

Top-down control in the pelagic Baltic ecosystem

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Abstract

This paper reviews evidence for and possible consequences of top-down control in the pelagic Baltic ecosystem. Two top-down control processes, cod predation on clupeids and clupeid predation on cod eggs, are considered important and tend to produce either a cod-dominated or a clupeid-dominated system. Several counteracting forces could prevent this from happening, including the side-effects of eutrophication, variable hydrographic conditions, cannibalism within species, the fishery, and separate spawning and nursing areas for herring. Top-down control of zooplankton is likely to be intense but variable with season. Zooplanktivores (primarily herring, sprat and mysids) are selective and consume a large proportion of the estimated zooplankton production (50-93%). In addition, zooplanktivory is at a peak in late summer and early autumn when zooplankton populations decline. Therefore, a negative correlation is expected between clupeid and zooplankton biomass although this was not found in available data sets (1974-1988). The lack of correlation could be due to relatively small changes (by a factor 2) in planktivore biomass over this time period and compensatory increases in other zooplanktivores (e.g. mysids and juvenile clupeids). Less is known about the top-down control of primary production in the Baltic Sea. Available information suggest that grazing rates on algae is maintained as metazooplankton decrease by compensatory responses of protozooplankton. A better understanding of top-down control processes is necessary for predicting the future development of the Baltic ecosystem.

Keywords: clupeids, mysids, cod, zooplankton, phytoplankton.

Introduction

This paper considers the possibility and consequences of top-down control in the Baltic ecosystem. Experimental studies in lakes have shown that piscivores can control planktivorous fish abundance and species composition, that planktivorous fish can control zooplankton abundance and species composition, and that zooplankton can control algal abundance and species composition. Top-down control can therefore cascade down the trophic levels from fish to phytoplankton (Carpenter *et al.* 1985, Mills *et al.* 1987). This paper primarily discusses the direct effects of predation, while acknowledging that indirect effects of predators on prey distributions and nutrient recycling rates may be as important in aquatic systems (Turner & Mittelbach 1990, Brabrand *et al.* 1990, Kraft 1992). Of course, trophic levels are also controlled from the bottom-up; nutrient levels do set a limit for the standing biomass in aquatic systems. Understanding how top-down and bottom-up control

processes interact is a current focus of both empirical and theoretical research in aquatic ecology (Food chain length and productivity – Oksanen *et al.* 1981, Fretwell 1987, Cascading trophic interactions – Carpenter *et al.* 1985, Carpenter & Kitchell 1993, 'top-down/bottom-up' – McQueen *et al.* 1986, 1992 among others).

Not all experimental manipulations of higher trophic levels show strong top-down control (see Gulati *et al.* 1990, McQueen 1990). Natural food webs are complex entities where compensatory responses are common; therefore top-down control can have strong effects on community structure but weak effects on aggregated ecosystem properties, such as biomass and production (Carpenter & Kitchell 1993). Also, different trophic levels operate at different spatial and temporal scales (Steele 1991). For example, a strong year class of a dominant planktivore may affect zooplankton community structure for a decade but it has no effect on peak zooplankton biomass in the spring because the predator cannot respond fast enough to parthenogenetically reproducing daphnids (Rudstam *et al.* 1993). Further, in some cases, the species present simply do not interact, such as small zooplankton and some blue-green algae.

Most of the above references to top-down control in open water systems are from lakes. This is unlikely to be because top-down control is less important in marine systems like the Baltic Sea than in lakes. Indeed, fish yield per unit of primary production is five to ten times higher in coastal areas including the Baltic Sea, than in lakes (Nixon 1982), suggesting a strong coupling between fish and lower trophic levels. An increasing interest in top-down control in marine systems is demonstrated by an increasing number of papers that consider top-down control of lower trophic levels (zooplankton and algae) (Landry 1978, Lonsdale 1981, Deason & Smayda 1982, Koslow 1983, Fulton 1984, Davis 1984, Ohman 1986, Verity 1987, Bollens 1988, Kimmerer & McKinnon 1989, Suthers & Frank 1990, Kuipers *et al.* 1990, Purcell 1992, Turner & Granéli 1992) and in the Baltic Sea (Möller 1979, Vuorinen *et al.* 1983, Arndt 1989, Hansson *et al.* 1990a, Rudstam *et al.* 1992, Johansson 1992, Kivi *et al.* 1993). In fisheries, there is a long tradition of implicitly accepting top-down control; human exploitation is assumed to be able to control the fate of fish stocks. Further, dome-shaped stock recruitment curves have been attributed to cannibalism by older fish. In recent years, explicit modelling of predatory interactions within fish communities has developed; in several cases top-down control within the fish community have been taken into account in fisheries management (Sissenwine & Daan 1991).

Although predatory interactions are likely to be important in marine systems, the boundary conditions set by the physical environment may affect both the appearance and importance of top-down control in at least two ways. Firstly, oceanographic conditions affect the overall structure of the biological system by being favourable to some species and excluding others. Only a limited number of species are abundant at the intermediate salinities present in the Baltic Sea and the salinity gradient from the southern to the northern Baltic strongly affects species composition (Voipio 1981). Secondly, oceanographic conditions may affect short and intermediate-term variability of particular populations and hence their importance as predators in the system. Oceanographic conditions are at least partly responsible

for the varying year class strength of several important Baltic fish species; the strongest and weakest year classes of cod and sprat differ by an order of magnitude. Even so, the evidence for top-down control should be more obvious in the Baltic Sea than in many other marine systems because of the relatively simple structure of the food web.

This paper reviews the evidence for top-down control in the Baltic Sea and concentrates on the pelagic system and the role of fish and the fishery. The paper briefly describes the Baltic systems and food web from a top-down perspective, then 1) presents estimates of food consumption by Baltic fish populations, 2) discusses top-down control within the fish community and 3) discusses the planktivore-zooplankton link and the possibilities of top-down control cascading from fish to the phytoplankton. The assessment concludes with discussion on the possibility of using top-down control to manipulate the Baltic ecosystem.

The Baltic food web

The Baltic is a large, semi-enclosed brackish sea. Surface salinity levels are over 15 psu in the southern Baltic proper and decrease to less than 2 psu in the northern Bothnian Bay. Three main areas are discussed: 1) the Baltic proper including the Gulf of Riga and the Gulf of Finland (257 441 km²), 2) the Bothnian Sea (79 257 km²) and 3) the Bothnian Bay (36 260 km²). These areas represent a gradient in salinity and the species composition is influenced by more marine species in the Baltic proper and more freshwater species in the Bothnian Bay (Voipio 1981). They also differ in average annual temperatures and in rates of primary production, the Baltic proper being the warmest and most productive area and the Bothnian Bay the coldest and least productive (Elmgren 1984).

The top piscivores are humans and (at least historically) seals throughout the Baltic Sea. Cod (*Gadus morhua*) and salmon (*Salmo salar*) are the main piscivorous fish. In the Baltic proper the biomass of cod is one to two orders of magnitude larger than that of salmon, but the relative importance of salmon increases in the Bothnian Sea and the Bothnian Bay (Thurow 1993). In the Baltic proper the major open water planktivores are herring (*Clupea harengus*) and sprat (*Sprattus sprattus*); in the Bothnian Sea herring dominates, but the planktivorous fish community also includes sprat, smelt (*Osmerus eperlanus*) and sticklebacks. In the Bothnian Bay, sprat is rare and vendace (*Coregonus albula*) is relatively abundant. A similar gradient in mysid species occur with *Mysis relicta* (possibly two species; Väinölä 1992) dominating in the Bothnian Bay, both *Mysis relicta* and *Mysis mixta* common in the Bothnian Sea and *Mysis mixta* dominating in the Baltic proper (Salemaa *et al.* 1990). Baltic Sea zooplankton are dominated by calanoid copepods of primarily estuarine origin (*Acartia*, *Eurytemora*, *Pseudocalanus*, *Temora*), but cladocerans and rotifers can be very abundant. Large freshwater daphnids and large marine copepods are rare (Ackefors 1969, Wulff *et al.* 1986, Kankaala 1987, Johansson 1992).

