

The role of fish and fisheries in Baltic Sea nutrient dynamics

Olle Hjerne¹ and Sture Hansson

Department of Systems Ecology, Stockholm University, SE-106 91 Stockholm, Sweden

Abstract

Many studies show that fish and fisheries management can be important to freshwater nutrient dynamics, but similar reports from marine environments are scarce. In the Baltic Sea, we estimate the removal of nutrients by the fishery to be 1.4% and 7% of the total nitrogen and phosphorus load to the Baltic Sea. Moreover, compared with the anthropogenic load of nutrients that reaches the open sea, the fishery removes 2.4% and 18% of the nitrogen and phosphorus. In addition, we show that the summer increase of fish biomass can explain up to one third of the summer decrease in “total phosphorus” in the upper 40 m of the water column. This suggests that fish may compete with primary producers (particularly cyanobacteria) for phosphorus. The fish and the fishery can thus influence nutrient dynamics in marine systems substantially, and this should be considered in ecosystem oriented fisheries management.

In freshwaters, fish can be important in nutrient dynamics, and sometimes most of the pelagic phosphorus is stored in fish biomass (Bartell and Kitchell 1978; Schindler et al. 1993). Fish stock fluctuations can influence the availability of nutrients to phytoplankton, and especially young-of-the-year (YOY) fish can be an important P sink relative to sedimentation losses (Bartell and Kitchell 1978; Kraft 1992). The removal of nutrients by fisheries landings can be substantial (Sarvala et al. 1984). Fish can influence nutrient dynamics through excretion (Schindler 1992; Schindler et al. 1993), especially benthic feeding fish, which mobilize nutrients from sediments (Lamarra 1975; Schaus et al. 1997). Furthermore, fish can influence nutrient dynamics indirectly through their effects on zooplankton. Intensive zooplanktivory can decrease nutrient regeneration, but size selective predation can also alter the zooplankton community structure, and increases in small species with high metabolic rate can increase nutrient regeneration (Bartell and Kitchell 1978; Carpenter et al. 1992). Yet another mechanism by which fish can influence nutrient dynamics is transport. Nutrients from the sea are moved to freshwater and terrestrial systems through the spawning migration and eventual death of anadromous Pacific salmon (Kline et al. 1990; see also Durbin et al. 1979 for the anadromous alewife, *Alosa pseudoharengus*). Within a lake, fish can move nutrients by migration (Kitchell et al. 1994) or indirectly by changing the migration

pattern of their prey (Schindler et al. 1993). Even in marine environments, nutrient transport with migrating fish can be substantial (Deegan 1993).

These effects on nutrient dynamics show the importance of fish as ecosystem components. Limnologists already take advantage of this in lake biomanipulations (i.e., reducing the effects of eutrophication by modifying food web structure, Stenson et al. 1978; Carpenter et al. 1985; Hansson et al. 1998). Our understanding of the role of fish in marine ecosystems is poorly developed. One reason for this is that marine fish research traditionally has focused on fisheries management issues rather than on integrating fish in an ecological perspective. Despite this lack of understanding, the sea fishery has been allowed to develop into a giant, uncontrolled biomanipulation, because naturally very abundant fish species are frequently seriously reduced through overfishing (FAO 2000; Steele and Schumacher 2000).

In this study, we explore whether some of the processes which make fish potentially important in freshwater nutrient dynamics are significant also in the Baltic Sea. We concentrate on two aspects of the role of fish. (1) Can the removal of biomass by the fishery constitute a significant flux of nutrients (nitrogen and phosphorus) from the ecosystem? (2) Can interannual fluctuations in fish biomass significantly influence phosphorus dynamics?

The Baltic Sea is a semienclosed brackish sea, with the highest salinities and temperatures in the southwest area and lowest in the north. The Baltic Proper (Fig. 1) has a permanent halocline at 40–70 m depth, and a thermocline develops at 15–20 m depth in summer (Kullenberg 1981). The brackish environment makes the Baltic Sea species poor, and the fish community is dominated by three species. Herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) are the dominant zooplanktivores. Herring migrate to coastal areas for spawning on bottom substrates, but they spend most of their life cycle in the open sea. Sprat spend their entire life in the open sea and spawn pelagically. Cod (*Gadus morhua* L.) is the dominant piscivore, although benthos constitutes about half of the population's diet (Uzars 1994). Herring, sprat, and cod make up ~80% of the total fish biomass (Elmgren 1984). The primary production in the Baltic Proper is generally nitrogen limited, but phosphorus limitation oc-

¹ Corresponding author (olle.hjerne@system.ecology.su.se).

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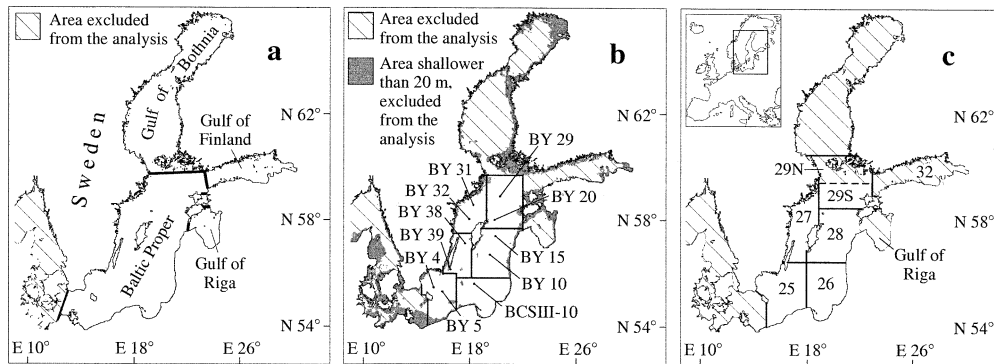


Fig. 1. (a) Basins in the Baltic Sea used for nutrient load estimations. (b) Sampling stations and areas used in the calculation of totP in the Baltic Proper and (c) corresponding ICES subdivisions used in the estimation of phosphorus in the fish biomass.

curs during summer blooms of nitrogen-fixing cyanobacteria (Granéli et al. 1990). Besides adding nitrogen (Larsson et al. 2001) and thus contributing to the eutrophication problems (e.g., Larsson et al. 1985; Rosenberg et al. 1990), some common cyanobacteria, like *Nodularia spumigena*, are toxic (Edler et al. 1985; Sellner 1997).

