

27 “Top-Down” Predation Control on Marine Harmful Algae

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27.1 Introduction

Removal of upper-trophic-level predators by industrialized fishing appears capable of disrupting and restructuring some marine ecosystems through a series of trophic cascades (Frank et al. 2005). There is the potential that such trophic cascades might favor harmful algal bloom (HAB) species of phytoplankton.

There is extensive literature on „top-down“ control of phytoplankton by predation-induced trophic cascades, whereby predation on herbivorous zooplankton leads to increases in phytoplankton and cyanobacteria. Such studies come primarily from freshwater ecosystems (reviewed by Carpenter et al. 1985; Carpenter 1988), and are rare in marine ecosystems. However, there are suggestions that predation on marine grazers such as on copepods by gelatinous predators such as scyphomedusae and ctenophores, or by fish may decrease zooplankton grazing pressure, and increase the biomass or alter species composition of phytoplankton, including HAB species.

Inverse field abundances of copepods and medusae (Möller 1980; Greve and Reiners 1988; Greve 1994; Schneider and Behrends 1998), copepods and ctenophores of the genus *Mnemiopsis* (Reeve and Walter 1978; Kremer 1979; Deason and Smayda 1982; Turner et al. 1983; French and Smayda 1995), or studies from mesocosms using ctenophores of the genus *Pleurobrachia* (Olsson et al. 1992; Granéli et al. 1993a), suggest that predation impact of gelatinous carnivores on copepods can be high. In contrast, there are indications of a relatively small predatory impact of the ctenophore *Pleurobrachia pileus* on copepods in European coastal waters (Miller and Daan 1989; Kuipers et al. 1990; Båmstedt 1998). However, such conclusions are usually equivocal, based upon correlations of field abundances, which might be due to advection or other factors, rather than predation effects.

Selective grazing by mesozooplankton may change phytoplankton species composition. Selective grazing on diatoms by copepods (Turner and Tester

1989) or euphausiids (Granéli et al. 1993b) could reduce grazing pressure on phytoflagellates and other non-diatom phytoplankters (Granéli et al. 1989). This could possibly contribute to events such as the ichthyotoxic Scandinavian bloom of *Chrysochromulina polylepis*, which began in the Skagerrak in late-spring of 1988 (Dahl et al. 1989; Maestrini and Granéli 1991). Alternatively, if ctenophore predation removes copepods, this could contribute to blooms of phytoplankters normally grazed by copepods.

We will review evidence for “top-down” influences on harmful algal blooms in the sea. These will include possible effects of gelatinous predators such as ctenophores and medusae, as well as fish. One hypothesized scenario is that predation by ctenophores, medusae and/or fish on mesozooplankton grazers such as copepods would reduce mesozooplankton grazing pressure on phytoplankton, possibly contributing to differential growth of certain phytoplankton taxa, some of which may include harmful algae. Also, global depletion of large piscivorous fishes by industrialized fishing (Myers and Worm 2003) may promote increases in smaller zooplanktivorous fish, increasing predation pressure on zooplankton, and diminishing zooplankton grazing on phytoplankton, including HAB species. Similar cascades might result from human “fishing down” marine food webs (Pauly et al. 2000), whereby industrialized fishing sequentially exploits organisms at lower trophic levels (such as small planktivorous fish), after severe depletion of larger apex predators