In aquatic systems, trophic levels are strongly correlated with individual size. However, a piscivore like cod grows over six orders of magnitude in weight from larva to adult (a cod larva weighs less than 0.01 g and an adult cod may exceed 10 kg).

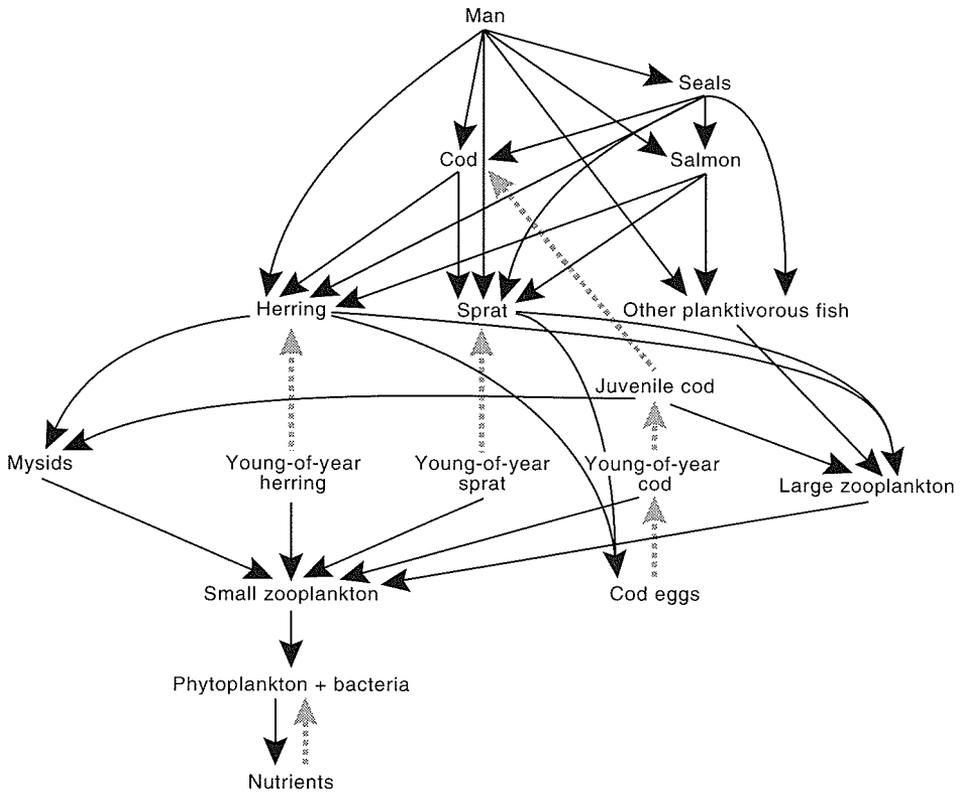


Figure 1. Outline of major potential top-down control pathways in the Baltic pelagic ecosystem (heavy black arrows) and feed back loops (dashed grey arrows). In the Bothnian Sea interactions through the cod egg component is absent and the role of sprat and juvenile cod is considerably reduced compared to the Baltic proper. In the Bothnian Bay, all interactions through sprat and cod are insignificant.

Therefore cod is a small planktivore at the larval stage, a large planktivore and a benthivore at the juvenile stage, and a benthivore and a piscivore as adult (ontogenetic niche shifts, Werner & Gilliam 1984). Figure 1 shows six trophic levels: 1) top piscivores (humans, seals), 2) large piscivores (cod, salmon), 3) large planktivores which are also small piscivores (adult herring, adult sprat), 4) small planktivores (fish larvae, larger *Mysis*, other predatory zooplankton), 5) zooplankton or grazers (copepods, cladocerans, juvenile *Mysis*), and 6) phytoplankton. Many of these groups feed on more than one trophic level. For example, large planktivores like adult herring and sprat feed on zooplankton and on small planktivores such as fish larvae and mysid shrimps. This type of multi-level omnivory is common in aquatic systems and results in a large number of interactions involving both predation and competition (intra-guild predation, Polis & Holt 1992). Ontogenetic niche shifts and intra-guild predation adds complexity to the Baltic food web and to aquatic food webs in general. For the sake of clarity, not all of these possible top-down interactions are included in Figure 1. For example the complexity of the zooplankton

and phytoplankton trophic levels are over-simplified; in reality zooplankton includes both omnivores and grazers and phytoplankton includes producers and mixotrophic flagellates. The microheterotrophic loop is also excluded as are additional components of the pelagic food web. The coelenterate *Aurelia aurita* can be a common and important predator on zooplankton and possibly on fish larvae in the southern Baltic (Möller 1979) but is not consumed by other trophic levels. Also the blue mussel (*Mytilus edulis*), although a benthic animal, may be an important grazer on pelagic phytoplankton but is not utilized much by higher trophic levels (Kautsky 1981).

Total food consumption by Baltic fish and its seasonal variation

The ICES database on herring, sprat and cod biomass (Figure 2) can be used to estimate predatory demand of these species in the Baltic. Several attempts have been made to use this database to estimate consumption by various fish species in the Baltic Sea (Załączowski *et al.* 1976, Aneer 1980, Elmgren 1984, Thurow 1984, Lankov 1988, Sparholt 1991, Anon. 1992a, Arrhenius & Hansson 1993). The dif-

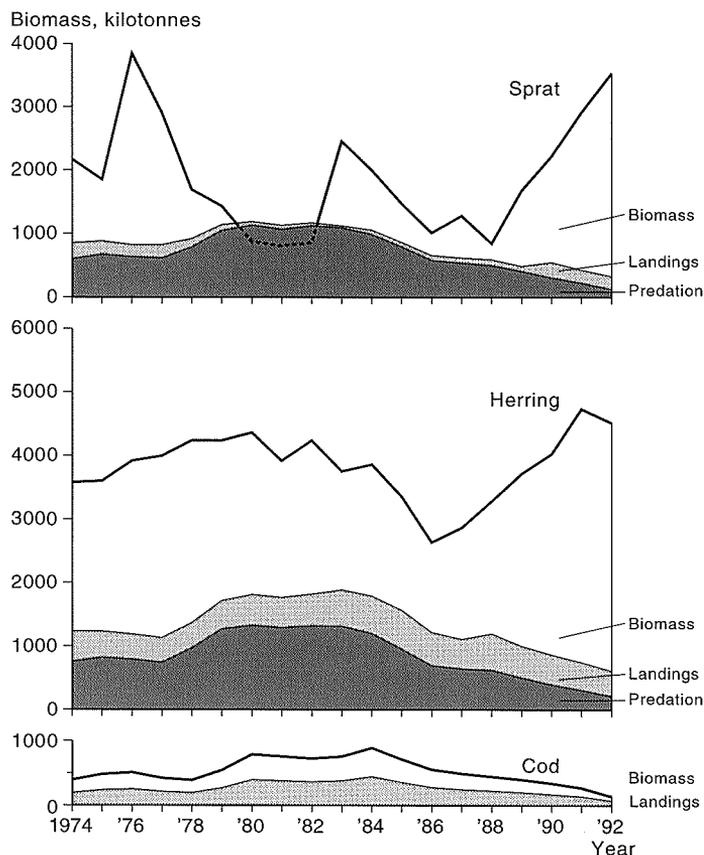


Figure 2. Development of the biomass of cod, herring and sprat in the Baltic Sea from 1974 to 1992 (from Anon. 1993a,b). The known landings of these species (Anon. 1993a,b) and our estimate of cod predation on herring and sprat (see text) are included. Note that predation and landings of sprat exceeded the year-end biomass during some years in the 1980s.

ferences between consumption estimates are substantial. Arrhenius & Hansson (1993), using a bioenergetics model for herring (Rudstam 1988), obtained estimates of zooplankton consumption by the clupeids that were a factor 4 higher than similar calculations by Elmgren (1984). Approximately half of this difference is due to the use of different years for the biomass estimates whereas the other half is due to differences in methods and assumptions. Consumption estimates require information on daily rations, fish diet, and early-age mortality rates. Although mortality rates of older age groups can be estimated from the ICES database, mortality rates of the 0-age group that are not vulnerable to the fishing gear are not known. Early-age mortality rates are needed to reconstruct the abundance of the younger fish age groups.

