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Food consumption by clupeids in the Central Baltic: evidence for top-down control?

Christian Möllmann and Friedrich W. Köster



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Considerable changes have taken place in the pelagic ecosystem of the Central Baltic Sea during the last decade. Owing to a combination of high fishing pressure and unfavourable hydrographic conditions, the cod (*Gadus morhua*) stock as the top predator in the system was reduced from a high level in the early 1980s to its lowest size on record in the early 1990s. The preferred prey species sprat (*Sprattus sprattus*) showed a significant increase in population size since the late 1980s to the highest level on record in recent years, while the herring (*Clupea harengus*), another important planktivore in the system, did not show such a response. We investigate whether fluctuations in clupeid stock size cascade down to the trophic level of mesozooplankton, based on stomach content data and daily ration estimates in combination with stock sizes estimated from Multispecies Virtual Population Analysis. Estimates of daily consumption by the populations of the two species for 1978–1990 were compared with standing stocks of mesozooplankton species. No evidence was found for food limitation as might be expected if clupeids exert a strong top-down control on mesozooplankton. Also no influence on interannual variability of mesozooplankton abundance was detected. However, predation did contribute to the seasonal development of two copepod species (*Pseudocalanus elongatus* and *Temora longicornis*).

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Key words: Central Baltic Sea, consumption, food limitation, herring, mesozooplankton abundance, sprat, top-down control.

C. Möllmann and F. W. Köster: Institute of Marine Sciences, Düsternbrooker Weg 20, 24105 Kiel, Germany [tel: (+49) 431 5973925; fax: (+49) 431 565876; e-mail: cmoellmann@ifm.uni-kiel.de, fkoester@ifm.uni-kiel.de]

Introduction

The trophic cascade hypothesis, derived from experimental studies in lakes, considers that the potential productivity of an aquatic ecosystem is dependent on nutrient input (Carpenter *et al.*, 1985). Deviations of the actual from the potential productivity are caused by variability in predator-prey interactions and their influence on community structure (Carpenter and Kitchell, 1987). Alterations at the top of the food web cascade through the lower trophic levels (top-down control; Kitchell and Carpenter, 1993). The major process involved is the concept of selective predation by consumers on prey types and sizes, which shapes the structure of each lower trophic level (Kitchell and Carpenter, 1993). Piscivores control size and species composition of the planktivorous fish populations, which in turn influence in concert with invertebrate predators the herbivorous zooplankton community. The zooplankton

finally determines the amount and structure of the phytoplankton competing for nutrients. Size-selective predation by abundant planktivorous fish is expected to result in a shift in dominance towards smaller individuals in the zooplankton community. In contrast, piscivore-dominated systems are associated with low abundance of planktivorous fish and the zooplankton size distribution shifts towards larger organisms (Brooks and Dodson, 1965; Hall *et al.*, 1976).

An example of a trophic cascade in marine pelagic systems has recently been described for the sub-arctic Pacific (Shiomoto *et al.*, 1997), where alterations in pink salmon abundance have resulted in decreasing zooplankton and increasing phytoplankton populations. For the pelagic ecosystem of the Central Baltic Sea, with cod as major piscivore and herring and sprat as abundant planktivores, two control processes, cod predation on clupeids (Sparholt, 1994) and clupeid predation on cod eggs (Köster and Schnack, 1994) have been

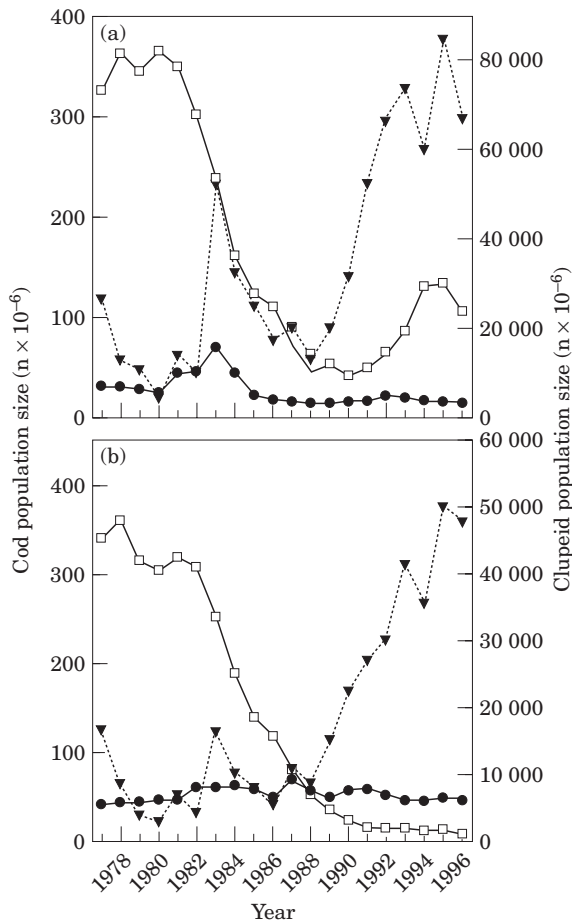


Figure 1. Cod, herring, and sprat population sizes [age 1+; 15th of July] in ICES Subdivisions (a) 26 and (b) 28 according to an area-disaggregated MSVPA, 1977–1996.

identified in the upper trophic levels, which may result in either a cod-dominated or a clupeid-dominated system (Fig. 1). Owing to a combination of high fishing pressure and climate-induced variations in the physical environment (Bagge *et al.*, 1994), the cod stock was reduced from a high level in the early 1980s to its lowest stock size on record in the early 1990s. The preferred prey species, sprat, had shown a significant increase in population size since the late 1980s to the highest level on record in recent years due to a combination of reduced predation mortality and high reproductive success (ICES, 1997a). Thus, the open-sea system of the Central Baltic exhibits a pronounced change from a cod- to a sprat-dominated system. The herring stock has not shown a similar response and has been fairly stable in numbers, although biomass has declined as a result of a substantial reduction in weight at age and condition (e.g. Parmanne *et al.*, 1994).

