 1998: *Ulva americana* (Ulvales, Chlorophyta) from the coasts of Brittany (France). II. Nuclear rDNA ITS sequence analysis. — *Eur. J. Phycol.* 33: 81–86.
- Fletcher, R. L. 1992: The “Green Tide” problem. — In: Delepine, R. & Morand, P. (eds.), *Production and exploitation of entire seaweed*: 29–33. Proc. 3rd Cost 48 Subgroup 3 workshop, Paimpol & Saint-Malo (France) 9–14 March 1991. EEC, Brussels.
- Fletcher, R. L. 1996: The occurrence of “Green tides”. A review. — In: Schramm, W & Nienhuis, P. H. (eds.), *Ecological studies, Vol. 123. Marine benthic vegetation*: 7–43. Springer Verlag, Berlin & Heidelberg.
- Hällfors, G., Viitasalo, I. & Niemi, Å. 1987: Macrophyte vegetation and trophic status of the Gulf of Finland. A review of Finnish investigations. — *Meri* 13: 111–158.
- Hein, M., Pedersen, M. F. & Sand-Jensen, K. 1995: Size-dependent nitrogen uptake in micro- and macroalgae. — *Mar. Ecol. Progr. Ser.* 118: 247–253.
- Isaksson, I. & Pihl, L. 1992: Structural changes in benthic macrovegetation and associated epibenthic faunal communities. — *Netherl. J. Sea Res.* 30: 131–140.
- Kautsky, L. 1982: Primary production and uptake kinetics

- of ammonium and phosphate by *Enteromorpha compressa* in an ammonium sulphate industry outlet area. — *Aq. Bot.* 12: 23–40.
- Kiirikki, M. & Blomster, J. 1996: Wind induced upwelling as a possible explanation for mass occurrences of epiphytic *Ectocarpus siliculosus* (Phaeophyta) in the northern Baltic Proper. — *Mar. Biol.* 127: 353–358.
- Kiirikki, M. & Ruuskanen, A. 1996: How does *Fucus vesiculosus* L. survive ice scraping. — *Bot. Mar.* 39: 133–139.
- Koistinen, M. 1989: Vesikasvillisuus Hankoniemen pohjoispuolen merialueella, teollisuuden ammoniumsulfaattipäästöjen vaikutuspiirissä v. 1987. — *Vesi- ja ympäristöhallituksen monistesarja* 186: 1–149.
- Lampolahti, J. 1997: *Uudenkaupungin merialueen kasvilisuiden kehitys 1990–1996*. Tutkimusraportti Kemira Agro Oy:n Uudenkaupungin tehtaille. Kemira Agro, Finland. 30 pp. + 36 figs.
- Luther, H. 1951: Verbreitung und Ökologie der höheren Wasserpflanzen im Brackwasser der Ekenäs-Gegend in Süd-Finland. II Spezieller Teil. — *Acta Bot. Fennica* 50: 1–370.
- McGlathery, K. J., Krause-Jensen, D., Rysgaard, S. & Christensen, P. B. 1997: Patterns of ammonium uptake within dense mats of the filamentous macroalga *Chaetomorpha linum*. — *Aq. Bot.* 59: 99–115.
- Mäkinen, A., Hänninen, J. & Vahteri, P. 1994: *Underwater mapping of the biodiversity in the Archipelago Nature Conservation Park, SW Finland*. — Archipel. Res. Inst. Turku Univ. 60 pp., 3 append.
- Moksnes, P.-O. & Pihl, L. 1995: Utbredning och production av fintradiga alger i grunda mjukbottensraden i Göteborgs och Bohus län. — *Miljövarsrapporter, Landstyrelsen i Göteborgs och Bohus län* 1995 (10): 1–15.
- Norkko, A. & Bonsdorff, E. 1996: Rapid zoobenthos community responses to accumulations of drifting algae. — *Mar. Ecol. Progr. Ser.* 131: 143–157.
- Pihl, L., Magnusson, G., Isaksson, G. & Wallentinus, I. 1996: Distribution and growth dynamics of ephemeral macroalgae in shallow bays on the Swedish West Coast. — *J. Sea Res.* 35: 169–180.
- Sfriso, A., Marcomini, A. & Pavoni, B. 1987: Relationships between macroalgae biomass and nutrient concentrations in the hypertrophic area of the Venice lagoon. — *Mar. Env. Res.* 22: 297–312.
- Sfriso, A., Pavoni, B., Marcomini, A. & Orio, A. A. 1992: Macroalgae, nutrient cycles and pollutants in the lagoon of Venice. — *Estuaries* 15: 517–528.
- Soulsby, P. G., Lowthion, D., Houston, M. & Montgomery, H. A. C. 1985: The role of sewage effluent in the accumulation of macroalgae mats on the intertidal mudflats in two basins in southern England. — *Netherl. J. Sea Res.* 19: 257–263.
- Sundbäck, K., Jonsson, B., Nilsson, P. & Lindström, I. 1990: Impact of accumulating drifting macroalgae on a shallow-water sediment system: An experimental study. — *Mar. Ecol. Progr. Ser.* 58: 261–274.
- Thorne-Miller, B., Harlin, M. M., Thursby, G. B., Brady-Cambell, M. M. & Dworetzky, B. A. 1983: Variation in the distribution and biomass of submerged macrophytes in five coastal lagoons in Rhode Island, USA. — *Bot. Mar.* 26: 231–242.
- Ulvinen, A. 1955: Die Armleuchteralgen (Characeae) an der Meeresküste von Kymenlaakso. — *Arch. Soc. Vanamo* 9: 386–395.
- Vadas, R. L. & Beal, B. 1987: Green algal ropes: A novel estuarine phenomenon in the Gulf of Maine. — *Estuaries* 10: 171–176.
- Vermaat, J. E. & Sand-Jensen, K. 1987: Survival, metabolism and growth of *Ulva lactuca* under winter conditions: A laboratory study of bottlenecks in the life cycle. — *Mar. Biol.* 95: 55–61.
- Wallentinus, I. 1979: Environmental influences on benthic vegetation in the Trosa-Askö area, northern Baltic Proper. II. The ecology of macroalgae and submerged phanerogams. — *Contr. Askö Lab.* 25: 1–210.