Diets determine the potential pathways of top-down control in the Baltic Sea. There are extensive stomach content data for cod, sprat and herring. Zooplankton, mysids, macro-crustaceans, herring, sprat and other macro-invertebrates are the most important food items for the Baltic fish community (Table 1). The proportions of mysids and zooplankton in herring diets vary among studies. Several authors report the proportion of mysids at over 20% (Załaachowski *et al.* 1976, Aneer 1980, Elmgren 1984). Ostrowski & Mackiewicz (1992) and Anon. (1992a) have observed an increasing share of mysids in the food of herring and cod. Arrhenius & Hansson

Table 1. Proportion of major food items in the diet of herring, sprat and cod in the Baltic Sea. Consumption by age-0 fish is included for herring and sprat but not for cod. Diets are based on Załaachowski *et al.* (1976), Aneer (1980, herring only), Arrhenius & Hansson (1993, herring and sprat), and ICES cod stomach database (Anon. 1992a, cod only). All values are in per cent. A small proportion of unidentified clupeids (7% of clupeids) in cod diets were assigned to sprat and herring in proportion to those identified.

Species and food item	Załaachowski <i>et al.</i> (1976)	Aneer (1980), herring Anon. (1992a), cod	Arrhenius & Hansson (1993)
Herring			
Zooplankton	68.5	46.7	88.9
Mysids	27.8	40.6	8.1
Macro crustaceans	0.6	8.5	3.0
<i>Antinoella sarsi</i>	2.6	1.1	
Fish	0.4	0.5	
Other food items	<0.1	2.6	
Sprat			
Zooplankton	99.9		100
Macro crustaceans	0.1		0
Cod			
Mysids	2.6	(included in other invertebrates)	
<i>Saduria entomon</i>	17.2	21.4	
Other invertebrates	15.6	15.9	
Sprat	23.9	26.5	
Herring	28.4	25.3	
Cod	4.3	3.8	
Other fish	7.9	7.2	

(1993) assumed that the proportion was less (about 5%) based on their review and interpretation of published data. As mysids are patchily distributed (for example there seem to be very few mysids over areas with anoxic bottoms, Salemaa *et al.* 1990), large differences are expected in the proportion of mysids in the diet between different areas.

Estimates of annual consumption rates (1974-1991) on mysids and zooplankton by Baltic cod, herring and sprat (Figure 3) are based on the diets of Załachowski *et al.* (1976) and assumption of daily consumption as follows. Older clupeids have a daily consumption rate of 2% (derived from observations of maintenance rations of larger herring kept in large aquaria, Aneer, unpubl. data). This daily consumption

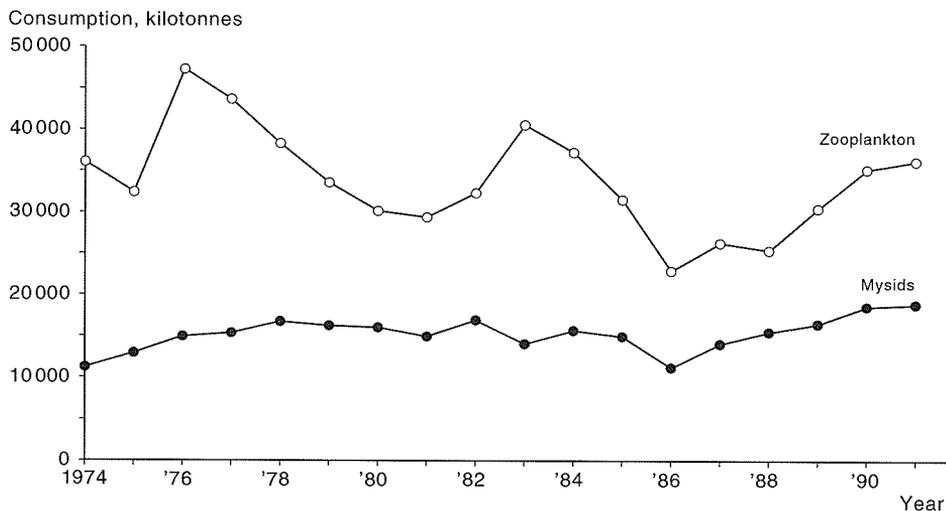


Figure 3. Estimated annual consumption of mysids and zooplankton by the Baltic fish population (herring, sprat and cod) from 1974 through 1991. These estimates have been obtained by using direct relationships between consumption estimates calculated for the 1991 stocks of herring, sprat and cod (see text) and the biomass for the 1974-1991 period as given in Anon. (1992b,c).

rate is close to the numbers of Załachowski *et al.* (1976) based on observations of stomach content and a linear digestion rate model. This is considered to represent a lower limit for clupeid consumption in the Baltic and these estimates are about half those given by Arrhenius & Hansson (1993). For cod, the daily ration estimates used are from Załachowski *et al.* (1976, based on stomach content and a linear digestion rate model), which are markedly higher than those used by the multi-species working group (Anon. 1992a). The values used by the multi-species working group resulted in unreasonably high conversion efficiencies (70% for age-1 cod). The estimates here include consumption from age-0 fish, assumed to be 33% of the total adult consumption for all three species.

With these assumptions, average annual consumption for the years 1974-1991 is 34 000 kilotonnes wet weight of zooplankton (range 23 000-47 000 kilotonnes) and 15 000 kilotonnes of mysids (range 11 000-19 000 kilotonnes). For the Baltic Sea as a whole, fish species other than cod, herring and sprat may represent about

20% of the total biomass (Elmgren 1984, Thurow 1993). Assuming an approximately linear relationship between biomass and consumption the data in Figure 3 should be increased accordingly to get an overall Baltic consumption estimate.

Predation rates by cod on herring and sprat can also be estimated with these assumptions. Predation rates are compared with landings from the Baltic fishery and the biomass of herring and sprat in Figure 2 (Anon. 1993a,b). Clearly, predation by cod is considerably higher for most of this time period than landings by fishermen for both sprat and herring.

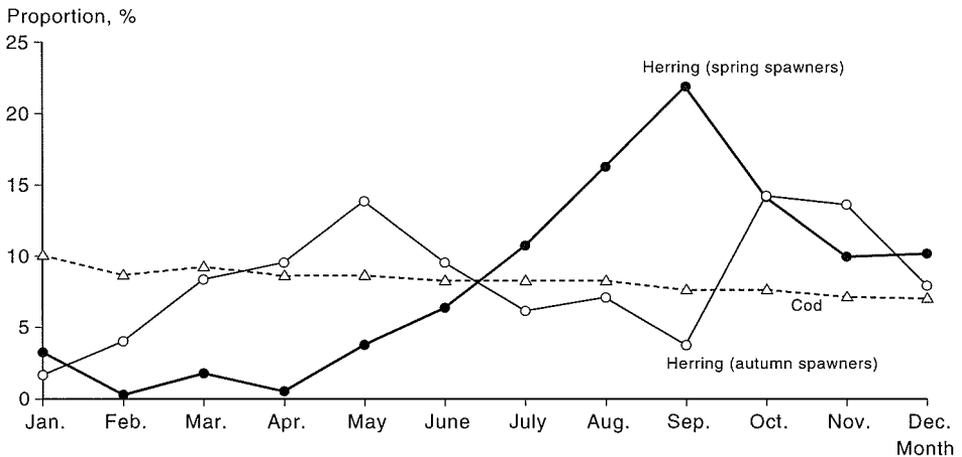


Figure 4. Proportion of total annual consumption occurring in each month for cod, autumn-spawning herring and spring spawning herring in the Baltic Sea. The seasonal pattern is based on data in Popiel (1951), Załachowski *et al.* (1976) and Aneer (1980, unpubl.) for herring and on data in Anon. (1992a,b) for cod.