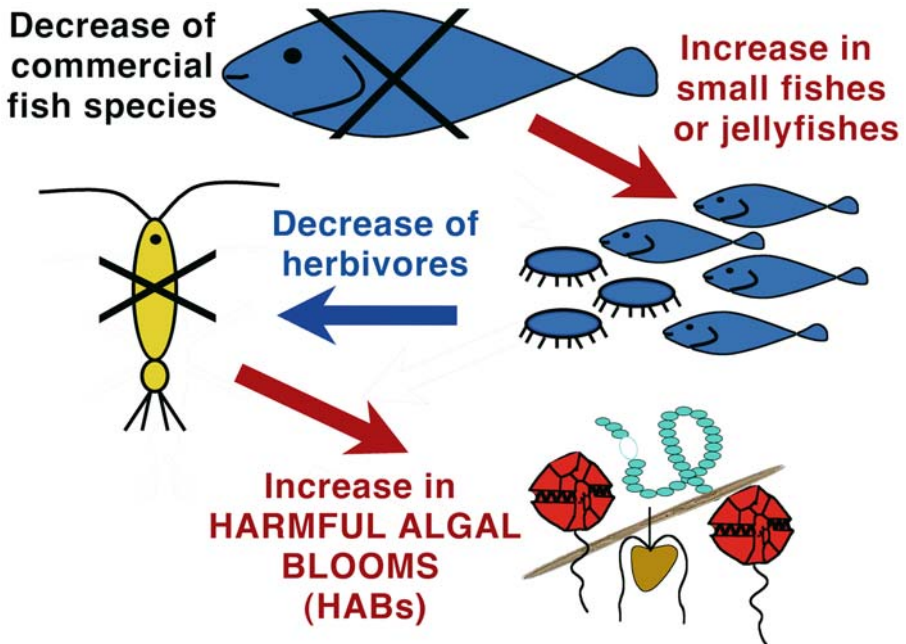


Fig 27.1. Possible pathway for HAB formation when the “top-down control” of the food chain is disrupted, as e.g., by overfishing. (Redrawn from Granéli 2004)

(Fig. 27.1). We will examine evidence for top-down predation-induced cascades in the Black Sea, and in mesocosm experiments designed to elucidate such effects. We will conclude that much more must be learned in order to clarify the extent of “top-down predation” effects on HABs, by either gelatinous predators such as medusae or ctenophores, or by fish.

27.2 “Top-down” Predators

27.2.1 Medusae

Greve (1994) reported that in July, 1989 in the German Bight of the North Sea, an increased population of the siphonophore *Muggiaea atlantica* was associated with lower than long-term mean levels of copepods, and higher than long-term mean levels of phytoplankton biomass. Greve concluded that siphonophore predation on copepods reduced grazing pressure on phytoplankton.

Schneider and Behrends (1998) found that abundant summer appearances of the scyphomedusa *Aurelia aurita* in Kiel Bight (western Baltic Sea) were associated with declines in mesozooplankton. This was particularly true for filter-feeding copepods such as *Pseudocalanus* spp., *Paracalanus* spp. and *Oithona similis*, compared to the copepods *Centropages hamatus* and *Acartia* spp. The latter two copepods reproduce throughout the summer in these waters, whereas *Pseudocalanus* reproduces only in the spring. The *Aurelia* increases were associated with increases in ultraplankton (<15 µm), which comprised 85 % of the summer chlorophyll. There was no change in the abundance of larger phytoplankton such as diatoms and dinoflagellates. Schneider and Behrends concluded that medusae exerted “top-down” predation on mesozooplankton copepods, causing reduced copepod grazing pressure on the most abundant phytoplankton.

Lindahl and Hernroth (1983) concluded that in Gullmar Fjord (west coast of Sweden) that spring and summer diatom blooms were related to low zooplankton grazing pressure because of predation on copepods and marine cladocerans by *Aurelia aurita*. When *Aurelia* declined in the fall, copepods increased in abundance and there were fall blooms of dinoflagellates such as *Gyrodinium aureolum* (= *Karenia mikimotoi*) and *Ceratium* spp. which may be toxic or difficult for zooplankton to graze. However, the hypothesis that these blooms were caused by top-down effects by jellyfish was later rejected by Lindahl (1987) who concluded that water exchange processes were more probable causes of the blooms (Granéli et al. 1993a).

Huntley and Hobson (1978) found that in Saanich Inlet, a fjord on Vancouver Island in British Columbia, Canada, that there was an initial spring diatom

bloom (*Thalassiosira nordenskioldii*) in April–May, followed by a second spring diatom bloom (*Skeletonema costatum* and *Chaetoceros* spp.) in June. The second bloom may have been caused by predation of the medusa *Phialidium gregarium* on mesozooplankton, thereby reducing zooplankton grazing pressure on the diatoms.

Other studies suggest a lesser role for medusae predation impact on other zooplankton, and by inference, phytoplankton. Barz and Hirche (2005) found that in the Bornholm Basin of the central Baltic Sea, predation by *Aurelia aurita* did not regulate abundances of copepods and marine cladocerans, consuming averages of only 0.1 % of the copepods and 0.5 % of the cladocerans per day. Maximal impact was only 7.9 % of the cladocerans.