The spring bloom is N limited and is generally dominated by heavy diatoms, which sink and strip the water column of nutrients (Elmgren 1984). This bloom is little used by the pelagic food-web (low zooplankton densities, Koski et al. 1999) but probably constitutes the most important energy input for the benthic fauna (Elmgren 1984). The most important energy input to the pelagic food web is primary production by summer phytoplankton, when the zooplankton biomass builds up and is consumed by zooplanktivorous fish and invertebrates (Rudstam et al. 1992).

The potential role of fish in the nutrient dynamics is particularly interesting because the Baltic Sea has eutrophication problems. Attempts to decrease loads of both N and P are made, and therefore assessments of the removal of nutrients by fish landings are relevant. Analyses of the effects of intra-annual fluctuations in fish biomass focuses on P, because the biomass of the relatively phosphorus-rich fish increases rapidly in summer, during the same period as cyanobacterial blooms become P limited.

Materials and methods

Overview—We calculated the removal of nutrients by the fishery by estimating the N and P content in fish body tissue and adding up commercial landings. For comparison, we compiled the total and anthropogenic nutrient load and estimated the retention of nutrients in estuaries to obtain the load to the open sea.

To investigate the role of fish in intra-annual P dynamics, we estimated the amount of P sequestered in fish biomass from the P content in fish body tissue and intra-annual biomass dynamics. We calculated the biomass of fish age ≥ 1 yr from International Council for Exploration of the Sea (ICES) fish number data and individual weight data and for YOY fish, also from literature-based assumptions. We estimated the amount of total phosphorus (totP) in the upper

water column from measurements and hydrographic data. For both fish and totP, we used average dynamics over several years, but the data periods differed because reliable data did not overlap fully in time. For totP, the sampling frequency and reliability of data were better for later years (1994–1998). In contrast, fish data from recent years have relied largely on uncertain catch per unit effort data, whereas earlier data were based on total commercial fishery landings and were considered more reliable (1977–1997). We completed the analysis with sensitivity tests of some assumptions for YOY fish and performed individual weight projections on the basis of bioenergetics.

Nitrogen and phosphorus content in fish—Eighteen herring (between 66 and 145 mm length) and 22 sprat (between 58 and 130 mm length), collected in 1999–2001 during different seasons and in various places, from the Bornholm basin in the south to Himmerfjärden area in the northern Baltic Proper, were analyzed for N and P content. Samples of dried and homogenized whole fish were analyzed for N by use of a Leco CHN-analyzer (CHN-900, 600-8000-3000, ethylene diaminetetraacetic acid as standard). For the P analyses, samples on glass-fiber filters were put into 15-ml glass tubes. After the addition of 0.2 ml $\text{MgSO}_4 \cdot 7\text{H}_2\text{O} \cdot \text{KNO}_3$ solution (125 and 50 g L^{-1} , respectively), the samples were combusted for 2 h at 500°C and digested in 6 ml persulfate solution (50 g L^{-1} for 1 h at 120°C). After addition of 4 ml 1.6 M NaOH, samples were analyzed for molybdate reactive orthophosphate with a flow injection system (Lachat Instruments, modified QuickChem method 31-115-01-3-A). Blanks were run by use of the same procedure. Standards were prepared by adding stock phosphate solution to vials before digestion. These analysis procedures are used within the Swedish national monitoring program.

Removal of nutrients by the fishery—Removal: To estimate the removal of nutrients, we compiled the landings of herring, sprat, and cod from the commercial fishery in the Baltic Sea (1977–1998, from ICES statistics provided by B. Sjöstrand) and assumed the nutrient content of cod to equal that of herring and sprat.

Nutrient load: We compiled the total nutrient load to the

Gulf of Bothnia, Gulf of Finland, Gulf of Riga, and Baltic Sea Proper (Fig. 1a) separately. Inputs from rivers and coastal point sources were from 1995 in HELCOM (1988). To estimate the atmospheric load of nitrogen (from 1995, HELCOM 1997), the total nitrogen load into the Baltic Proper was divided between the Gulf of Riga and the rest of the Baltic Proper proportionally to their areas. The atmospheric load of P (from 1984, HELCOM 1986) was apportioned between areas proportionally to the atmospheric load of N. Nitrogen fixation by cyanobacteria was added to the load as 305,000 tons yr⁻¹ for the Baltic Proper (Larsson et al. 2001; report 180,000–430,000 tons) and 3,800 tons for the Gulf of Bothnia (Larsson et al. 1985).

Of the total loads of N and P, we also estimated the anthropogenic fraction and how much of this that reaches the open sea. On the basis of data from Larsson et al. (1985), the anthropogenic part of the atmospheric load of P and N was estimated to be 50% and 80%, whereas human activities have doubled the nitrogen fixation. For the riverine loads, we based our calculation on HELCOM (1998) and assumed that the anthropogenic fraction of both N and P to the Gulf of Bothnia was 50% and that in the other basins was 85%. All nutrients from coastal point sources were considered anthropogenic.