The seasonal distribution of predation pressure will also influence top-down control. Smoothed data for spring-spawning herring suggest peak consumption in late summer and autumn (Figure 4, see also Arrhenius & Hansson, 1993). The pattern is probably similar for sprat (Załachowski *et al.*, 1976, Arrhenius & Hansson 1993). This pattern arises as a result of changing temperature, low food consumption during spawning, growth and mortality of herring, and recruitment of the 0-group. Hence, it can vary from year to year, particularly as a result of variable recruitment. In contrast, the seasonal consumption pattern of the presently rare autumn-spawning herring has two peaks, one in May and the other in October–November (Figure 4). Autumn-spawning herring may have been dominant in the first half of this century (Hessle 1925, Ehnholm 1951) and the seasonal pattern of zooplankton consumption would then have been more evenly distributed over the season with possible implications for the seasonal dynamics of zooplankton (see below). The consumption of cod, excluding the 0-group, appears to be more evenly distributed throughout the year (Anon. 1992a,b, Figure 4). This is similar to expectations based on a cod bioenergetics model (Hildén 1991). Piscivory, which is unaffected by recruitment of the 0-group, is expected to have an even seasonal distribution.

Top-down control within the fish community and the gadoid/clupeid interaction

The Baltic proper

On an aggregate level, the cod is the most important piscivore in the Baltic fish community. The peak biomass of cod in the early 1980s was two orders of magnitude greater than that of salmon. Even in its present depressed state the spawning biomass of cod is about 30 times larger than the salmon biomass. Other stocks of predatory fish are also small in comparison.

Cod recruitment peaked in 1976 although there were strong year classes of cod (resulting in more than 500 million two-year-old fish) in 1977, 1979 and 1980. The reasons for these fluctuations have received considerable attention (St. John & MacKenzie, in press, Bagge *et al.* 1994). Hydrographical conditions combined with the effects of human-induced eutrophication are important as cod eggs require relatively high salinities for successful fertilization and development (over 11 psu, Westin & Nissling 1991, Nissling & Westin 1991). These salinities are only available in the deeper basins of the Baltic proper (Bornholm, Gdańsk and Gotland Basins) although these waters have low oxygen content unless oxygenated by inflow of more saline waters through the Danish Sounds. Cannibalism also appears to be significant in the cod stock (Sparholt 1994, Köster & Schnack 1994).

The food consumption data show that herring and sprat are important prey items for piscivorous cod (Table 1). It is, however, difficult to obtain reliable time series of the consumption because the data on stomach contents are incomplete. The present assumptions on cod consumption of herring and sprat (Figure 2) should be considered a first approximation. As young cod are mostly benthivorous, the spawning stock biomass of cod rather than the total biomass can be used as an approximation for the piscivore biomass. In the early 1970s, the ratio of clupeid biomass to the spawning stock of cod was approximately 16:1. During the period of maximal cod biomass between 1980 and 1984, the ratio was as low as 4:1 and in the early 1990s the ratio had increased to above 90:1 (Figure 5). The growth of cod has responded

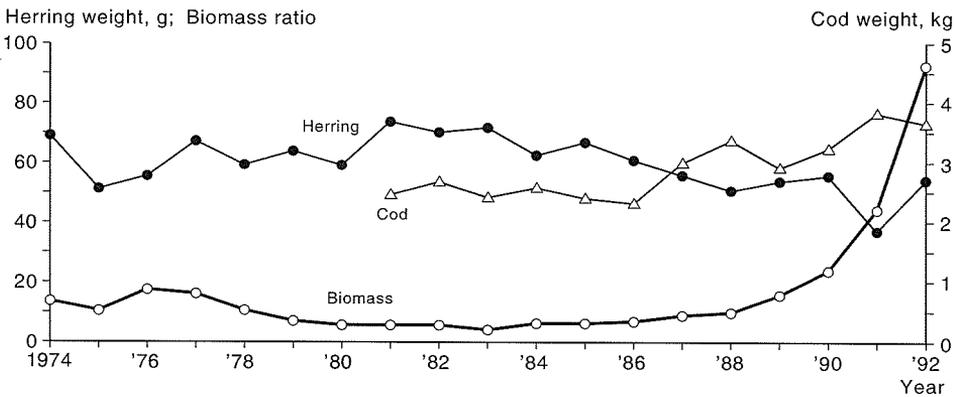


Figure 5. Changes in the ratio between clupeid biomass and cod spawning stock biomass (Biomass ratio), weight at age 5 for herring and weight at age 7 for cod between 1974 and 1992 (Source: Anon. 1993a,b).

to this change in prey availability per predator. Growth of age-7 cod is highly correlated with the clupeid to cod ratio (Spearman's rank correlation = 0.8, $p < 0.001$).

In the Baltic proper, the cod stock and consequently the amount of fish consumed by cod has varied with a factor of 4 since the 1970s and is currently at its lowest level since 1974. Since cod is the dominant predator on clupeids, the clupeids should respond to these changes in the cod stock if cod predation is an important top-down control mechanism in the Baltic. There are several indications that the clupeids have responded. Herring biomass is currently at its highest level since 1974 (Figure 2) and the growth rates of older herring have decreased, suggesting food limitation. A general decrease in the growth rate and fat content of herring was observed in the late 1980s in the southern Baltic (Karnicki 1993) but similar changes have not been observed in sprat or in age-0 herring. Sprat biomass has also increased and is now reaching the levels present in the late 1970s (Figure 2). Multi-species VPA analysis indicates that cod contributed to the decline of the sprat stock in the early 1980s (Sparholt 1994). The annual change in biomass of both sprat and herring are negatively correlated with cod spawning stock biomass (Figure 6), although these relationships are not statistically significant unless two outlier years are removed for each species. Biomass changes also depend on recruitment success, which is usually variable in clupeids partly as a result of oceanographic conditions (Sissenwine 1984). Strong year classes of sprat have occurred only three times since 1974 (Anon. 1992c); this adds to the variability in Figure 6. Herring recruitment is less variable, possibly because herring spawn in the coastal area and use near-shore areas as nursing grounds (Urho & Hildén 1990, Rudstam *et al.* 1992). Data on the