27.2.2 Ctenophores

Various field sampling programs have revealed precipitous declines in abundance or biomass of mesozooplankton such as copepods coincident with increases in ctenophores (reviewed by Reeve and Walter 1978; Kremer 1979; Deason and Smayda 1982; Turner et al. 1983; Frank 1986). In some of these cases (Deason and Smayda 1982; Turner et al. 1983), these patterns were coincident with increases in total phytoplankton abundance or biomass. Deason and Smayda (1982) found that for 4 of the 6 years studied in Narragansett Bay, Rhode Island, summer/fall pulses of the ctenophore *Mnemiopsis leidyi* were accompanied by rapid declines in zooplankton abundance and phytoplankton blooms. Yearly variations in the summer abundance of the diatom *Skeletonema costatum* were positively related to ctenophore abundance. Deason and Smayda (1982) concluded that *M. leidyi* regulated summer dynamics of phytoplankton and zooplankton in Narragansett Bay, and that such influence on phytoplankton dynamics through predation by a carnivore two trophic levels above the phytoplankton was analogous to other predation-induced trophic cascades reported for benthic marine communities.

In an extension of these studies in Narragansett Bay, French and Smayda (1995) proposed that the toxic flagellate *Heterosigma akashiwo* (formerly *Olisthodiscus luteus*, and *Heterosigma carterae*) can bloom in late spring even though the diatom *S. costatum* can outcompete it in growth rate. This can occur if copepod grazing on *H. akashiwo* is impaired by toxicity (Tomas and Deason 1981), but absence of ctenophore predation allows copepods to eat substantial amounts of *S. costatum*.

27.2.3 Fishes

There is little convincing evidence for putative top-down effects on marine phytoplankton communities through fish predation on zooplankton grazers.

As with most of the papers on “top-down” predation by gelatinous carnivores such as ctenophores and medusae, such effects due to fish remain more speculated than demonstrated. The primary reason for this is that there is very little information on the impact of predation by planktivorous fish on zooplankton communities.

Several attempts to estimate the importance of ichthyoplankton predation on zooplankton concur that such predation has little impact on the zooplankton. Dagg and Govoni (1996) estimated that at three localities in the northern Gulf of Mexico, predation by larval fish induced daily mortality of <1 % of the abundance of copepod eggs, nauplii or copepodites within the size range ingested by the fish larvae. Maximum potential predation by unusually high numbers of fish larvae concentrated in the plume of the Mississippi River was only 2–18 % of the copepodites per day, but most values were <2.5 % per day. Munk and Nielsen (1994) estimated that ichthyoplankton in frontal zones in the North Sea ingested only 2.3–3.5 % of copepod biomass per day. Pepin and Penney (2000) calculated that daily predation by a coastal Newfoundland larval fish community on the zooplankton community was <0.1 % of zooplankton abundance.

In estuarine enclosure studies, the predation effects of fish on zooplankton communities can range from weak (Granéli et al. 1993a) to substantial (Horsted et al. 1988; Riemann et al. 1988). Granéli et al. (1993a) found in mesocosm experiments, that the introduction of zooplanktivorous fish decreased the copepod biomass by half in enclosures where copepods were at natural abundance levels, as well as those where copepods were added at 10x their natural abundance. The resulting effect was that *Gyrodinium aureolum* (= *Karenia mikimotoi*) increased in abundance in these cylinders where grazing on dinoflagellates by copepods was released by the predation on the copepods by fish. However, there were no such effects apparent for another large dinoflagellate, *Ceratium furca*. Thus, different phytoplankton species were affected differently by fish predation on zooplankton.

27.3 Case Studies

27.3.1 Black Sea

The Black Sea is thought to be a major site of intense top-down predation effects on marine food webs. There has been an overall deterioration in the pelagic ecosystems of the Black Sea since introduction of the North American ctenophore *Mnemiopsis leidyi*, first detected in 1982 (Zaitsev 1992). These changes include increases in harmful algal blooms (Kideys 1994, 2002; Moncheva et al. 2001a, 2001b), suggesting the possibility of links to top-down

predation by ctenophores on mesozooplankton, reducing grazing pressure on phytoplankton. However, it is difficult to separate effects of ctenophore predation from those of concurrent eutrophication due to increases in nutrient loading and changes in nutrient ratios due to damming of the Danube (Humborg et al. 1997; Lancelot et al. 2002), overfishing (Daskalov 2002; Gucu 2002) and climate change (Daskalov 2003).