Because herring, sprat, and cod are mainly caught (and produced) in the open Baltic (on average, 99% of the Swedish catches; B. Sjöstrand pers. comm.), the nutrient removal by fish landings should be compared with the nutrient load that actually reaches the open sea. Nixon et al. (1996) estimated the retention of N and P in Atlantic estuaries to be 30%–65% and 10%–55%, respectively. We have not found similar analyses of the total retention in Baltic estuaries published. For the rivers Neva, Daugava, Vistula, and Odra, which contribute ~70% and ~80% of the total N and P river load to the Baltic Sea, Savchuk and Swaney (1999), Savchuk (2000), and C. Humborg (Dept. of Systems Ecology, Stockholm University, pers. comm.), reported substantial retention, and, on the basis of their studies, we have assumed 33% retention of N and 52% of P (estimated from river estuary specific retention values, weighted by the river loads). There is also some retention of the atmospheric load that reaches the coastal areas, but we ignored that fraction herein. Furthermore, some of the nutrients that enter the sea are not bioavailable (Pitkänen 1994), but information is insufficient to allow subtraction of this fraction. On the basis of these assumptions, we estimated the anthropogenic load of nutrients to the open sea.

The role of fish in annual phosphorous dynamics—Estimation of totP in the Baltic Proper: Data on totP concentrations were derived from analyses of unfiltered water samples (large organisms like fish excluded) from 11 offshore stations in the Swedish national monitoring program (Fig. 1b). We used the Baltic Environmental Database (Sokolov et al. 1997) and the software NetStations (Sokolov and Wulff 1999) to process raw data provided by the Swedish Meteorological and Hydrological Institute (SHARK database, 10 sampling stations) and the Department of Systems Ecology, Stockholm University (one sampling station). Averaging over the period 1994–1998, we calculated mean monthly

totP concentrations at 1.25, 5, 10, 15, 20.75, 29.5, and 40 m depth in six areas (Fig. 1b). The total amount of totP was derived by multiplying the depth specific concentrations with volumes in corresponding depth intervals by use of a hypsographic grid with 1 nautical mile horizontal resolution and 1 m vertical resolution (Data Assimilation System; Sokolov et al. 1997). Because we were interested in the dynamics of the open sea, areas shallower than 20 m were excluded (~10% of the surface area).

Fish stocks: After ICES assessment stock units (ICES 1999b), we based our analysis on the herring and sprat stocks in ICES subdivisions (SD, Fig. 1c) 25–29 and 32. Because this area is larger than the area covered by the calculations of totP, fish stock sizes had to be reduced. We decreased both herring and sprat numbers in proportion to the catches in SD 29N and 32 relative to total catches between 1977 and 1997. When catch data from SD 29N were unavailable, they were assumed to constitute 50% of the total catches in SD 29. Herring numbers were also reduced in proportion to the average biomass in the Gulf of Riga relative to the average total biomass over the period (ICES 1999a). This procedure overestimated the fish biomass in the open Baltic Sea by including fish in coastal areas (depth <20 m), especially YOY herring. However, because we are interested in the total fish biomass, overestimated herring and sprat stocks will at least partly be compensated for by the exclusion of other species (e.g., cod and threespined stickleback, *Gasterosteus aculeatus* L.).

Fish numbers: We used data on fish numbers and individual weights between 1977 and 1997 from a multispecies virtual population analysis (MSVPA) with a quarterly time step (ICES 1999b, data provided by M. Vinter, Dansk Fiskeri Undesøgelse, Charlottenlund, Copenhagen). Daily stock numbers were derived from fish numbers at the beginning and the end of a quarter under the assumption of a constant mortality rate.

Larval and YOY herring and sprat account for about half of the total consumption by these species (Arrhenius and Hansson 1993), which indirectly indicates their importance to the biomass dynamics. To account for YOYs in our analysis, we modeled abundances according to the method of Arrhenius and Hansson (1993), who assumed 50% of the spawning stock biomass (SSB) to be females, that gonads constitute 20% of the females' weight, and that 90% of this is eggs. We estimated the SSB on the spawning day (1 May) from biomass estimates and proportions of sexually mature fish at different age (ICES 1999b). From the SSB and the individual egg weight (herring, 0.53 mg and sprat, 0.26 mg), the total number of eggs was calculated. The eggs were assumed to hatch after 10 d, and the mortality until then was 10%. During the yolk sac stage (5 d), the mortality was also 10%, but during the period between first feeding and metamorphosis (70 d, 16 May–24 July), we used a 90% monthly larval mortality. A constant YOY mortality during the post-larval period was estimated by interpolation between the number of surviving fish at the beginning and end of this period (the latter number derived from the MSVPA analysis). We believe that this approach to calculate YOY fish abundance gives more realistic numbers than the MSVPA,