Rudstam *et al.* (1994) provided several indications for a cascading effect of planktivorous fish on zooplankton

in the Baltic: (i) selective predation on zooplankton species, (ii) a more pronounced vertical migration of selected copepods, possibly to avoid spatial overlap with predators, (iii) consumption of up to 70% of the annual zooplankton production by the predators, and (iv) effects of clupeid predation during late summer on the seasonal succession of zooplankton. However, no evidence was found for a correlation between zooplankton abundance and clupeid biomass in different years (Rudstam *et al.*, 1994).

Investigations on mesozooplankton abundance and species composition in the Central Baltic Sea have revealed a shift from larger to smaller copepods and cladocerans in the Baltic Proper (HELCOM, 1996) and in the Gulf of Finland (Flinkman *et al.*, 1998). These changes have so far not been related to top-down control effects, but to decreased salinity caused by lack of inflows of saline water from the North Sea (Matthäus and Franck, 1992) and exceptionally high rain fall (Bergström and Carlsson, 1994).

We investigate the potential contribution of clupeid predation to the observed changes in the mesozooplankton community by addressing indications for food limitations of herring and sprat that might be caused by strong predation pressure, and seasonal and interannual effects of clupeid consumption on mesozooplankton development.

Material and methods

Diet

Stomach content weights and diet composition were derived from an international database (TemaNord, 1994). Data from 9314 herring and 13 350 sprat stomachs collected during 1978–1990 have been included in the analysis. Arithmetic mean weights of stomach contents of all stomachs sampled by month were derived for ICES Subdivisions 26 and 28 separately (Fig. 2). This simple procedure could be applied because samples were representative of the catches by station and variations in length distribution between stations were low. However, since 1983/1984 only arithmetic means by length-group by station are available. Consequently, average stomach contents had to be computed by averaging group means.

The available information includes a detailed diet composition, including developmental stages of copepods. However, we grouped the information in six classes: *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia* spp. (*A. bifilosa*, *A. longiremis*, and *A. tonsa*), other copepods (*Eurytemora hirundo*, *Centropages hamatus*, and *Limnocalanus grimaldii*), cladocerans (*Evadne nordmannii*, *Podon* spp., and *Bosmina coregoni maritima*), and macrozooplankton (species belonging to Mysidacea, Amphipoda, Cumacea, Isopoda, Decapoda,

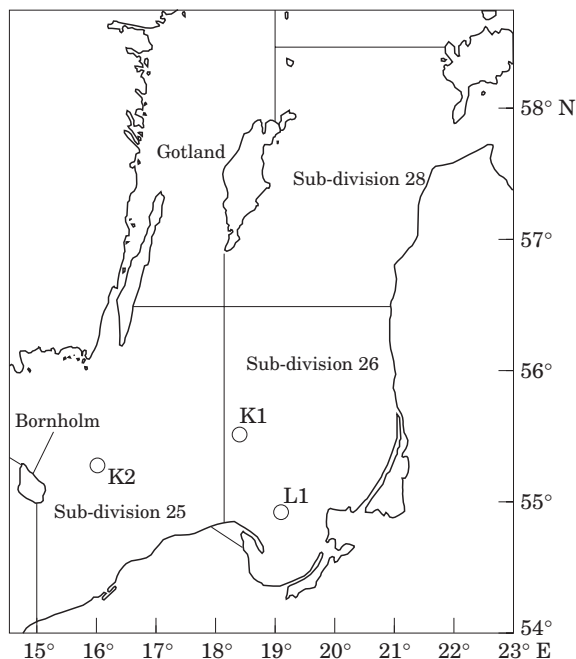


Figure 2. The Central Baltic Sea with ICES Subdivisions and HELCOM stations K1, K2, and L1 indicated.

and Polychaeta). If only prey numbers were available, a conversion to wet weight was made using a set of individual standard weights for each food organism (Hernroth, 1985).

Daily ration

To estimate the daily food intake by individual herring and sprat, an exponential form of the general gastric evacuation model (Jones, 1974) was applied, which incorporates ambient temperature as a variable (Temming, 1996):

$$S_t = S_0 \cdot \exp(-R' \cdot t \cdot \exp(A \cdot C)),$$

where S is stomach content (g), R' a food type constant, A a temperature coefficient, C the ambient temperature ($^{\circ}\text{C}$), and t the time interval. The exponential simplification appears reasonable because the coefficient B of the general evacuation model was close to 1 for both species (Köster and Schnack, 1994; Temming, 1996). The data sets for fitting the function were derived during 24-h fisheries and deck tank experiments (Köster, 1994) performed in the Bornholm Basin. A detailed description of data sets and estimation procedures are given for herring by Temming (1996) and for sprat by Anon. (1998). Following Pennington (1985), daily rations (F_T) were estimated as:

$$F_T = R' \cdot S \cdot T \cdot \exp(A \cdot C) + S_t - S_0,$$

where T is duration of the feeding period, S_t the average stomach content at the end and S_0 the average stomach content at the beginning of the feeding period.

Values of R' (herring: 0.084; sprat: 0.108) and A (herring: 0.129; sprat: 0.073) were derived from Temming (1996) and Anon. (1998), respectively. Average ambient temperatures per month and year were derived by 20-m depth layers (0–20 m, . . . , ≥ 100 m) from the ICES hydrographic database. Assuming an even distribution of fish within an area, weighted averages for the entire water column were calculated using the area of each depth stratum as weighting factor. Values of the average stomach content at the end and beginning of the feeding period (S_t and S_0) were estimated according to Köster (1994).

To describe the seasonal development of clupeid food consumption, daily rations were calculated based on monthly averages of the stomach content, 1978–1990 (Table 1). Interannual variations were investigated using daily rations in July (Table 2), because this was the month best covered by data and falls within the period when consumption is highest. To study the relation with interannual changes in growth, July daily rations were expressed per unit of body weight.

Clupeid populations

Population sizes of herring and sprat were derived by Multispecies Virtual Population Analysis using the model set up by ICES (1999), but adapted to apply to Subdivisions 26 and 28 separately (Fig. 2). Quarterly international catch- and weight at age of the three species were extracted for each Subdivision (ICES, 1997b). The international cod stomach content database, recompiled for single Subdivisions, and corresponding new quarterly consumption rates were incorporated using the model suggested by Temming (1996). The MSVPA was tuned by an Extended Survivor Analysis (XSA) as suggested in ICES (1997a). Detailed information is given in ICES (1999). Clupeid stock numbers (age-group 1+) on July 15 were calculated by applying equivalent proportions of the fishing and natural mortality rates within the third quarter to the abundance values obtained at the beginning of quarter 3.