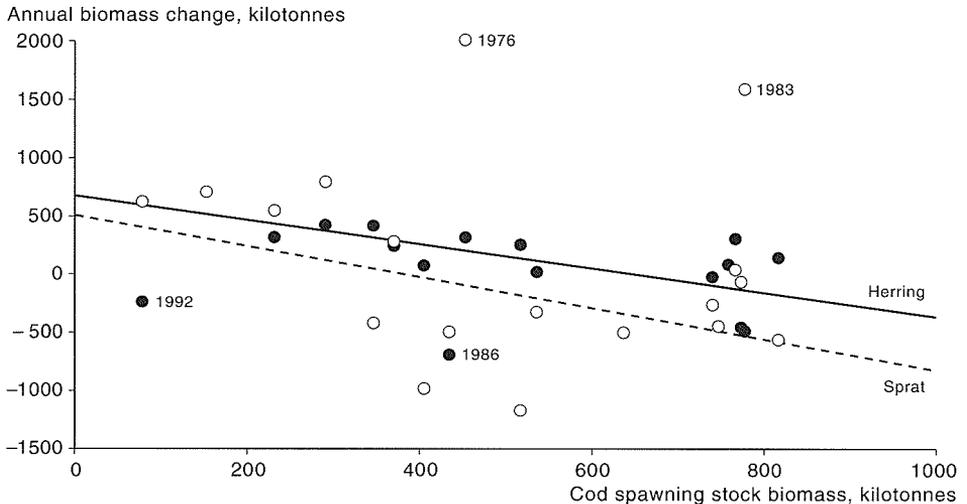


Figure 6. The annual biomass change (ΔB) of sprat (open circles) and herring (solid circles) as a function of cod spawning stock biomass (CSSB, Anon. 1993a,b). The sprat regression (dashed line, $\Delta B = -1.34 \cdot \text{CSSB} + 522$, $r = 0.540$, $p = 0.03$, $n = 16$) does not include the years 1976 and 1983 when sprat biomass increased drastically due to strong recruitment events. The herring regression (solid line, $\Delta B = -1.05 \cdot \text{CSSB} + 681$, $r = 0.674$, $p = 0.004$, $n = 16$) does not include the years 1986 and 1992. Neither relationship is significant if all data points are included ($r = 0.37$ for herring, $r = 0.23$ for sprat).

effects of cod on other fish stocks have not been quantified, but fishermen's reports suggest that stocks of cottids were severely reduced when cod abundance was high, especially in the northern Baltic proper where the density of cod increased up to ten fold relative to the early 1970s (Suuronen 1981, Savolainen & Vepsäläinen 1991).

But top-down control within the fish community can also involve clupeids as predators, not only as prey. Because of the ontogenetic shifts in trophic levels within the fish community, it is conceivable that planktivorous fish can control cod recruitment through predation on early life history stages. Herring feed to some extent on fish larvae (Popiel 1951, Anon. 1992a) while sprat does not; more importantly, predation on cod eggs, especially by sprat, is considerable (Anon. 1992a). Cod eggs are concentrated in a narrow layer where herring and sprat feed on them during the day (Müller 1988, Wieland 1988, Köster & Schnack 1994), at rates that have been estimated to between 20 and 100% of the cod eggs per day in March-April. An ICES working group (Anon. 1992a) found a strong negative correlation between the commercial catch of sprat and cod for the period 1960-1991. As there was a time lag between the decrease in the sprat stock and the increase in the cod stock at the end of the 1970s, the working group judged that sprat predation on cod eggs could be a cause for this negative relationship.

We suggest that there are two competing top-down control processes in the Baltic Sea, one leading to gadoid (cod) dominance and the other leading to clupeid dominance (Figure 7). An increase of the cod stock depresses the stocks of clupeids,

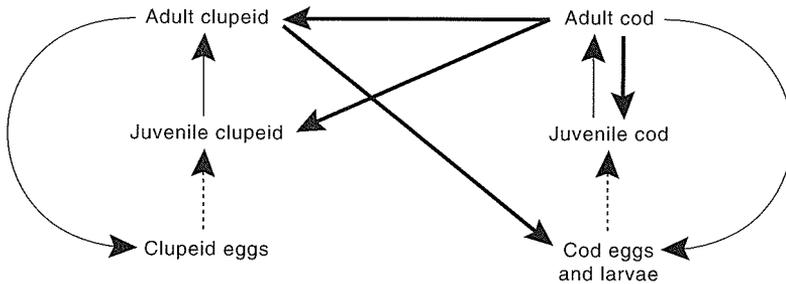


Figure 7. Conceptual model structure of the predatory interactions in the cod-clupeid system. Top-down control through predation is marked by thick arrows. Thin arrows represent the life-cycle progression of the two species; solid thin lines are well established relationships and dashed thin lines are relationships strongly affected by hydrographical conditions.

further increasing the probability of strong year classes of cod. Alternatively, an increase of the clupeid stocks depresses cod recruitment and hence reduces predation on clupeids leading to a clupeid-dominated system. At some high cod or herring abundances, cannibalism and other compensatory mechanisms will control the stocks.

Both of these top-down control processes are plausible and have been observed in the Baltic Sea (Sparholt 1994, Köster & Schnack 1994) although it is not yet clear to what extent they determine the dynamics of the fish community in the Baltic proper. The first strong year class of the most recent cod outburst developed in

1976, when clupeid biomass was at a high level. The other two strong year classes, however, occurred when the sprat stock was depressed. Therefore the reduction of the clupeid biomass may have increased the probability of strong cod year classes. Renewal of the bottom water creates necessary, but insufficient, conditions for strong cod year classes for several years. When other factors (such as weather conditions, food availability and, as argued above, predation rates on early life history stages) are favourable, strong year classes can develop.

Although cod predation likely reduces total clupeid biomass and therefore predation by clupeids, it is less clear whether clupeid recruitment is affected. This is because there is little evidence of any dependency of clupeid recruitment on spawning stock size (but this may partly be due to the limited range of clupeid spawning stock biomass observed in the Baltic since 1974).

Humans are the only major non-fish predators on Baltic fish. Seal populations in the Baltic were much larger during the first half of this century and must have been important fish predators at that time. But active hunting and toxic pollutants have reduced seal populations to less than 2% of their earlier numbers (Elmgren 1989). Although the seal populations are increasing in some areas (Helander & Bignert 1992), they are far from abundant enough to exert any significant predation pressure on fish populations.

The commercial fishery may amplify or attenuate the fluctuations in the Baltic fish community by acting as a highly selective piscivore. At present, fishing mortality rates of cod are high whereas those of clupeids are low for most stocks (Anon. 1993a,b, Figure 2). By reducing the cod stock, the fishery has further depressed the predation rates on clupeids and has indirectly increased the clupeid stocks. The eutrophication of the Baltic tends to affect cod more than clupeids by reducing the area suitable for cod reproduction (Anon. 1992b), although herring recruitment may also be affected through increased egg mortality on the spawning grounds (Aneer 1985, 1987, Oulasvirta *et al.* 1985). The Baltic proper has become a planktivore-dominated system and the size spectrum of the entire system has shifted towards smaller individuals and a relative lack of large piscivorous predators. At present the most important predatory processes within the fish community may be those affecting the early life history stages.

The Bothnian Sea and the Bothnian Bay

The fish communities in the Bothnian Sea and the Bothnian Bay are dominated by planktivores. The ratio of planktivorous fish to piscivorous fish is approximately 30-40 to 1. In these areas, other predatory fish than cod are also important. There are no exact stock size estimates for these basins separately, but catch data can be used as an indication of abundance because all the main predatory fish species are important for both commercial and recreational fisheries.

In the Gulf of Bothnia (the Bothnian Sea and the Bothnian Bay), the main part of the planktivorous biomass is herring (60-150 kilotonnes). In the northernmost Bothnian Bay, there are at the most 3 kilotonnes of vendace (Hildén *et al.* 1984). In addition, there are abundant populations of smelt and sticklebacks. Rough estimates based on data from the Finnish side of the Quark region, between the

Bothnian Sea and the Bothnian Bay, suggest that the total smelt stock in the Bothnian Bay may be around 10 kilotonnes (R. Hudd, Finnish Game and Fisheries Research Institute, pers. comm.). An acoustic survey of sticklebacks in 1991 estimated the total biomass to be approximately 25 kilotonnes in the Gulf of Bothnia (V. Mamylov *et al.*, pers. comm.). These results indicate that sticklebacks are an important species in the fish community in the Gulf of Bothnia and the total biomass of smelt, vendace and sticklebacks can thus reach 40 kilotonnes. But herring is more abundant with 60-150 kilotonnes, reaffirming the dominance of herring in the Baltic Sea in general.