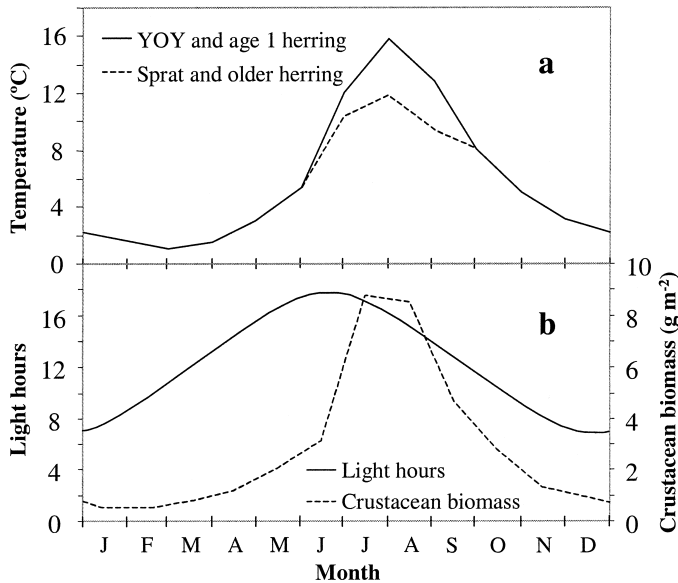


Fig. 2. (a) Temperatures assumed to be inhabited by herring and sprat. (b) Length of daily feeding period (light hours) and crustacean biomass used as input in the food \times light bioenergetic model.

which predicts a lower mortality rate of YOYs than of age 1 fish.

Individual body weight: Data on the quarterly weights from age 1, second quarter, and older fish were average values for 1977–1997 on the basis of ICES (1999b). Daily average weights were from linear interpolations between the middle of the quarters.

ICES data on YOY weights are probably biased because of gear selectivity (P. O. Larsson, National Board Fisheries, Sweden, pers. comm.), and we used alternative estimates for YOY and age 1 fish up to the second quarter. According to the methods of Arrhenius and Hansson (1993), we assumed that egg weights of herring and sprat were 0.53 and 0.26 mg at spawning. Until hatching, they lose 20% of their weight, but at the start of exogenous feeding weights have increased to 0.7 and 0.5 mg for herring and sprat. From the day of first feeding until metamorphosis, the weight increased exponentially to 0.13 g.

From metamorphosis until the end of the first year, we assumed growth of herring and sprat to follow the shape of a function found by Arrhenius and Hansson (1996), where length depends on the number of degree-days after hatching (temperatures in Fig. 2a and weight of $3.01 \times 10^{-6} \times \text{length}^{3.15}$, F. Arrhenius, National Board Fisheries, Sweden, pers. comm.). The weight curve obtained was then rescaled to intersect the weight at metamorphosis and the weight at the end of the year, which we assumed to be the same as that given by ICES for age 1 fish in the middle of the second quarter. We assumed that the weight was constant from the end of the YOY period (31 December) until the middle of the second quarter the following year.

Sensitivity analysis of some assumptions for YOYs: Mortality rates and abundances of larvae and YOYs of herring and sprat are uncertain. To analyze whether our assumptions were crucial to the results, a sensitivity analysis was per-

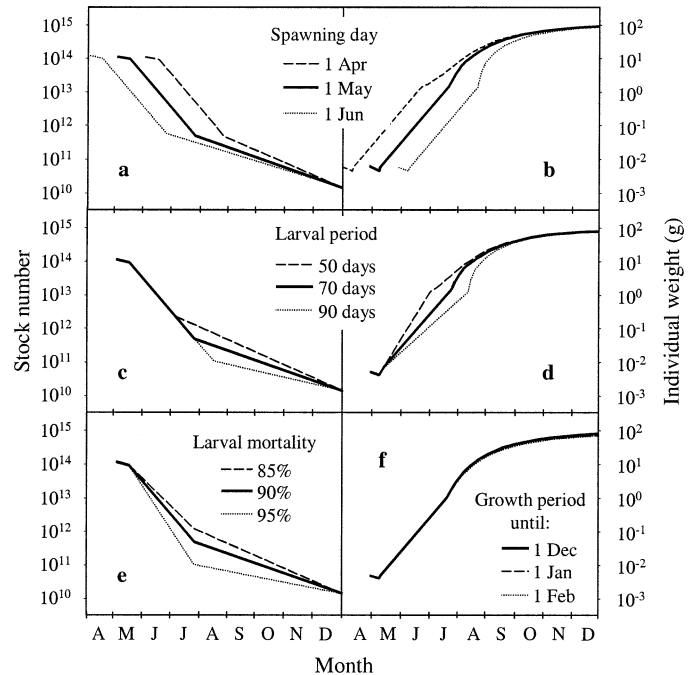


Fig. 3. Variation in (a, c, e) stock numbers and (b, d, f) individual weight of herring in the sensitivity analysis. We tested changes in (a, b) spawning day, (c, d) larval period length, (e) larval mortality, and (f) growth period length. The solid line shows the standard run in all panels.

formed. We varied the spawning day (1 April, 1 May, and 1 June), the larval period length (50, 70, and 90 d), and the monthly larval mortality (85%, 90%, and 95%) independently of each other (Fig. 3a,c,e), where the middle alternative represents the standard run, described above. Keeping the assumptions on growth (see above), sensitivity tests of spawning day and larval period duration indirectly also bring about changes in the weights (Fig. 3b,d). In the standard run, we assumed that the growth period terminated at the end of the year and that weight after that stays constant until 15 May. Sticking to the same growth calculation as described above, we also extended the growth period until 1 February and 1 March. (Fig. 3f).