Daily population consumption rates for July were estimated by multiplying daily rations per fish by population numbers (Table 2).

Mesozooplankton

Data were extracted from three different sources:

- (1) Monthly abundance and biomass values of total mesozooplankton were taken from Wolska-Pys and Ciszewska (1991). The abundances were

Table 1. Number of years (n) and of stomachs sampled (N), average stomach content (S; g ww*) 1978–1990, with standard error (s.e.), average ambient temperature (T; °C), and daily ration (R; g ww) by month (M).

M	n	N	S	s.e.	T	R
a. Sprat in Subdivision 26						
1	5	815	0.012	0.006	3.60	0.027
2	4	301	0.012	0.005	3.54	0.027
3	9	1093	0.023	0.009	3.68	0.050
4	3	173	0.042	0.019	3.75	0.094
5	9	1608	0.029	0.004	4.06	0.066
6	4	373	0.032	0.018	4.38	0.074
7	12	1632	0.038	0.004	5.48	0.093
8	1	60	0.031	—	7.94	0.084
9	9	976	0.043	0.007	5.64	0.105
10	6	471	0.019	0.004	5.99	0.046
11	—	—	—	—	—	—
12	1	55	0.012	—	4.99	0.028
b. Sprat in Subdivision 28						
1	5	303	0.010	0.005	3.08	0.021
2	3	311	0.016	0.004	3.55	0.034
3	6	701	0.007	0.002	3.43	0.014
4	3	259	0.018	0.014	3.07	0.039
5	9	1550	0.032	0.003	3.68	0.071
6	4	350	0.025	0.006	3.88	0.054
7	10	1122	0.036	0.004	5.64	0.086
8	1	46	0.045	—	6.64	0.114
9	8	742	0.044	0.009	5.80	0.107
10	3	345	0.029	0.007	6.18	0.072
11	—	—	—	—	—	—
12	1	64	0.017	—	6.05	0.042
c. Herring in Subdivision 26						
1	3	206	0.036	0.004	4.13	0.072
2	1	333	0.043	—	3.66	0.083
3	5	428	0.097	0.040	3.55	0.184
4	4	336	0.202	0.119	3.82	0.393
5	4	580	0.091	0.022	4.54	0.189
6	4	312	0.094	0.039	4.88	0.201
7	12	1667	0.117	0.027	5.47	0.264
8	—	—	—	—	—	—
9	4	523	0.174	0.083	5.57	0.396
10	5	543	0.040	0.005	6.34	0.098
11	—	—	—	—	—	—
12	—	—	—	—	—	—
d. Herring in Subdivision 28						
1	4	247	0.058	0.031	3.17	0.105
2	2	448	0.114	0.058	3.27	0.209
3	5	347	0.075	0.022	2.88	0.132
4	3	265	0.159	0.041	3.93	0.308
5	6	840	0.064	0.017	4.04	0.126
6	1	25	0.128	—	3.74	0.243
7	12	1357	0.080	0.021	5.68	0.182
8	1	30	0.034	—	6.64	0.084
9	4	270	0.028	0.005	6.05	0.065
10	5	404	0.097	0.023	5.99	0.226
11	1	143	0.023	—	5.97	0.052
12	—	—	—	—	—	—

*ww: wet weight.

averaged over depth layers and years, 1979–1988. Sampling for both parameters took place at HELCOM stations K1 (southern Gotland Basin,

Subdivision 26) and L1 (Gdańsk Deep, Subdivision 26; Fig. 2). To obtain a species-specific resolution of the total biomass, a relative copepod

Table 2. Stomach content (S) with standard error (s.e.), average ambient temperature (T), daily ration (R), daily coefficient (C; ration per unit body weight), population size (N; $\times 10^{-6}$) and daily population consumption (P; tonnes) in July by year (Y), 1978–1990 (for units see also Table 1).

Y	S	s.e.	T	R	C	N	P
a. Sprat in Subdivision 26							
1978	0.023	0.002	5.22	0.076	0.0052	12 736	996
1979	0.066	0.007	4.81	0.210	0.0142	10 753	2261
1980	0.045	0.005	4.33	0.138	0.0083	4678	645
1981	0.045	0.006	6.06	0.151	0.0091	13 812	2090
1982	0.044	0.004	5.76	0.147	0.0111	9684	1426
1983	—	—	5.45	—	—	50 193	—
1984	0.041	0.008	5.56	0.134	0.0130	32 210	4324
1985	0.027	0.003	4.64	0.085	0.0082	24 758	2103
1986	0.042	0.008	4.72	0.132	0.0105	17 479	2306
1987	0.053	0.013	4.88	0.170	0.0156	19 798	3370
1988	0.029	0.005	5.49	0.097	0.0065	12 339	1193
1989	0.039	0.005	6.36	0.135	0.0089	19 955	2690
1990	0.037	0.003	7.94	0.141	0.0115	31 554	4451
b. Sprat in Subdivision 28							
1978	0.017	0.003	5.81	0.056	0.0049	8627	482
1979	0.039	0.003	4.97	0.126	0.0085	4028	507
1980	0.044	0.005	5.21	0.144	0.0085	2981	430
1981	0.021	0.002	5.56	0.071	0.0048	6997	498
1982	—	—	5.39	—	—	4445	—
1983	—	—	6.59	—	—	15 886	—
1984	0.035	0.004	5.94	0.119	0.0105	10 105	1200
1985	0.030	0.007	5.08	0.098	0.0077	8137	797
1986	0.061	0.006	5.29	0.202	0.0138	5363	1082
1987	0.036	0.011	4.84	0.114	0.0096	10 969	1256
1988	0.043	0.003	6.12	0.150	0.0090	8583	1283
1989	0.044	0.011	6.55	0.160	0.0081	15 087	2352
1990	0.050	0.003	6.65	0.178	0.0109	22 344	3987
c. Herring in Subdivision 26							
1978	0.152	0.013	5.22	0.469	0.0078	6812	3194
1979	0.369	0.045	4.81	1.097	0.0124	6470	7097
1980	0.121	0.009	4.33	0.343	0.0041	5481	1877
1981	0.141	0.013	6.06	0.477	0.0055	9519	4542
1982	0.055	0.004	5.76	0.179	0.0022	10 188	1821
1983	0.018	0.004	5.45	0.058	0.0014	14 821	859
1984	—	—	5.56	—	—	10 179	—
1985	0.185	0.022	4.64	0.540	0.0077	4950	2673
1986	0.072	0.004	4.72	0.211	0.0048	4043	852
1987	0.095	0.009	4.88	0.283	0.0040	3672	1040
1988	0.072	0.006	5.49	0.228	0.0030	3211	733
1989	0.063	0.008	6.36	0.218	0.0032	3121	681
1990	0.059	0.007	7.94	0.245	0.0055	3512	862
d. Herring in Subdivision 28							
1978	0.073	0.005	5.81	0.245	0.0056	5784	1417
1979	0.081	0.010	4.97	0.247	0.0052	5824	1437
1980	0.304	0.032	5.21	0.953	0.0154	6197	5905
1981	0.068	0.017	5.56	0.222	0.0064	6109	1357
1982	0.043	0.004	5.39	0.136	0.0026	8037	1091
1983	0.010	0.003	6.59	0.035	0.0007	7921	280
1984	—	—	5.94	—	—	8193	—
1985	0.037	0.005	5.08	0.113	0.0018	7772	880
1986	0.041	0.002	5.29	0.123	0.0039	6465	839
1987	0.086	0.008	4.84	0.258	0.0066	9225	2380
1988	0.068	0.031	6.12	0.236	0.0056	7437	1754
1989	0.056	0.005	6.55	0.202	0.0043	6503	1313
1990	0.082	0.015	6.65	0.299	0.0078	7532	2251