Several simulations using physical-biological models have investigated changes in the pelagic ecosystems of the Black Sea in relation to increased predation by the ctenophore *Mnemiopsis leidyi* and the medusa *Aurelia aurita* during the last two decades (Oguz et al. 2001; Daskalov 2002, 2003, and references therein). The model of Oguz et al. (2001) reproduced reasonably well the observed planktonic community and food web structures in a typical eutrophic coastal location in the late 1970s and early 1980s prior to introduction of ctenophores. Simulations for the ctenophore-dominated ecosystems of the late 1980s indicated that outbreaks of either medusae or ctenophores reduced mesozooplankton grazing and led to increased phytoplankton blooms, as actually observed throughout the late 1980s and early 1990s. However, except for the omnivorous non-toxic dinoflagellate *Noctiluca scintillans*, simulated linkages between ctenophore or medusae predation and harmful algal blooms in the Black Sea remain inconclusive. Also, simulated trophic “cascades” caused by overfishing are complicated by other factors such as eutrophication and climate change (Daskalov 2002, 2003), and eutrophication-related changes in phytoplankton are complicated by climate-related changes in hydrography (Yunev et al. 2005). Effects of the invasion of the Caspian Sea by *Mnemiopsis leidyi* in 1995, probably from the Black Sea, are similarly complicated, and blaming such effects on a ctenophore-induced trophic cascade is uncertain (Bilio and Niermann 2004).

27.3.2 Mesocosm Studies

The Role of Ciliates

Planktonic ciliates are both grazers of phytoplankton, including HAB species, as well as prey for larger omnivorous zooplankters such as copepods (Turner and Roff 1993). Thus, predation on ciliates by copepods may actually remove the major grazers of HAB phytoplankton, enhancing their blooms.

Granéli and Turner (2002) performed mesocosm experiments (west coast of Sweden) to investigate whether ctenophore predation caused a cascade of “top-down” effects on phytoplankton abundance and species composition. A major result, which emerged from these experiments, was the unanticipated importance of ciliates in such interactions. Although copepod biomass levels in treatments with and without added *Pleurobrachia pileus* were not signifi-

cantly different except for the last day of the experiment, it appeared that ctenophore predation diminished copepod abundance or slowed copepod growth enough to reduce copepod predation pressure on ciliates, which were the major grazers of smaller phytoflagellates. In mesocosms with natural copepod abundances, ctenophore predation contributed to increased ciliate biomass by removal of copepods. Resultant ciliate increases led to reductions in small phytoflagellates due to ciliate grazing. These effects were particularly magnified in mesocosms with added zooplankton (primarily copepods) at 10x natural abundance. There, copepod predation decimated ciliate biomass, both in the presence and absence of ctenophores. Differences in ciliate biomass and the presence versus absence of ctenophores in these enclosures were minor compared to differences in ciliate biomass in mesocosms with and without added zooplankton. This was because copepods were dramatically effective in removing ciliates. Consequently, small phytoflagellates and monads actually increased in mesocosms with added zooplankton (mainly copepods) at 10x natural concentrations, either with or without ctenophores. The toxic dinoflagellate *Karenia mikimotoi* was somewhat reduced (presumably by grazing) in the containers with 10x natural copepod abundance, but in treatments with natural abundances of copepods and ctenophores, *K. mikimotoi* increased in abundance, as ctenophores reduced the grazing pressure on *K. mikimotoi* by preying on copepods, promoting growth of this dinoflagellate.

The implication that copepods in the mesocosms were substantial predators on ciliates and grazers on the diatom *Skeletonema costatum* was supported by independent grazing experiments (Turner and Granéli 1992), which were performed concurrently with the Granéli and Turner (2002) mesocosm studies. In the grazing experiments, the copepod *Acartia clausi* grazed *S. costatum* and was predatory on ciliates, whereas *Centropages hamatus* only fed upon ciliates. These experimental results matched the mesocosm observations that there were practically no *S. costatum* ever, and no ciliates present after 3 days in the mesocosms with added zooplankton. Similarly, Olsson et al. (1992) and Nejstgaard et al. (1997) found that copepods preferred eating ciliates to most phytoplankters in mesocosm experiments. Other studies on the importance of ciliates as a food source for copepods have been reviewed by Turner and Roff (1993), Levinsen et al. (2000), Calbet and Saiz (2005) and references therein.