Individual weights generated by a bioenergetics model: Input data on herring weight at age from the MSVPA follow a strange annual bimodal pattern (Fig. 4a). Between the fourth and first quarter, which is the darkest and coldest period of the year with the lowest food availability, the weights increase by an unexpectedly large amount. This has most likely to do with sampling biases. To obtain alternative growth data for metamorphosed fish, we also generated weights at age with a bioenergetics model (Hanson et al. 1997; Fig. 4b). The model is a mass balance equation in which growth (G) equals food consumption (C) minus losses through metabolism (R), specific dynamic action (S), egestion (F), and excretion (U):

$$G = C - [(R + S) + (F + U)] \quad (1)$$

The growth in this model is driven by food consumption, which is a function of the weight dependent maximum pos-

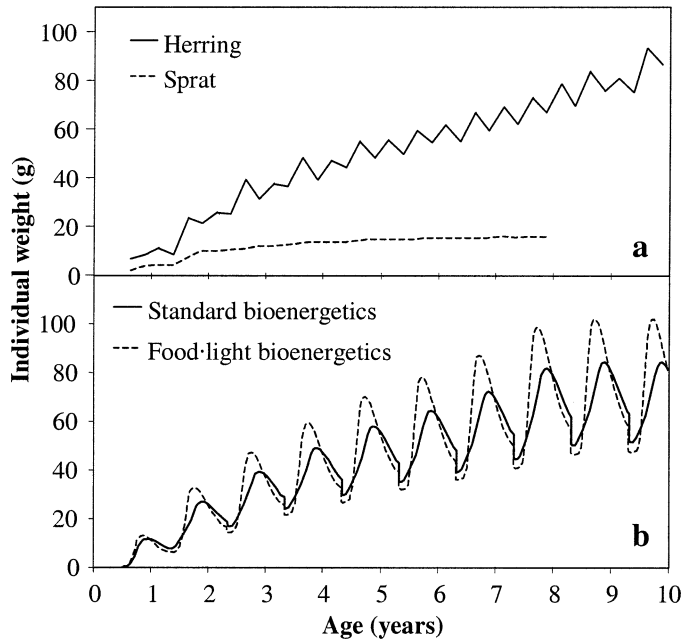


Fig. 4. (a) Average individual herring and sprat weights, from ICES data (1977–1997). Note the strange annual bimodal pattern in herring weight. (b) The herring weights derived from bioenergetics models show pronounced annual fluctuations.

sible consumption (C_{\max}) and temperature [$f(T)$]. Within a year, the daily consumption is set to a fixed proportion (P) of the maximum food consumption, given the temperature and fish size. This relationship is described as

$$C = P \times C_{\max} \times f(T) \quad (2)$$

The model parameters for YOY fish are from Arrhenius (1998), and those for older fish are from Rudstam (1988). The modeling started with newly metamorphosed fish (0.13 g), and these were grown to fit the weights at the end of each year (weight data from the average individual weights [1977–1998] during the first quarter are from ICES 1999b). We accounted for seasonal changes in fish energy density (generally decreasing during winter and spring and increasing during summer and fall) according to the method of Arrhenius and Hansson (1996).

When the bioenergetics model is run with a constant P value over an entire year, this assumes constant feeding conditions. An alternative approach is to assume that consumption is proportional to food availability. Furthermore, Arrhenius assumed that the consumption by herring, which is a visual predator, depend on the length of the daily feeding period. Combining these assumptions transforms Eq. 2 to

$$C = P \times \text{daily feeding period} \times \text{food availability} \quad (3)$$

The use of this relationship to derive consumption rates instead of Eq. (2), growth and weights were obtained through iteration in the same way as in Hanson et al. (1997). For daily food availability, we used crustacean zooplankton biomasses in the northern Baltic Proper (58°48'N, 17°38'E, Fig. 2b, based on data provided by S. Johansson, Swedish Environmental Protection Agency). We used the time between

sunrise and sunset at latitude 56°30'N as the length of the daily feeding period (Fig. 2b).

Phosphorus in fish biomass: The quantity and annual dynamics of phosphorus in the fish biomass was calculated from the P content in fish, combined with weight and abundance data. Furthermore, we made an alternative and conservative estimate on the basis of the annual production of herring and sprat in the Baltic Proper. This production was calculated as landings of herring and sprat (ICES statistics provided by B. Sjöstrand, National Board Fisheries, Sweden) plus the estimated fish biomass eaten by cod (ICES 1999b, with cod food consumption based on Hansson et al. 1996, averages 1977–1997). To calculate the increase in biomass and the amount of P sequestered from the water column by fish during summer, we assumed landings and the biomass eaten by cod to be constant for all months and that all net fish production (production based on nonfish food) occurs during the summer half of the year (May–November), when zooplankton are abundant.

For comparison, we made a third estimate of the accumulation of P in fish biomass during summer (between the middle of the second and third quarter, 15 May–15 September) solely (even for YOY) on the basis of quarterly data from the MSVPA (ICES 1999b; M. Vinter pers. comm.). These data allow us to estimate the annual differences in fish P increase during the period (1977–1997) but has the drawback of uncertain data for young fish, as discussed above.

Results

N and P content in fish—The content of N and P in herring and sprat was 2.4% (standard deviation [SD] 0.2%) and 0.43% (SD 0.07%) of the wet biomass, which correspond well with values from other teleosts (Sterner and George 2000). We found no obvious differences in nutrient concentrations among species, fish size, seasons, or areas; therefore, we assume constant N and P content.

Removal of nutrients by the fishery—The commercial landings of herring, sprat, and cod are on average 650,000 tons yr^{-1} and remove, on average, 15,000 tons of N and 3,000 tons of P annually. This removal is 1.4% of the annual N load and 8% of the P load (Table 1). We estimate the anthropogenic load to be 820,000 tons and 30,000 tons of N and P. This corresponds to a fourfold increase in nutrient load of both N and P due to human activities. Of this load, we estimate that 650,000 tons and 16,000 tons reach the open sea. Compared with this load, the removal of N and P by fish landings is 2.5% and 18%, respectively (Table 1).