species composition (Dahmen, 1997) derived on HELCOM station K2 (Bornholm Basin, Subdivision 25) (Fig. 2) in 1988–1992 was applied.

- (2) Abundance values (1979–1990) of *P. elongatus* (summer/Gdańsk Deep; April–May/southern Gotland Basin; June–September/Subdivision 28), *T. longicornis*, and *Acartia* spp. (both summer/Gdańsk Deep) were taken from HELCOM (1996);
- (3) Abundance values (1978–1990) of *P. elongatus* (August and October/Subdivision 28) were extracted from Naglis and Sidrevics (1993) as modified by TemaNord (1994).

Data from source (1) were used to investigate the influence of clupeid consumption on the seasonal succession of mesozooplankton, whereas data from (2) and (3) were used to check the influence of predation on inter-annual development of the main mesozooplankton populations.

Results

Seasonal variability

Daily rations for sprat showed highest values from April to September (Table 1a, b), with maxima in September and August in Subdivisions 26 and 28, respectively, and without consistent differences between the two areas. For herring (Table 1c, d), daily rations were also highest in April and September in Subdivision 26, and in April, June, and October in Subdivision 28. However, the pattern over the year deviated in the latter with lowest values during August, September, and November, and relatively high values during the winter months.

The most important food items for sprat (Fig. 3a and b) were *P. elongatus* and *T. longicornis* with relative contributions up to 90% of the diet. The seasonal pattern is similar for the two areas, with *P. elongatus* showing an increase at the beginning of the year to maximum values in April, while *T. longicornis* declined concurrently to minimum values. During summer, *P. elongatus* was largely replaced by *T. longicornis*, while in autumn the share of the latter species decreased again. From May to October, *Acartia* spp. and cladocerans contributed significantly to the diet of sprat. The relative contribution of other copepods and macrozooplankton was insignificant (maximum 1%).

Also for herring *P. elongatus* and *T. longicornis* were the most important food organisms (Fig. 3c and d). However, the latter were of less importance compared to sprat. The seasonal patterns were largely similar to sprat, although the large contribution of *P. elongatus* extended up to later in the season. In September/October the importance of both food items decreased. During the first months of the year, macrozooplankton contributed significantly to the diet, but this prey declined gradually

towards summer. Only in Subdivision 28, did the proportion of macrozooplankton increase again during late summer. *Acartia* spp. was observed in herring stomachs mostly in spring and early summer, but their contribution remained relatively low compared to sprat. The contribution of other copepods, too, was low and comparable to sprat during most of the year, with one exception in February. Cladocerans were observed only from early summer to autumn, with values mostly below 10%. In June and September/October, outstanding values were found for Subdivisions 28 and 26, respectively.

Interannual variability

Maximum individual daily rations per body weight in July for sprat were calculated for 1987 and 1986 in Subdivisions 26 and 28, respectively, and rations were lowest in 1978 and 1981 (Table 2a, b). No clear trends with time were obvious. In contrast, rations for herring did show a time trajectory (Table 2c, d). Relatively high rations were obtained at the beginning of the time series, with outstanding values in 1979 and 1980 for Subdivisions 26 and 28, respectively, followed by a decline to very low values in 1983 in both areas. At the end of the period, daily rations were stable at an intermediate level.

The estimated daily consumption by sprat in July in both areas varied considerably from year to year, but increased in both areas. They were consistently higher in Subdivision 26 than in Subdivision 28, reflecting the difference in population size (Table 2a, b).

The development in daily consumption by the herring population reflects the variations in daily rations (Table 2c, d). Consumption diminished until 1983 in both areas, even though population size increased. Recent years were characterized by fairly constant values. Consumption by herring was higher in Subdivision 26 during the first part of the time series, whereas values were higher for Subdivision 28 from 1987 onwards.

T. longicornis was in general the most important food organism for sprat in July (Fig. 4a and b) with a maximum contribution of 96% in 1979 in Subdivision 26 and a minimum of 4% in 1986 in both areas. In 1978 and again in the mid-1980s, *Acartia* spp. was very important. *P. elongatus* and other copepods were preyed upon in high quantities sporadically, whereas cladocerans contributed more consistently to the diet (generally 5–25%).

P. elongatus and *T. longicornis* formed the main part of the herring diet in July (Fig. 4c and d). The early years were characterized by a clear prevalence of *P. elongatus* (up to 97%). *T. longicornis* took over rapidly. A similar event occurred in 1990.