In the Bothnian Bay, the cod outburst of the 1980s did not significantly change the ratio of planktivorous fish to piscivorous fish and although cod was commonly observed in the southern parts of the bay, it never became an important predator. The peak catches were less than 100 tonnes, which is less than the estimated catches of salmon, sea trout, pike and turbot for which the total catch has exceeded 500 tonnes in recent years.

In the Bothnian Sea, the change in cod abundance was significant. Data on catch per unit of effort (Suuronen 1981, Savolainen & Vepsäläinen 1991) suggest that the amount of cod increased up to ten fold in Finnish coastal waters during the cod outburst in the early 1980s. But the biomass of piscivorous fish did not increase ten fold because a large fraction of the cod migrated southward upon reaching maturity (and becoming more piscivorous). Two years after tagging at the Eland Island, most fish were recaptured in the central part of the Baltic proper (Aro 1989). In the Bothnian Sea, catches of cod increased to more than 3000 tonnes per year in the mid-1980s, but present landings are approximately 1000 tonnes (Anon. 1992c). The catches of other predatory fish (salmon, sea trout, pike, turbot, pike-perch, large perch) since the 1980s have been above 1000 tonnes. These catch data for the Bothnian Sea indicate at least a doubling of the total biomass of piscivorous fish during the cod outburst in the early 1980s.

However, the ratio of planktivorous fish to piscivorous fish in the Bothnian Sea remained well above levels observed in the Baltic proper even during the recent cod outburst. Therefore, it is unlikely that piscivory strongly affects planktivores in the Bothnian Sea. But observations by fishermen suggest that the stocks of sculpins diminished during the cod outburst (Suuronen 1984). Other non-commercial benthic species such as eel-pout and gobies may also have been affected, but there are no data to support such trends.

The Gulf of Bothnia clearly differs from the Baltic proper with respect to the structure of the fish community. The relative importance of adult piscivores is much less than in the Baltic proper suggesting that predation on early life history stages by clupeids and other small fishes like sticklebacks is the most important top-down process among the pelagic fish in this area. Coastal fish communities may, however, differ from the basin-wide communities (Hildén *et al.* 1988) and other predatory processes may influence the dynamics in these areas.

The fish community of the Gulf of Bothnia also differs quantitatively from the Baltic proper. The maximal biomass of clupeid fish per unit area is less than half of the minimal densities of clupeids per unit area in the Baltic proper (about 40

$\text{kg} \cdot \text{ha}^{-1}$ cf. $110 \text{ kg} \cdot \text{ha}^{-1}$, Anon. 1992b, c). Consequently, the conditions for piscivorous fish are rather different in the Gulf of Bothnia compared to the Baltic proper. The difference in prey availability probably explains why the migrations of salmon from the rivers in the northern Bothnian Bay extend to the Baltic proper.

Top-down control of lower trophic levels

Top-down control of zooplankton abundance and species composition is a common phenomenon in lakes, especially when the dominant planktivore is a clupeid (Hrbacek *et al.* 1961, Brooks & Dodson 1965). Fish will selectively remove larger zooplankton, which are generally the most efficient grazers on phytoplankton. As a result, grazing rates on algae decrease and the algal biomass increases. The converse, a decrease in fish biomass leading to an increased abundance of large grazers (*Daphnia*) and to lower algal abundance, is the basis for biomanipulation of lakes to improve water clarity (Shapiro & Wright 1984, Carpenter *et al.* 1985, Gulati *et al.* 1990). What are the evidence for such cascading trophic interactions in the Baltic Sea?

The interactions between zooplankton and zooplanktivores have been examined in a coastal area of the northern Baltic proper in the vicinity of the Askö Laboratory in a series of articles by Hansson, Rudstam, Johansson and co-workers. The studies combined abundance estimates of fish from hydroacoustics and vertical gill nets, abundance estimates of mysids from net samples, and bioenergetics models to calculate predation rates on zooplankton along a nutrient gradient. Predation rates were then compared to zooplankton abundance and production along the same gradient. The main zooplanktivores in this area were herring, sprat and *Mysis mixta*. Young-of-year herring were particularly important in late summer and autumn and predation by mysids was higher than predation by fish at one station. Growth of mysids was food limited. Several observations suggest top-down control of zooplankton in this area: 1) mysids and clupeids selected certain zooplankton species over others (*Eurytemora* over *Acartia* and cladocerans over copepods), 2) the selected copepods had a stronger vertical migration than the less selected species, 3) the predators consumed up to 70% of the estimated annual zooplankton production in 1985, and 4) an increase in planktivory in late summer coincided with a decrease in zooplankton biomass (Hansson *et al.* 1990a,b, Rudstam *et al.* 1989, 1992, Johansson 1992). These authors suggest that the seasonal dynamics of zooplankton in this area is the result of seasonal changes in the importance of bottom-up and top-down forces. In early summer, zooplankton increase as a response to warmer temperature, adequate food resources, and relatively low predation rates. In late summer, predators cause a decline in zooplankton biomass. Later in the season, zooplankton are restricted by cold temperatures and low food supplies (Johansson 1992). Planktivory has also been compared to zooplankton production in the Darß-Zingst Estuary, southern Baltic (Arndt 1989). As in the Askö area, mysids (in this case *Neomysis integer*) and juvenile fishes (herring and smelt) were the important planktivores and these predators appeared to strongly affect the zooplankton community. Predation by *Neomysis* is considered an important structuring force also in shallow brackish lakes (Irvine *et al.* 1990, Jeppesen *et al.* 1994).

Available data from the open Baltic Sea suggest similar patterns to the Askö area, but the data are less complete. Clupeids are also selective planktivores in other areas of the Baltic Sea (Sandström 1980, Flinkmann *et al.* 1992) and the vertical migration of *Eurytemora* is likely to be a response to high predation risk (Vuorinen *et al.* 1983, Vuorinen 1987) suggesting that top-down processes at least affect habitat utilization of selected prey species. This deserves more attention, as zooplankton need to avoid both clupeid feeding during the day and mysids feeding at night.

Top-down control is likely to be more intense if a large portion of the zooplankton production is consumed by the planktivores. The average zooplankton consumption for the period 1974-1991 is $32 \text{ g} \cdot \text{m}^{-2}$ for sprat and $85 \text{ g} \cdot \text{m}^{-2}$ for herring based on the ICES database (all rates and biomass values in this paper are in units of wet weight). These values could be twice as high depending on methods for calculating daily rations and on assumptions for early mortality (Arrhenius & Hansson 1993). Age-0 clupeids are likely to be important planktivores as they are abundant and have high specific consumption rates (Hewett & Stewart 1989, Rudstam *et al.* 1992). Arrhenius & Hansson (1993) calculated that 45-50% of the total consumption of zooplankton by clupeids in the Baltic Sea is from the age-0 fish whereas the present study obtained around 33% with slightly different assumptions on age-0 mortality rates (see also Elmgren 1984). Both mortality and growth rates of the age-0 are important components of such estimates. Given the dominating proportion of planktivory attributed to age-0, more accurate estimates are required of age-0 growth rates, abundance, diet, energetics, and spatial distribution.