The role of fish in annual nutrient dynamics—TotP in the Baltic Sea Proper: The concentration of totP in the upper 20 and 40 m follows an annual cycle (Fig. 5), building up during the winter as a result of vertical mixing and metabolic activities by organisms not compensated for by the low nutrient assimilation by plants. This period is interrupted by a rapid decrease due to sedimentation during and after the spring bloom. During the summer, the decrease continues at a slower rate until September, when the concentration starts

Table 1. Compilation of the total annual nutrient load (in thousands of tons) to the Baltic Sea from different sources, the anthropogenic load, and the estimation of how much of this that reach the open sea. On average, the fishery removes a considerable part of the load (15,000 tons of N and 3,000 tons of P).

Area	Riverine load		Coastal point sources		Atmospheric load		Nitrogen fixation		Total load		Anthropogenic load		Anthropogenic load to the open sea	
	N	P	N	P	N	P	N	P	N	P	N	P	N	P
Gulf of Bothnia	89	5.0	10	0.6	34	0.8	4		137	6.4	83	3.5	65	1.9
Gulf of Finland	103	4.7	30	3.4	16	0.4	—*		149	8.5	130	7.6	92	3.8
Gulf of Riga	85	1.8	1	0.4	9	0.2	—*		96	2.4	81	2.0	—†	—†
Baltic Proper	298	16	18	1.7	141	3.4	305		762	21	537	17	504	10
Total Baltic Sea	575	28	59	6.1	200	4.8	309		1,143	39	831	30	661	16
Removed by the fishery (%)									1.4	7.2	1.9	9.2	2.4	18

* We had no estimations on N fixation in the Gulf of Finland and the Gulf of Riga.

† The Gulf of Riga is not part of the open sea.

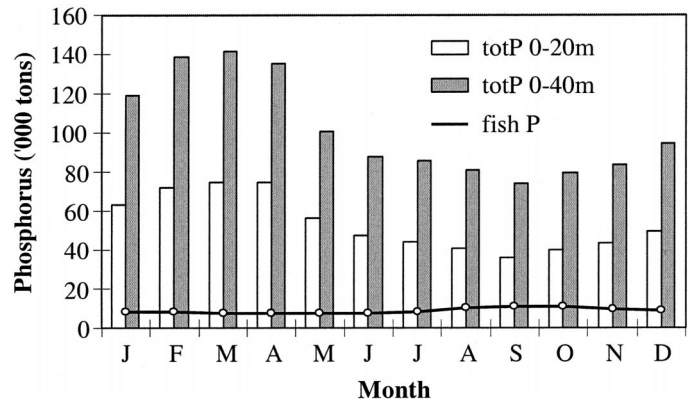


Fig. 5. Average annual dynamics of fish P in the standard run (1977–1997) and totP in the upper 20 and 40 m (1994–1998) in the Baltic proper.

to increase. This basic pattern occurred in all basins and in all years.

Fish P and totP: We assume the same P content in larvae as in metamorphosed fish, and because the P content is constant over time, changes in the amount of P in fish follow the fluctuations in fish biomass over the year. In our standard run, the P in fish biomass in April is only 10% and 5% of totP in 0–20 and 0–40 m but increases to 30% and 15% in September (Fig. 5). The range of variation in fish P over the year only corresponds to 10% and 6% of the range in variation of totP in 0–20 and 0–40 m. However, in the summer when totP in the water decreases slowly and the fish biomass builds up, changes in fish P and totP are of the same magnitude (Table 2, Figs. 5, 6). Between July and August, for example, the fish P in our standard run increases >1,500 tons, and this corresponds to 48% and 33% of the decrease in totP in 0–20 and 0–40 m, respectively.

This estimated build-up of phosphorus in fish biomass is based on a number of assumptions, and by changing some of these assumptions we explored the sensitivity in our estimates. A 50-d larval period duration and a 85% monthly larval mortality almost doubled the increase in fish P between May and September, whereas a 90-d larval period or a 95% mortality rate reduced it by more than half (Fig. 6a, Table 2). However, changes in the length of the growth period (Fig. 3f) hardly influenced the results. The assumptions about spawning time did not influence the total increase in fish P much either, but with a later spawning time (1 June), the biomass peak was 1 month later than that for the standard run (Fig. 6b, Table 2). When weights at age were derived from the bioenergetics model, the fish P dynamics changed dramatically (Fig. 6b). The increase in biomass almost doubles with the standard bioenergetics model and increases even more with weight data from the “food-light” model. The biomass increase was also shifted in time, so that the biomass peaked about a month later than in the standard run.

The average annual biomass production of herring and sprat, as based on landings and cod consumption is 1.1 million tons yr⁻¹. This conservative estimate gives a fish P increase of 2,100 tons during the summer half of the year, which is almost 60% of the estimate in the standard run

Table 2. The size of the monthly fish P increase in percentage of the totP decrease in depth intervals 0–20 and 0–40 m. Values >100% means that the fish P increase is bigger than the totP decrease and is theoretically possible if there is transport (horizontal, from coastal areas, or vertical, from deeper water layers) of P to the water column. The standard run has 90% monthly larval mortality, a 70-d larval period length, and spawning on 1 May.