With the exception of a high contribution of macrozooplankton in 1985, the contribution of the other prey

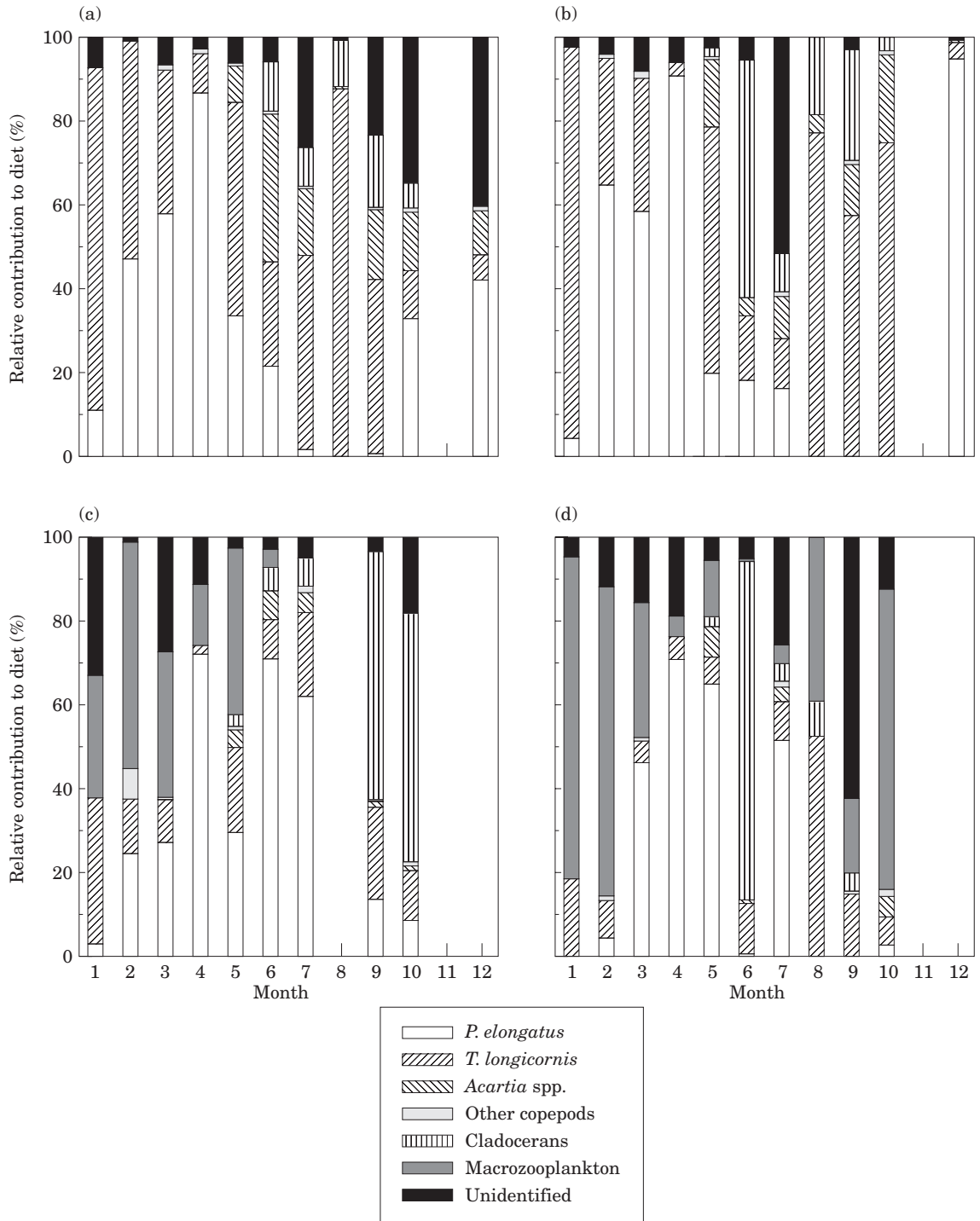


Figure 3. Average seasonal development of diet composition of clupeids. a. Sprat in Subdivision 26; b. sprat in Subdivision 28; c. herring in Subdivision 26; d. herring in Subdivision 28.