Mysids may also contribute significantly to zooplanktivory in the Baltic Sea. Here, a first order estimate of mysid planktivory based on a bioenergetics model for mysids (Rudstam 1989) is attempted. Assumptions are 1) densities are $50 \text{ ind.} \cdot \text{m}^{-2}$ in the Baltic proper ($100 \text{ ind.} \cdot \text{m}^{-2}$ over oxic bottoms and none over anoxic bottoms), $150 \text{ ind.} \cdot \text{m}^{-2}$ in the Bothnian Sea and $50 \text{ ind.} \cdot \text{m}^{-2}$ in the Bothnian Bay on 1 September, and 2) the observed growth rates of mysids in these areas, and 3) a constant mortality calculated by assuming that one female on the average produce two mature offspring. Growth, abundance and fecundity data are from Simm & Kotta (1992a, b), Salemaa *et al.* (1986, 1990), Rudstam (1989) and Rudstam & Hansson (1990). These calculations suggest that mysids consume $20 \text{ g} \cdot \text{m}^{-2}$ in the Baltic proper, $49 \text{ g} \cdot \text{m}^{-2}$ in the Bothnian Sea and $16 \text{ g} \cdot \text{m}^{-2}$ in the Bothnian Bay. Compared to clupeids, mysids are less important as planktivores in the Baltic proper, but at least as important in the Bothnian Sea and Bothnian Bay. Over the whole area, mysids would consume $26 \text{ g} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, sprat $32\text{-}64 \text{ g} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ and herring $85\text{-}170 \text{ g} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ (using clupeid biomass from 1991).

These calculations indicate that between $143 \text{ g} \cdot \text{m}^{-2}$ (the present calculations for 1991) and $260 \text{ g} \cdot \text{m}^{-2}$ (Arrhenius & Hansson's (1993) calculations applied to the biomass available in 1991) are consumed annually by clupeids and mysids in the Baltic Sea. This represents between 50 and 93% of the zooplankton production estimated by Elmgren (1989) ($14 \text{ g C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$) assuming a carbon content of 5% of wet weight (Mullin 1969). This is high considering that 1) other fish species must also consume some zooplankton and 2) Elmgren's estimate of zooplankton production may be high. Johansson (1992) calculated annual zooplankton production to

be $6.3 \text{ g C} \cdot \text{m}^{-2}$ at a coastal station close to Askö and $12 \text{ g C} \cdot \text{m}^{-2}$ in a nutrient enriched station. Thus, available data indicate that a substantial proportion, if not most, of the zooplankton production is consumed by planktivores in the Baltic Sea. This suggests that top-down control of zooplankton is intense.

Planktivory is not equally distributed over seasons. As in the Askö area, planktivory by clupeids peaks in late summer and autumn (Figure 4, Arrhenius & Hansson 1993). This is caused by an increased biomass of age-0 clupeids. A late summer peak in planktivory is common in systems where age-0 fish are important planktivores (Mills *et al.* 1987, Hewett & Stewart 1989). Therefore, stronger top-down control of zooplankton is expected in late summer and autumn than in spring. Unfortunately, zooplankton data from the open Baltic have insufficient temporal resolution to investigate whether zooplankton in this area decline at the time when zooplanktivory increases. It is of note that the seasonal pattern of planktivory was probably different in the first half of this century when autumn-spawning herring were more abundant (Figure 4).

The combined biomass of clupeids has varied with a factor 2 between 1974 and 1991. Additional evidence for strong top-down control of zooplankton in the Baltic would be provided if zooplankton abundance tends to be low when clupeid biomass is high. Because of the seasonal patterns discussed previously, such a negative correlation should be most pronounced in late summer and autumn. The periodic assessment of the Baltic Sea (Anon. 1990) presents some zooplankton data from the open Baltic. The longest data series is from the southern Baltic, from 1953 to 1988. Contrary the hypothesis here, August zooplankton abundance does not correlate with the present estimates of clupeid biomass (Figure 8). In addition, there were no inter-annual patterns in zooplankton abundance that correlate with measured fish abundance in the Askö area from 1985 to 1991 (fish data in Hansson & Rudstam 1990 and Hansson 1993, zooplankton data in Johansson 1992). A detailed re-analysis of the available zooplankton data series from Finland (Vuorinen & Ranta 1987, Viitasalo *et al.* 1990, Viitasalo 1992) may allow for further tests of this hypothesis. However, it is difficult to determine patterns between planktivory and zooplankton abundance without data series where both fish, mysids and zooplankton have been collected concurrently. Such series are rare in the Baltic.

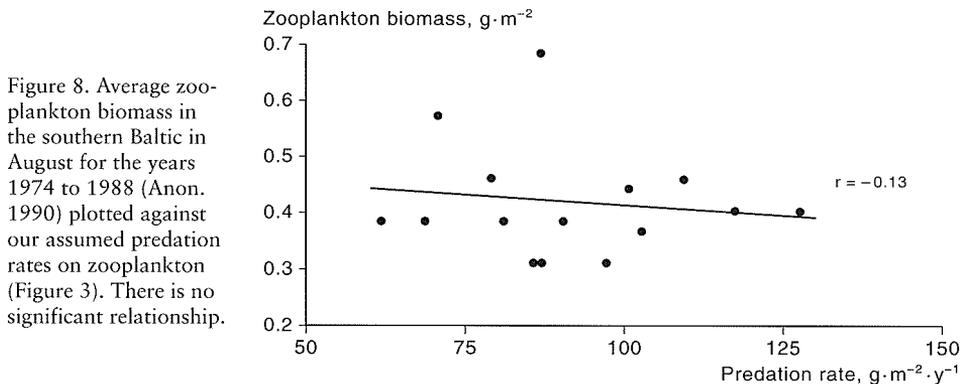


Figure 8. Average zooplankton biomass in the southern Baltic in August for the years 1974 to 1988 (Anon. 1990) plotted against our assumed predation rates on zooplankton (Figure 3). There is no significant relationship.

If top-down control of zooplankton is important, changes are expected in zooplankton species composition associated with gradients in predation rates or inter-annual differences in predation rates. Viitasalo (1992) discusses selective predation as a possible cause for onshore-offshore species changes in the Gulf of Finland, but lacks data on the distribution of fish and mysids. Daphnids, generally the most predator-sensitive zooplankton group, are absent from most of the Baltic proper. This may be the result of high predation rates. Planktivore biomass in the Baltic proper is similar or higher (minimum $110 \text{ kg} \cdot \text{ha}^{-1}$) than the biomass that depresses *Daphnia* populations in eutrophic lakes ($20\text{-}40 \text{ kg} \cdot \text{ha}^{-1}$, Mills *et al.* 1987, $30\text{-}50 \text{ kg} \cdot \text{ha}^{-1}$ McQueen & Post 1988). However, salinity may explain more of the observed species changes and trends over time than changes in predation rates (Vuorinen & Ranta 1987, Viitasalo *et al.* 1990, Lumberg & Ojaveer 1991). *Daphnia* is not common unless salinity is less than 2 psu in brackish lakes in Denmark (Jepesen *et al.* 1994) and growth and reproduction of *Daphnia magna* are reduced at 8 psu compared to 4 psu and fresh water (Arnér & Koivisto 1993).

To summarize, the current understanding of the degree and effect of top-down control on zooplankton in the Baltic Sea is inconclusive. Several observations do suggest top-down control: 1) overall zooplanktivory rates are comparable to estimates of zooplankton production, 2) selected zooplankton species avoid predation through vertical migrations, and 3) the seasonal decline of zooplankton coincide with a seasonal increase in predation rates (at least in coastal areas). However, low zooplankton abundance was not observed during years with high clupeid biomass.