Depth interval (m)	Month	Standard run (%)		Monthly larval mortality (%)			Larval period length			Spawning time (%)			Bioenergetics (%)		
		Standard	run (%)	85	95	50 days	90 days	1 April	1 June	Standard	Food × light	Standard	Food × light		
0–20	May–Jun	6	6	9	3	15	3	5	9	3	1				
	Jun–Jul	15	15	29	10	64	10	21	18	21	27				
	Jul–Aug	48	48	90	23	82	13	42	15	54	102				
	Aug–Sep	21	21	32	6	19	12	12	40	66	111				
0–40	May–Jun	4	4	6	2	10	2	4	6	2	1				
	Jun–Jul	26	26	49	17	108	18	36	30	36	45				
	Jul–Aug	33	33	62	16	56	9	29	10	37	70				
	Aug–Sep	15	15	22	5	13	9	9	28	46	78				

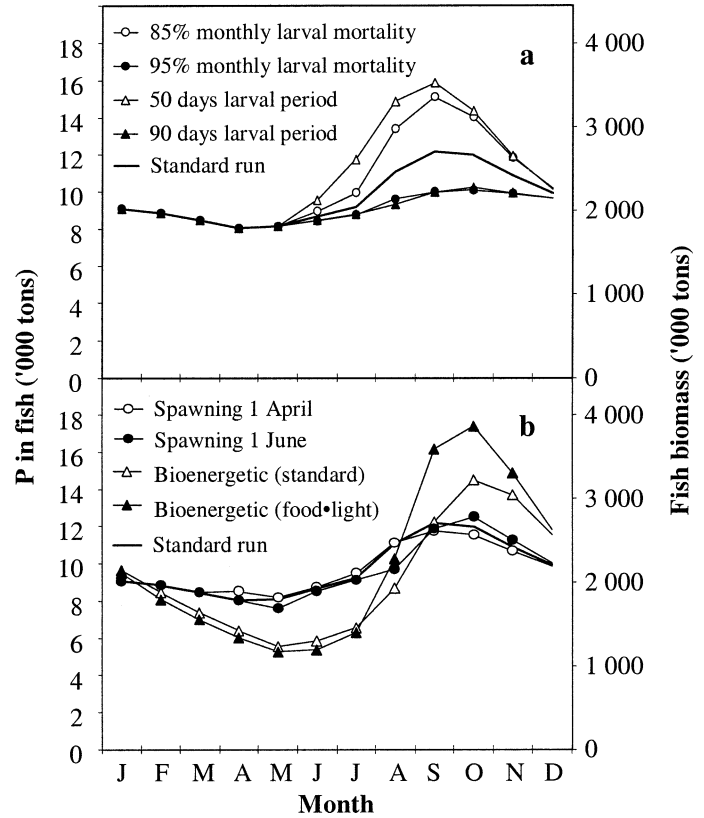


Fig. 6. Annual dynamics in fish biomass and P in fish with different assumptions about (a) monthly larval mortality, larval period length, and (b) spawning day and individual weights estimated by two different bioenergetic models. The standard run assumes 90% monthly larval mortality, a 70-d larval period, and spawning on 1 May.

above (~3,700 tons, Fig. 6). The average fish P increase estimated solely from ICES data is 2,400 tons, with an annual variation between 700 and 3,900 tons.

Discussion

Removal of nutrients by the fishery—The fishery removes a relatively large proportion of the estimated anthropogenic load of, especially, P that reaches the open Baltic Sea (18%). However, the estimation of the nutrient retention in coastal areas used, probably reflects the situation over a relatively short timescale (months–year), and it is uncertain whether these estimates can be extrapolated to longer timescales (years–decades). Nevertheless, the removal of P compared with that of the total load is still substantial (7%) and is actually underestimated, because we have included only the commercial landings of herring, sprat, and cod. Noncommercial catches of these species and catches of other fish species have been estimated to be 10%–15% of the total Baltic fish catch (A. Lindquist, National Board Fisheries, Sweden, pers. comm.). Considerable removal of nutrients with fish landings has been reported from freshwaters (Sarvala et al. 1984), and we now show that this could happen also in marine systems.

Because eutrophication is considered an environmental problem in the Baltic, substantial efforts are made to reduce nutrient discharge. Depending on the type of measures taken, nutrient reduction costs varies between 7 and 9,500 Swedish crowns (SEK) kg^{-1} N and 20–6,700 SEK kg^{-1} P (Gren et al. 1995). The value of the nutrients removed through the fishery (15,000 tons of N and 3,000 tons of P annually) thus corresponds to at least 170 million SEK. Conventional nutrient reduction in a modern Swedish sewage treatment plant (Henriksdalsverket, Stockholm) costs 31 SEK kg^{-1} N (Gren et al. 2000), and the marginal cost for P reduction is 24–41 SEK kg^{-1} (Gren et al. 1995). Applying these costs, the value of the nutrient removal through the fishery totals 550–600 million SEK. For comparison, the total first sale value of landings of herring, sprat, and cod was estimated to 3,000 million SEK (landings in 1999 [ICES 2000b] and average Swedish fish prices, herring 4.07, sprat 0.77, and cod 13.50 SEK kg^{-1} ; L. Melin, National Board of Fisheries, Sweden, pers. comm.). The value of the nutrient removal by the fishery may be even higher, because substantial parts of the anthropogenic nutrient load are biologically unavailable or is retained in coastal areas. To result in the same open sea reduction in nutrients as the fishery removal, load reductions at point sources must thus be larger than the quantities removed by the fishery.