The high copepod predation on ciliates in the mesocosms of Granéli and Turner (2002) allowed total phytoplankton and small phytoflagellates to increase. Ciliates may even compete with copepods for consumption of prey larger than 4 μm (Rassoulzadegan et al. 1988). While the ciliates appear to have been extensively consumed by copepods, it appears that small phytoflagellates were not. This was confirmed by independent experiments of Turner and Granéli (1992). The high copepod grazing on diatoms and predation on ciliates gave the small phytoflagellates release from copepod grazing pressure.

The increase in ungrazed small phytoflagellates in the presence of abundant copepods was similar to mesocosm experiments from the Adriatic (Turner et al. 1999), where small phytoflagellate growth proceeded relentlessly until terminated by nutrient depletion (Granéli et al. 1999). This suggests that trophic transfer from phytoplankton communities dominated by flagellates through copepods to higher consumers may be inefficient, ultimately leading to a limited production of fish (Legendre 1990).

The original hypothesis of Granéli and Turner (2002) that ctenophore predation might contribute to blooms of all non-diatoms (i.e., all sizes of dinoflagellates and phytoflagellates) by removing copepods that are selective feeders on diatoms was not upheld. There was a trophic cascade effect of ctenophore predation that was transmitted down the food chain to the level of the phytoplankton, but it was not the effect that was hypothesized. Although copepods quickly grazed down *Skeletonema costatum* in enclosures and feeding experiments, this was a sideshow. The primary copepod trophic interaction was predation on ciliates, and ciliate grazing on small phytoflagellates was a major determinant of phytoplankton abundance and composition. Copepod grazing was ineffective in controlling small phytoflagellate abundance. Most larger dinoflagellates (except for *K. mikimotoi*) and small phytoflagellates (which include most nuisance algal bloom taxa in the Skagerrak) were unaffected by copepod grazing and ctenophore predation. Thus, either direct or indirect top-down influences on harmful algal blooms appear to be complicated.

Since *Chrysochromulina polylepis*, the flagellate which caused the 1988 toxic bloom in the Skagerrak, is only 10 μm in size, results of Granéli and Turner (2002) suggest that it would likely be grazed primarily by ciliates rather than copepods. Thus, if ctenophore predation on copepods was sufficient to reduce copepod predation pressure on ciliates, this would increase ciliate grazing pressure on *Chrysochromulina*.

27.4 Conclusions

The notion that top-down predation cascade effects on marine phytoplankton result in harmful algal blooms is theoretically attractive, and has often been suggested in the literature. However, this notion has prompted surprisingly little experimental investigation resulting in data from marine ecosystems. To date, only a few mesocosm studies demonstrate that trophic cascade effects of predation by zooplanktivorous fishes or gelatinous predators can promote increases in some HAB species. In one mesocosm study (Granéli et al. 1993a), the introduction of zooplanktivorous fish appeared to decrease copepod biomass and increase that of the dinoflagellate *Karenia mikimotoi* (= *Gyrodinium aureolum*). This was presumably because predation on the copepods by fish

reduced grazing on dinoflagellates by copepods. However, the large dinoflagellate *Ceratium furca* appeared unaffected even when copepods were present in high abundance. In another mesocosm study (Granéli and Turner 2002), there were surprises by the unanticipated importance of trophic interactions involving ciliates. Ctenophore predation on copepods appeared to promote increases in the dinoflagellate *K. mikimotoi*, concurrent with ciliate increases and decreases in small phytoflagellates such as *Chrysochromulina polylepis*. Thus, different trophic cascades appear to work differently for different HAB phytoplankton species. Other complications with marine trophic cascades are that poorly understood effects of water advection on plankton in open marine systems confuse inverse field correlations between different trophic levels, unlike the elegant trophic cascades that have been demonstrated in some closed lake ecosystems. Further, there is a growing realization that heterotrophic protists, rather than metazoans such as copepods, are the primary grazers of phytoplankton, including HAB species, in most marine systems (Calbet and Landry 2004; Landry and Calbet 2004). Thus, scenarios based on top-down predation, which assume that metazoans such as copepods are the primary grazers of phytoplankton are oversimplified, and may actually work in the reverse way as hypothesized. Demonstration of top-down predation effects on marine plankton by fish that extend down the food chain to the phytoplankton lack clarification because, with a few exceptions, the effects of fish predation on zooplankton populations thus far remain poorly quantified. In view of recent indications that fishing is substantially altering the structure of marine food webs (Frank et al. 2005), it seems that connections between human industrialized fishing, top-down predation and trophic cascades, and harmful algal blooms should be more intensely investigated.