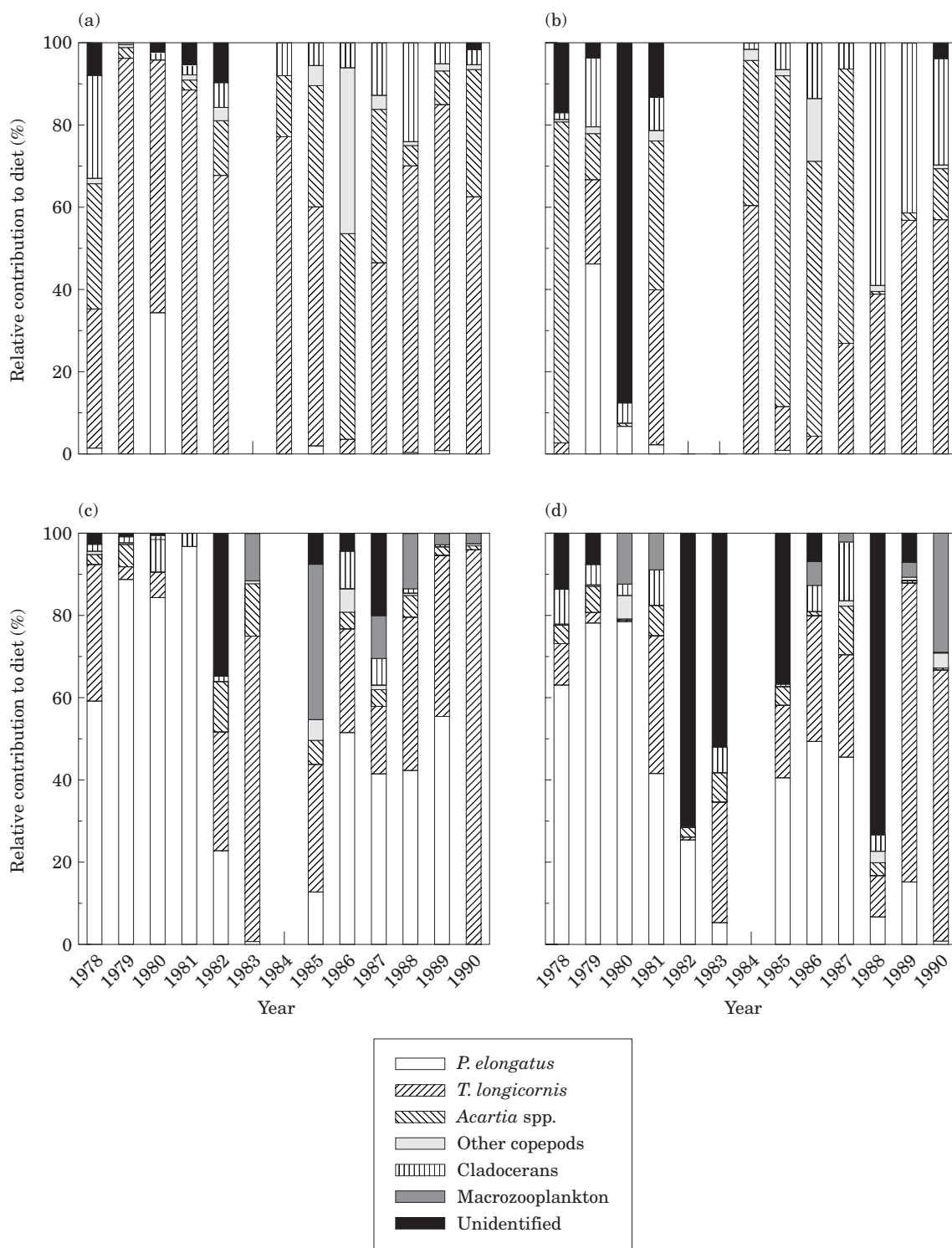


Figure 4. Interannual development of diet composition of clupeids in July. a. Sprat in Subdivision 26; b. sprat in Subdivision 28; c. herring in Subdivision 26; d. herring in Subdivision 28.

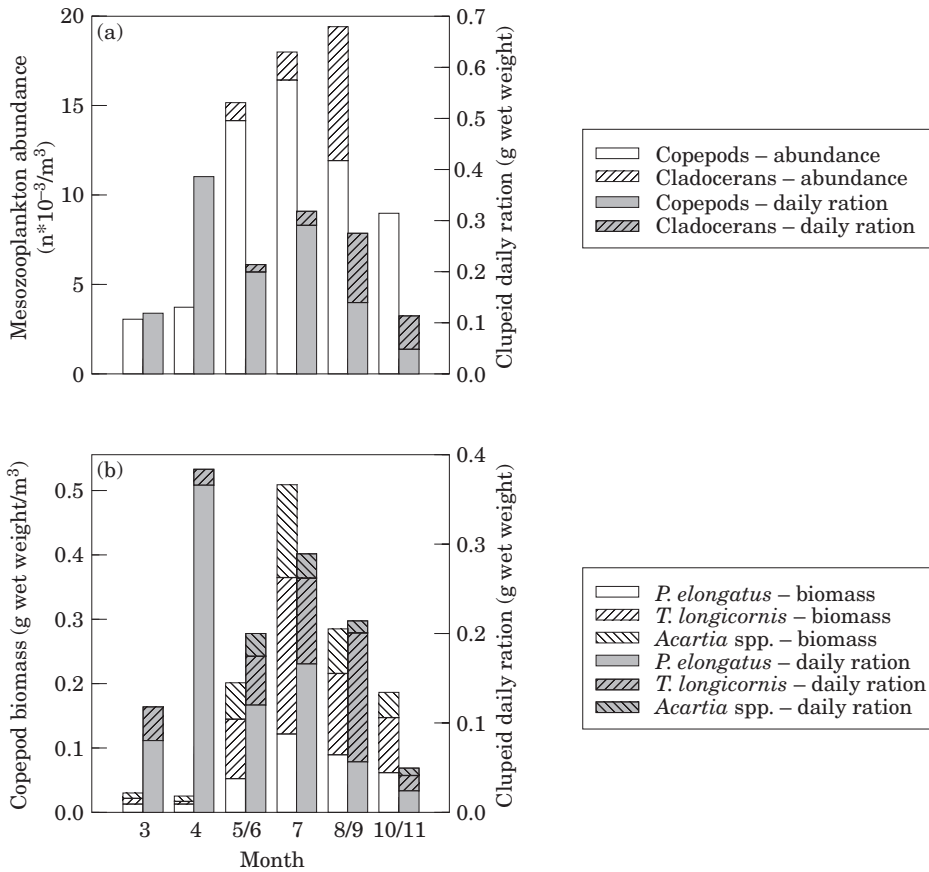


Figure 5. Comparison of summed daily rations of herring and sprat in Subdivision 26 and standing stock by prey species (group). a. Copepods and cladocerans; standing stock: abundance in the southern Central Baltic Sea; b. copepod species *P. elongatus*, *T. longicornis*, and *Acartia* spp.; standing stock: biomass in Subdivision 26.

types remained generally below 10%, but the variations between years were large.

Mesozooplankton abundance and consumption

The abundance of copepods and cladocerans in Subdivision 26 shows a typical seasonal cycle with low values in spring and a maximum in late summer/early autumn (Fig. 5a). The maximum for the copepods was found in July, while cladocerans were most abundant in August/September. Daily rations of sprat and herring combined largely followed the abundance pattern with high predation pressure on copepods in July and on cladocerans in August/September, but copepod consumption peaked already in April. Predation in spring was directed mainly on *P. elongatus*, even though the biomass was low (Fig. 5b). Biomass of the three most important copepod species increased until July, while daily rations were reduced, though still considerable. Highest predation pressure on *T. longicornis* was observed in August/September, while abundance of this species peaked already in July.

Comparing the shares of the three copepod species in the diet with their shares in the plankton (Fig. 6) revealed that the high contributions of *P. elongatus* to the diet of both predators in spring were associated with a dominance of this species in the plankton. In summer sprat switched to the more abundant *T. longicornis*, whereas herring still fed mainly on *P. elongatus*. In August/September, *T. longicornis* also became more important for herring, while in September/October sprat showed a slight preference again for *P. elongatus*. Throughout the season, predation on *Acartia* spp. by herring was low compared to the fraction in the plankton, but for sprat diet contribution and plankton fraction were comparable from May onwards.