Before concluding that the fishery decreases society costs for nutrient reductions and really counteracts eutrophication, some assumptions have to be fulfilled. One is that the nutrients would have been recycled if the fish were not caught, so that the fishery removal not only replace another nutrient sink (like sedimentation). We have little knowledge about the situation in the “unfished” Baltic Sea, but generally marine systems had larger stocks of predatory fish and higher predation on small pelagics before intensive fishing started (Steele and Schumacher 2000). This suggests that much of the nutrients in fish were recycled to the water in a highly bioavailable form. However, before advocating an intensive fishing as a measure to counteract eutrophication, it must be understood that sustainable and rich catches can only derive from large and well-managed fish populations. In the Baltic Sea today, the cod stock is seriously depleted, herring is at record low biomass, and the fishing for sprat is unusually intensive (ICES 2000a). Another important assumption is that the fishery does not, directly or indirectly, increase the negative effects of eutrophication in other ways (discussed below).

The role of fish in annual phosphorus dynamics—Our results show that the summer build-up of fish biomass sequesters considerable quantities of P. The conservative estimation of increase in fish P, based on fish production from landings and cod consumption data, is smaller but confirms that the results are reasonable. This production estimate is conservative because there are also other causes of herring and sprat mortality than fishing and cod predation. As expected, the estimate based solely on ICES data are also slightly smaller, because young fish are treated differently. This analysis also indicates that there may be a great inter-annual variation in fish P increase.

Although the results seem reasonable, the magnitude of

fish effects on annual P dynamics depends on our assumptions. We may have overestimated the offshore fish biomass by including YOY herring in the estimates. At least some of these fish inhabit the archipelago during summer. On the other hand, we have not included fish like cod and three-spined sticklebacks in the analyses. We cannot make a reliable estimation of the biomass of other fish, and the proportion of YOY herring in the archipelago relative to the open sea is also unknown. Nevertheless, even completely excluding YOY herring from the analysis would only decrease the sequestered P between July and August by, on average, 30%, fluctuating between 8% and 71%.

Regarding other assumptions for YOY fish, we consider egg numbers from SSB to be rather robust, and we did not test alternative values in our sensitivity analysis. Alternative spawning dates did not alter the results much and are thus not crucial to our analysis. The larval period length, however, influenced the results substantially, but the alternative larval period lengths (50 and 90 d) are probably rather extreme (Arrhenius and Hansson 1993). Arrhenius and Hansson (1996) reported the herring larval period in the northern Baltic Proper as ~ 70 d. A sensitive link is the assumption on larval mortality. Variation in the monthly mortality (85%–95%) influenced the dynamics of P in fish considerably. However, for some years, a monthly mortality of 95% produced unrealistic results, with numbers at metamorphosis that were lower than the expected number from the same cohort ~ 5 months later (MSVPA results for 1 January). This indicates that a mortality of 95% is unrealistically high.

Scenarios with different assumptions on the duration of the growth period of YOY fish (Fig. 3f) did not change biomass dynamics substantially (not shown). That reliable growth data are important is, however, shown by the big difference in biomass development between our standard run and runs based on weight data derived from the bioenergetics models (Fig. 6b). Standard growth data from ICES show some unrealistic features (see Materials and Methods section), which probably leads to an underestimation of the biomass increase during summer. The bioenergetics model, on the other hand, shows intra-annual weight fluctuations (Fig. 4b) that are not supported by data and probably overestimate the biomass increase.

The summer decrease in totP in the water column has traditionally been explained by sedimentation. Data from sedimentation traps indicate that the summer sedimentation rates are 1.3–4.3 times higher than the decrease in totP in the upper 15 m (Larsson et al. 2001). As a consequence, there must be a compensatory flux of P to the upper water layer through turbulent mixing and erosion of the thermocline, external sources, or transport by migrating organisms. Because the summer thermocline in the Baltic is located at a depth of 15–20 m in offshore areas (Kullenberg 1981), we have internalized the fluxes across and occasional erosion of the thermocline by including the upper 40 m in the analysis. Furthermore, the upper 40 m is where all phytoplankton production takes place and where the highest summer zooplankton densities are found (Dahmen 1997) and hence is also where most of the net production of fish biomass occurs.

Freshwater studies have shown that large quantities of P can be built into fish biomass during summer (Bartell and

Kitchell 1978; Schindler et al. 1993), and we show that this might happen also in marine systems. One consequence of this is that fish, by sequestering phosphorus from the water column, may compete with phytoplankton both in P-limited freshwater systems (Bartell and Kitchell 1978; Kraft 1992) and in the Baltic Sea. During summer, phosphorus-limited cyanobacteria are important primary producers in the Baltic Sea (Larsson et al. 2001). The occurrence and intensity of cyanobacterial blooms (including toxic species) vary considerably between years and areas, and our understanding of the controlling factors is limited (Paerl 1996). Our results suggest that variation in fish stock sizes may influence the nutrient conditions for cyanobacteria (e.g., the termination of blooms). As a consequence, the fishery may, by changing stock sizes, influence the production and blooms of cyanobacteria. The overall picture is, however, complicated by the possibility that fish can also influence phytoplankton and nutrient dynamics through nutrient transport with migrating fish and by changing the behavior or structure of the gazer community, which results in changed nutrient transport and recycling. However, it is not the objective of this article to reveal the overall effect of fisheries or the entire role of fish on nutrient dynamics in the Baltic Sea.

Our results suggest that the fishery counteract eutrophication, particularly in the open Baltic Sea, by removing considerable amounts of nutrients through fish landings. However, other effects of fishing may counterbalance this positive effect. For example, we show that fish sequester considerable amounts of P during summer and might compete with algae, in particular nitrogen-fixing cyanobacteria, for P. Our main conclusion is that fish and fisheries, as in freshwater, can influence the nutrient dynamics in marine systems, and this should be considered in both fisheries and eutrophication management.

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