Can these observations be reconciled? We offer a few suggestions. Firstly, abundance of age-0 clupeids is inferred from abundance of age-1 fish in the ICES database. Little is known about how mortality rates of age-0 fish vary among years or about where age-0 clupeids feed and if this change over time. Planktivory from this group may compensate for changes in the biomass of older clupeids. The same is true for mysids. Such compensatory effect can be expected since the older clupeids feed on their own larvae and on mysids. Thus, when the biomass of older clupeids is relatively low, mysids and age-0 clupeids may be more common. Secondly, the current seasonal pattern of zooplanktivory may leave zooplankton relatively unaffected by predation during spring and early summer, allowing their populations also to build up in years with relatively high planktivory rates later in the season. Thirdly, other factors structuring zooplankton populations may eclipse the effect of interannual changes in predation rates. The estimated range in zooplanktivory in the 1974-1991 data is not large (factor 2) compared to the order of magnitude changes observed in lakes after strong manipulations or natural die-off (e.g. McQueen *et al.* 1992, Rudstam *et al.* 1993). With such small changes in predation rates, inter-annual changes in primary productivity, nutrient inputs and temperature may be more important in determining inter-annual changes in zooplankton abundance, even if fish exert a strong top-down control on zooplankton in the Baltic.

Finally, it is necessary to assess evidence that the hypothesized strong top-down control of zooplankton cascades to phytoplankton. Kivi *et al.* (1993) did not observe much grazing control of phytoplankton in experiments where metazooplankton and nutrients were manipulated. However, they noted that protozooplankton

increased as a response to metazooplankton removal, possibly compensating for the decreased grazing rates of metazooplankton. Johansson (1992) did observe a negative correlation between zooplankton biomass and chlorophyll-*a* at a nutrient enriched station but not at a reference station, suggesting that grazing can affect phytoplankton in some areas of the Baltic Sea. Grazing effects may be less marked than in lakes, however, because of the lack of *Daphnia*. In lakes, a grazing suppression of algae seems to be coupled with the presence/absence of large *Daphnia* (Mills *et al.* 1987, McQueen 1990, Carpenter & Kitchell 1993). But large effects of grazing on phytoplankton are not expected if zooplankton were strongly controlled by top-down interactions. Long-term data sets indicate a positive response of chlorophyll to increased nutrient levels, but no increase in zooplankton biomass (Wulff *et al.* 1986, Anon. 1990), as expected by the theories on cascading trophic interactions.

The Baltic future: can top-down control be used actively?

The countries around the Baltic Sea have formulated several objectives for the management of the sea and its resources. The Convention on the Protection of the Marine Environment of the Baltic Sea Area from 1992 states that the contracting parties declare 'their firm determination to assure the ecological restoration of the Baltic Sea, ensuring the possibility of self-regeneration of the marine environment and preservation of its ecological balance'. Individual countries have formulated more specific goals. For example the Swedish Environmental Protection Agency (SNV) has stated that overall goals include: 'to maintain vigorous, balanced populations of naturally occurring species, and to achieve a natural zoning of flora and fauna' (Anon. 1990). The Convention on Fishing and Conservation of the Living of the Baltic Sea has asked ICES, on an annual basis, to 'analyse the state of exploitation of the stocks of herring, sprat, cod and flatfish in the Baltic Sea and to advice as to regulations which might be used for approaching optimum yield of the stock of the said species' (Anon. 1974).

The means for achieving these goals for the Baltic Sea have been a reduction of fluxes of nutrients and pollutants entering the sea and management of the fishery through gear restrictions, catch quotas and stock enhancement. The programmes for the reduction of pollutant and nutrient loads have partly been successful, but the eutrophication of the Baltic Sea has continued (Ferm 1993). The fishery management has until recently been based on a species-by-species assessment. The introduction of multi-species approaches has significantly changed the nature of the management (Hildén 1993). Extensive stocking programmes have released more than 4 million smolts of salmon, about 2 million smolts of sea trout, more than 5 million sea trout fry, several hundred thousand smolt of rainbow trout and more than 5 million one-summer-old whitefish over time (Hildén *et al.* 1982, Anon. 1991). The stocking programmes have primarily been regarded as a way to restore the fish community and to compensate for the reduced spawning areas of anadromous fish brought about by the development of hydropower. Few substantial attempts have been made to manipulate fish communities or the environment at large in a desirable direction.

The Baltic Sea at present is dominated by planktivorous fish. Bergstrand (1990) suggested that great abundance of planktivores would retard the recovery of an eutrophic lake following reduction of nutrient loads. This could also be valid for the Baltic Sea. That stocks of sprat and herring are increasing suggests an increased predation on zooplankton. In lakes, a sometimes successful strategy involves manipulation of top predators to reduce planktivores and improve water quality (Shapiro & Wright 1984). Can this be done at the scale of the Baltic Sea? Large-scale stocking programmes have successfully established important salmonid fisheries in the Laurentian Great Lakes with multi-million dollar returns to local communities from tourism associated with this fishery (Talhelm 1987). These salmonids do affect their forage base (Kitchell & Crowder 1986), but it is still open to question as to what degree zooplankton affect algae and water clarity in these large lakes (Scavia *et al.* 1986, Lehman 1988). In the Baltic Sea, the annual rate of stocking per unit area is less than 0.15 juvenile piscivorous fish per hectare of surface water (primarily salmonids). Comparable figures for Lake Michigan and Lake Ontario are 1-4 fish · ha⁻¹ (Hartig *et al.* 1981). Thus there appears to be a considerable potential for increasing the stocking of piscivorous fish in the Baltic. Economic considerations are, however, different in the Baltic and in the Great Lakes. Commercial fisheries generally generate much less economic return per fish than sport fisheries and it will be very difficult to support large stocking programmes on revenues generated by commercial fisheries alone. Attempts to manipulate the entire Baltic pelagic system through massive stocking of piscivores would also be a high-risk venture. Experience from the Great Lakes suggests that it is difficult to establish sustainable stocking rates at levels that are close to the carrying capacity of the forage base and that public expectation can be difficult to reconcile with sound management based on an understanding of the underlying biological processes (Kitchell 1992). Also, successful large-scale stocking could aggravate conflicts between the conservation of wild stocks and the exploitation of fishery resources already observable in the Baltic Sea. In addition, fisheries are difficult to regulate because markets and not fisheries managers determine what and how much is fished. Further, diseases, such as M74 or Bacterial Kidney Disease, can jeopardize any large-scale stocking programmes. But local use of top-down control in semi-enclosed areas may be a viable strategy (S. Hansson, Department of Systems Ecology, University of Stockholm, pers. comm.).

In the Baltic Sea, the fishery has increased the dominance of planktivores by contributing to the depletion of the cod stock. The fishery for cod is likely to remain more valuable than the fishery for clupeids. Above is discussed the possibility that clupeids negatively affect cod stocks by predation on cod eggs. In addition to possible effects on water quality, there may be reasons for decreasing the currently high population of clupeids in the Baltic. The fishing fleets of the Baltic Sea are efficient enough to reduce the planktivore stocks, but at present it is not an economically viable option on a basin-wide scale because of the low market price for clupeids. Restoration of the ratio between planktivores and piscivores through fishing would require subsidies of the fishing fleet unless markets for clupeids improve. This may still be desirable if clupeids indeed do prevent cod recruitment as suggested in this review. Restricting fishing for cod has been attempted, but until recently the attempts

have been largely unsuccessful (Karnicki 1993). The present situation for the Baltic cod stock is alarming. The fishery is still reducing the stock and deteriorating hydrographical conditions impede successful reproduction. The role of cod as the most important top predator is at stake and the system may move to a clupeid-dominated system in which cod reproduction is prevented by top-down control from clupeids.

The investigations of top-down control processes in the Baltic Sea and in marine systems in general are just beginning and questions remain to be answered. Further research on top-down processes will be a productive avenue to increase our understanding of the Baltic ecosystem. The interactions between fish, mysids, zooplankton and algae should be amenable to experimental investigations in laboratory and mesocosms. Unfortunately, in contrast to limnology, whole sea manipulations are not feasible and there are few comparable water bodies to use for comparative studies. This is a continuing challenge for marine biologists interested in top-down control.

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