References

- Båmstedt U (1998) Trophodynamics of *Pleurobrachia pileus* (Ctenophora, Cydippida) and ctenophore summer occurrence off the Norwegian north-west coast. *Sarsia* 83:169–18
- Barz K, Hirche H-J (2005) Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea). *Mar Biol* 147:465–476
- Bilio M, Niermann U (2004) Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. *Mar Ecol Prog Ser* 269:173–183
- Calbet A, Landry MR (2004) Phytoplankton growth, microzooplankton grazing and carbon cycling in marine systems. *Limnol Oceanogr* 49:51–57
- Calbet A, Saiz E (2005) The ciliate-copepod link in marine ecosystems. *Aquat Microb Ecol* 38:157–167
- Carpenter SR (ed) (1988) Complex interactions in lake communities. Springer, Berlin Heidelberg New York, 283 pp
- Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. *BioScience* 35:634–639

- Dagg MJ, Govoni JJ (1996) Is ichthyoplankton predation an important source of copepod mortality in subtropical coastal waters? *Mar Freshw Res* 47:137–144
- Dahl E, Lindahl O, Paasche E, Thronsdén J (1989) The *Chrysochromulina polylepis* bloom in Scandinavian waters during spring 1988. In: Cosper EM, Bricelj VM, Carpenter EJ (eds) Novel phytoplankton blooms: causes and impacts of recurrent brown tides and other unusual blooms. Springer, Berlin Heidelberg New York, pp 383–405
- Daskalov GM (2002) Overfishing drives a trophic cascade in the Black Sea. *Mar Ecol Prog Ser* 225:53–63
- Daskalov GM (2003) Long-term changes in fish abundance and environmental indices in the Black Sea. *Mar Ecol Prog Ser* 255:259–270
- Deason EE, Smayda TJ (1982) Ctenophore-zooplankton-phytoplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972–1977. *J Plankton Res* 4:203–217
- Frank KT (1986) Ecological significance of the ctenophore *Pleurobrachia pileus* off southwestern Nova Scotia. *Can J Fish Aquat Sci* 43:211–222
- Frank KT, Petrie B, Choi JS, Leggett WC (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308:1621–162
- French DP, Smayda TJ (1995) Temperature regulated responses of nitrogen limited *Heterosigma akashiwo*, with relevance to its blooms In: Lassus P, Arzul G, Le Denn EE, Gentien P, Marcaillou C (eds) Harmful marine algal blooms. Lavoisier Intercept, Paris, pp 585–590
- Granéli E (2004) Eutrophication and harmful algal blooms. In: Wassmann P, Olli K (eds) Drainage basin nutrient inputs and eutrophication: an integrated approach. ISBN 82-91086-36-2, pp 99–112 (Also: <http://www.ut.ee/~olli/eutr/>)
- Granéli E, Turner JT (2002) Top-down regulation in ctenophore-copepod-ciliate-diatom-phytoflagellate communities in coastal waters: a mesocosm study. *Mar Ecol Prog Ser* 239:57–68
- Granéli E, Carlsson P, Olsson P, Sundström B, Granéli W, Lindahl O (1989) From anoxia to fish poisoning: the last ten years of phytoplankton blooms in Swedish marine waters. In: Cosper EM, Bricelj VM, Carpenter EJ (eds) Novel phytoplankton blooms: causes and impacts of recurrent brown tides and other unusual blooms. Springer, Berlin Heidelberg New York, pp 407–427
- Granéli E, Olsson P, Carlsson P, Granéli W, Nylander C (1993a) Weak „top-down“ control of dinoflagellate growth in the coastal Skagerrak. *J Plankton Res* 15:213–237
- Granéli E, Granéli W, Rabbani MM, Daugbjerg N, Fransz G, Cuzin-Roudy J, Alder VA (1993b) The influence of copepod and krill grazing on the species composition of phytoplankton communities from the Scotia-Weddell Sea. *Polar Biol* 13:201–213
- Granéli E, Carlsson P, Turner JT, Tester PA, Béchemin C, Dawson, R, Funari E (1999) Effects of N:P:Si ratios and zooplankton grazing on phytoplankton communities in the northern Adriatic Sea. I. Nutrients, phytoplankton biomass, and polysaccharide production. *Aquat Microb Ecol* 18:37–54
- Greve W (1994) The 1989 German Bight invasion of *Muggiaea atlantica*. *ICES J Mar Sci* 51:355–358
- Greve W, Reiners F (1988) Plankton time – space dynamics in German Bight – a system approach. *Oecologia* 77:487–496
- Gucu AC (2002) Can overfishing be responsible for the successful establishment of *Mnemiopsis leidyi* in the Black Sea? *Est Coast Shelf Sci* 54:439–451
- Horsted SJ, Nielsen TG, Riemann B, Pock-Steen J, Bjørnsen PK (1988) Regulation of zooplankton by suspension-feeding bivalves and fish in estuarine enclosures. *Mar Ecol Prog Ser* 48:217–224
- Humborg C, Ittekkot V, Coclasu A, Von Bodungen B (1997) Effect of Danube River dam on Black Sea biogeochemistry and ecosystem structure. *Nature* 386:385–388
- Huntley ME, Hobson LA (1978) Medusa predation and plankton dynamics in a temperate fjord, British Columbia. *J Fish Res Bd Can* 35:257–261