Time series of abundance of *P. elongatus*, *T. longicornis*, and *Acartia* spp. from the two Subdivisions at different times of the year are compared to the corresponding daily population consumption estimates for July in Figures 7–9. All abundance time series of *P. elongatus* show a high variability, but also a downward long-term trend (Fig. 7). Consumption estimates of sprat are negligible compared to herring, but the latter

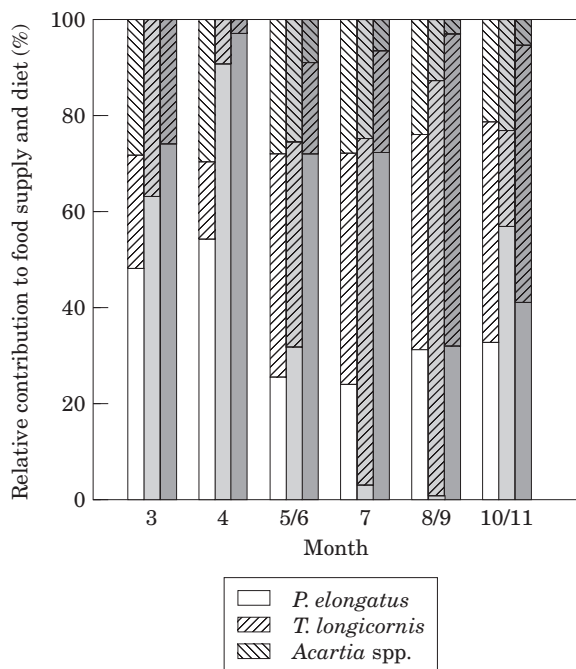


Figure 6. Comparison of relative contributions of *P. elongatus*, *T. longicornis*, and *Acartia* spp. to the diet of sprat (light grey bars) and herring (dark grey bars) in Subdivision 26 and to the available biomass (white bars) in the southern Central Baltic

indicate a period of high predation pressure in the late 1970s and early 1980s. From 1982 onwards, consumption was generally low, with the exception of 1987 in Subdivision 28.

The data set of *T. longicornis* (Fig. 8), too, indicates highly variable abundance values, with on average higher values after the mid-1980s. Daily population consumption of herring and sprat were also highly variable, but they suggest an increase in predation pressure in recent years.

In contrast, consumption of *Acartia* spp. by sprat increased clearly throughout most of the 1980s, with the exception of 1988/1989 (Fig. 9). The abundance of *Acartia* spp. in the Gdańsk Deep increased too, but the exceptionally high value in 1984 disturbs the general upward trend.

Discussion

The general food composition of sprat and herring in both Subdivisions concurs with earlier findings. *P. elongatus* in late winter/spring, *Acartia* spp., and especially *T. longicornis* in summer and autumn, and to a lesser extent cladocerans in late summer/early autumn, are known to constitute important parts of the diet (e.g. Hinrichs, 1985; Patokina, 1996). A decreasing importance of *P. elongatus* and an increasing importance of

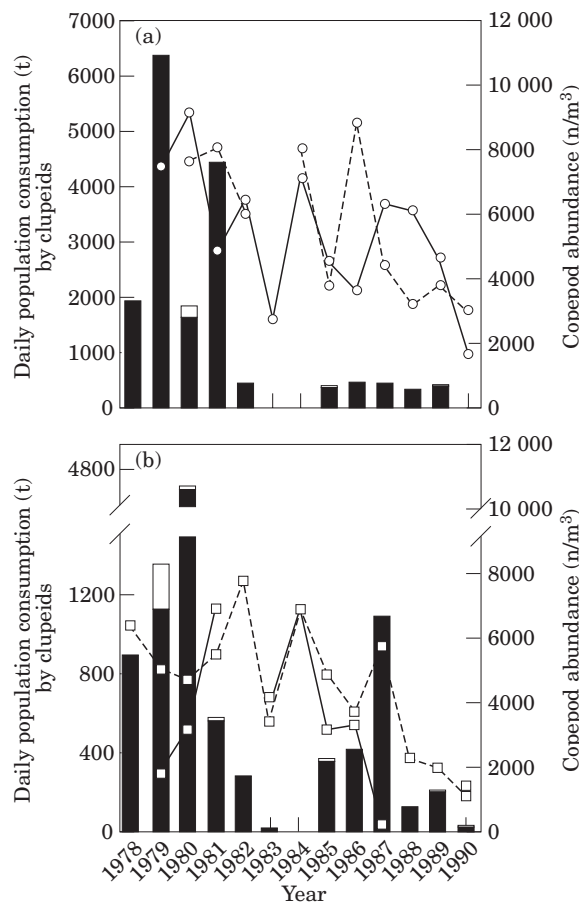


Figure 7. Daily population consumption of *P. elongatus* by sprat (white bars) and herring (black bars) in July in comparison with data on abundance, 1978–1990. a. Subdivision 26; abundance in summer in the Gdańsk Deep (solid line) and in April–May in the southern Gotland Basin (dotted line); b. Subdivision 28; abundance in June–September (solid line) and August–October (dotted line).

T. longicornis in the late 1980s and early 1990s have also been described for sprat in Subdivisions 26 and 28 by Starodub *et al.* (1992) and Davidyuka (1996) and for herring by Fetter and Davidyuk (1993).