- Kideys AE (1994) Recent dramatic changes in the Black Sea ecosystem: the reason for the sharp decline in Turkish anchovy fisheries. *J Mar Syst* 5:171–181
- Kideys AE (2002) Fall and rise of the Black Sea ecosystem. *Science* 297:1482–1484
- Kremer P (1979) Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Estuaries* 2:97–105
- Kuipers BR, Gaedke U, Enserink L, Witte H (1990) Effect of ctenophore predation on mesozooplankton during an outburst of *Pleurobrachia pileus*. *Neth J Sea Res* 26:111–124
- Lancelot C, Staneva J, Van Eeckhout D, Beckers J-M, Stanev E (2002) Modelling the Danube-influenced north-western continental shelf of the Black Sea. II: ecosystem response to changes in nutrient delivery by the Danube River after its damming in 1972. *Est Coast Shelf Sci* 54:473–499
- Landry MR, Calbet A (2004) Microzooplankton production in the oceans. *ICES J Mar Sci* 61:501–507
- Legendre L (1990) The significance of microalgal blooms for fisheries and for the export of particulate organic carbon in the oceans. *J Plankton Res* 12:681–699
- Levinsen H, Turner JT, Nielsen TG, Hansen BW (2000) On the trophic coupling between protists and copepods in Arctic marine ecosystems. *Mar Ecol Prog Ser* 204:65–77
- Lindahl O (1987) Plankton community dynamics in relation to water exchange in the Gullmar Fjord, Sweden. PhD Thesis, Univ Stockholm, 138 pp
- Lindahl O, Hernroth L (1983) Phyto-zooplankton community in coastal waters of western Sweden – an ecosystem off balance? *Mar Ecol Prog Ser* 10:119–126
- Maestrini SY, Granéli E (1991) Environmental conditions and ecophysiological mechanisms which led to the 1988 *Chrysochromulina polylepis* bloom: an hypothesis. *Oceanol Acta* 14:397–413
- Miller RJ, Daan R (1989) Planktonic predators and copepod abundance near the Dutch coast. *J Plankton Res* 11:263–282
- Möller H (1980) Population dynamics of *Aurelia aurita* medusae in Kiel Bight, Germany (FRG). *Mar Biol* 60:123–128
- Moncheva S, Doncheva V, Kamburska L (2001a) On the long-term response of harmful algal blooms to the evolution of eutrophication off the Bulgarian Black Sea coast: are the recent changes a sign of recovery of the ecosystem – the uncertainties? In: Hallegraeff GM, Blackburn SI, Bolch CJ, Lewis RJ (eds) *Harmful algal blooms 2000*. IOC-UNESCO, Paris, pp 177–181
- Moncheva S, Gotsis-Skretas O, Pagou K, Krastev A (2001b) Phytoplankton blooms in Black Sea and Mediterranean coastal ecosystems subjected to anthropogenic eutrophication: similarities and differences. *Est Coast Shelf Sci* 53:281–295
- Munk P, Nielsen TG (1994) Trophodynamics of the plankton community at Dogger Bank: predatory impact by larval fish. *J Plankton Res* 16:1225–1245
- Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283
- Nejstgaard JC, Gismervik I, Solberg PT (1997) Feeding and reproduction by *Calanus finmarchicus*, and microzooplankton grazing during mesocosm blooms of diatoms and the coccolithophore *Emiliania huxleyi*. *Mar Ecol Prog Ser* 147:197–217
- Oguz T, Ducklow HW, Purcell JE, Malanotte-Rizzoli P (2001) Modeling the response of top-down control exerted by gelatinous carnivores on the Black Sea pelagic food web. *J Geophys Res* 106:4543–4564
- Olsson P, Granéli E, Carlsson P, Abreu P (1992) Structuring of a post spring phytoplankton community by manipulation of trophic interactions. *J Exp Mar Biol Ecol* 158:249–266
- Pauly D, Christensen V, Froese R, Palomares ML (2000) Fishing down aquatic food webs. *Am Sci* 88:46–51

- Pepin P, Penney R (2000) Feeding by a larval fish community: impact on zooplankton. *Mar Ecol Prog Ser* 204:199–212
- Rassoulzadegan F, Laval-Peuto M, Sheldon RW (1988) Partitioning of food ration of marine ciliates between pico- and nanoplankton. *Hydrobiologia* 159:75–88
- Reeve MR, Walter MA (1978) Nutritional ecology of ctenophores – a review of recent research. *Adv Mar Biol* 15:249–287
- Riemann B, Nielsen TG, Horsted SJ, Bjørnsen PK, Pock-Steen J (1988) Regulation of phytoplankton biomass in estuarine enclosures. *Mar Ecol Prog Ser* 48:205–215
- Schneider G, Behrends G (1998) Top-down control in a neritic plankton system by *Aurelia aurita* medusae – a summary. *Ophelia* 48:71–82
- Tomas CR, Deason EE (1981) The influence of grazing by two *Acartia* species on *Olisthodiscus luteus* Carter. *PSZNI: Mar Ecol* 2:215–223
- Turner JT, Granéli E (1992) Zooplankton feeding ecology: grazing during enclosure studies of phytoplankton blooms from the west coast of Sweden. *J Exp Mar Biol Ecol* 157:19–31
- Turner JT, Roff JC (1993) Trophic levels and trophospecies in marine plankton: lessons from the microbial food web. *Mar Microb Food Webs* 7:225–248
- Turner JT, Tester PA (1989) Zooplankton feeding ecology: copepod grazing during an expatriate red tide. In: Coper EM, Bricelj VM, Carpenter EJ (eds) *Novel phytoplankton blooms: causes and impacts of recurrent brown tides and other unusual blooms*. Springer, Berlin Heidelberg New York, pp 359–374
- Turner JT, Bruno SF, Larson RJ, Staker RD, Sharma GM (1983) Seasonality of plankton assemblages in a temperate estuary. *PSZNI: Mar Ecol* 4:81–99
- Turner JT, Tester PA, Lincoln JA, Carlsson P, Granéli E (1999) Effects of N:P:Si ratios and zooplankton grazing on phytoplankton communities in the northern Adriatic Sea. III. Zooplankton populations and grazing. *Aquat Microb Ecol* 18:67–75
- Yunev OA, Moncheva W, Carstensen J (2005) Long-term variability of vertical chlorophyll-*a* and nitrate profiles in the open Black Sea: eutrophication and climate change. *Mar Ecol Prog Ser* 294:95–107
- Zaitsev YP (1992) Recent changes in the trophic structure of the Black Sea. *Fish Oceanogr* 1:180–189