The estimated daily rations during summer (0.5–1.6% body weight d^{-1} for sprat and 0.1–1.5% for herring) are lower than former estimates (2.5–4.2% and 1.1–1.7%, respectively), which were derived by applying a simple linear evacuation model coupled to a Bajkov (1935) approach (Zalachowski *et al.*, 1976; Szypluła, 1985). Our estimates for the winter/spring season (0.2–0.8% for sprat and 0.1–0.5% for herring) fall within the range (0.1–0.8% and 0.1–1.7%) given by these authors for the two species, respectively. For herring, average daily rations of 1.1% body weight d^{-1} have been estimated by Fetter and Davidyuka (1996) on the basis of a series of 24-h fisheries conducted in Subdivisions 26 and 28

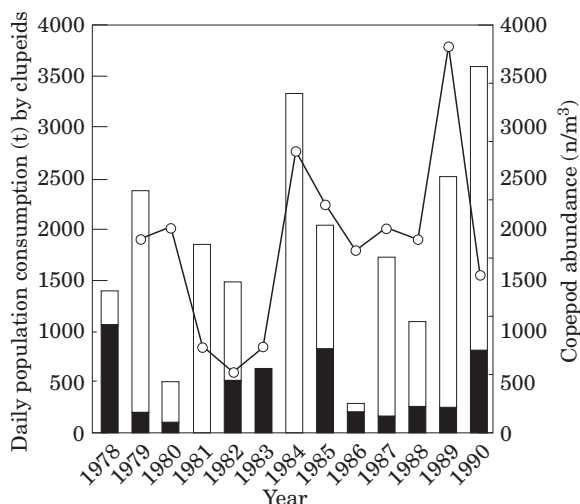


Figure 8. Daily population consumption of *T. longicornis* by sprat (white bars) and herring (black bars) in July in Subdivision 26 in comparison with data on abundance in summer in the Gdańsk Deep, 1978–1990.

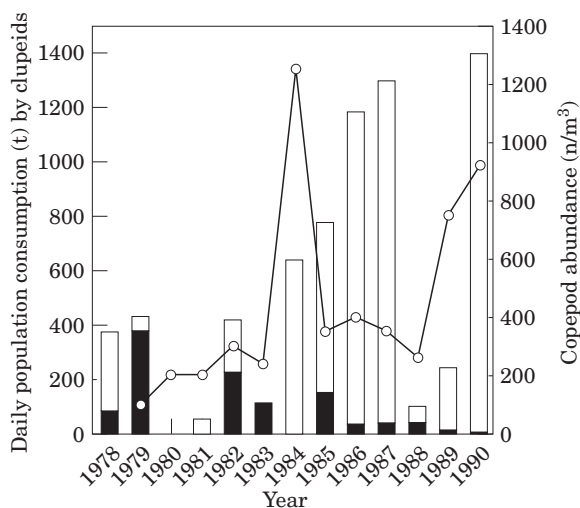


Figure 9. Daily population consumption of *Acartia* spp. by sprat (white bars) and herring (black bars) in July in Subdivision 26 in comparison with data on abundance in summer in the Gdańsk Deep, 1978–1990.

during the summers of 1978–1987. Patokina (1996), using a similar approach, estimated higher daily rations (1.5–2.9% and 1.3–5.4% for sprat and herring, respectively). Estimates of yearly averages derived from bioenergetics are, in general, also considerably higher. Values of 3.4–3.5% have been reported for sprat in the Northern Baltic by Lankov (1988); for herring in Swedish coastal waters 1.2–1.9% by Aneer (1980) and 3.3–4.7% by Rudstam (1988); and for herring in the Eastern Baltic 2.6–2.8% of body weight d^{-1} by

Chekunova (1979). Thus, our consumption estimates are obviously conservative compared to former estimates. Nevertheless, the evacuation model used is thought to be a considerable improvement compared to earlier approaches (Temming, 1996; Köster and Schnack, 1994).

The area-disaggregated MSVPA is a first attempt to quantify population sizes of sprat and herring within single Subdivisions. One objection may be that migration between areas has not been accounted for and tests to validate the results are still in progress. Because the tuning procedure caused problems for sprat in Subdivision 26, the estimated population sizes of this species for recent years are uncertain. However, this problem does not affect the estimates up to 1990 utilized here.

The mesozooplankton data were mainly derived from sampling within the framework of the Baltic Monitoring Programme (HELCOM, 1996). With the exception of the data from Naglis and Sidrevics (1993), sampling was performed on single stations only. Thus, mesoscale variability in zooplankton abundance in relation to hydrographic features was not reflected in the samples. Moreover, the samples were collected by a vertically integrating gear. As predators as well as their prey perform daily vertical migrations and may exhibit specific vertical distributions at the time of sampling, the data may not resemble the actual food environment of clupeids.

Food selection studies as conducted by Flinkman *et al.* (1992) for herring and by Cuesta-Linker (1997) for sprat have demonstrated selection for larger sizes of zooplankton (adult calanoid copepods, especially females with egg sacs and cladocerans with embryos). Also, in the material presented here, a clear dominance of late juvenile stages and adult copepods in the diet of both clupeid species has been described (Möllmann, 1996). Therefore, a comparison between diet and plankton in the sea, which does not take into account developmental stages is of limited validity. Nevertheless, these shortcomings would not be expected to change the general seasonal and interannual trends in mesozooplankton standing stocks.

For a sound evaluation of the impact of clupeids on their prey populations, production rates of mesozooplankton populations by season and Subdivision would be required. However, only limited data are available for the open sea areas of the Central Baltic Sea. Ackefors and Lindahl (1979) report a daily production value of $60 \text{ mg C m}^{-2} \text{ d}^{-1}$ for July 1976 at one station east of Gotland. Applying this value to Subdivisions 26 and 28 results in a mesozooplankton production of $10.8 \cdot 10^3$ and $5.7 \cdot 10^3 \text{ t d}^{-1}$, respectively. The estimated average consumption by the two clupeid populations in July (1978–1990) of $4.5 \cdot 10^3$ and $3.2 \cdot 10^3 \text{ t d}^{-1}$ in Subdivisions 26 and 28, respectively, would correspond to an average predation pressure of 41 and 57% of the

production. This rough comparison indicates that a large fraction of mesozooplankton production is removed through clupeid predation and thus supports the hypothesis of a potential top-down control (Rudstam *et al.*, 1994).

If clupeids exert a strong top-down control on the mesozooplankton, this would be expected to result in food limitation, and consequently in a reduction of daily rations with increasing population sizes. However, for neither sprat nor herring was the correlation between daily ration and population size significant. Although the daily rations of herring in both areas in July were relatively low in 1982 and 1983 (Table 2), when stock sizes were relatively high, the evidence that food limitation occurs is not convincing. The average daily rations (April to August, 1978–1990; Table 1) in Subdivisions 26 and 28 were considerably (a factor of 4 for sprat and 5–8 for herring) lower than comparable estimates from the Bornholm Basin (Subdivision 25; 1988–1996; Köster and Möllmann, 2000) after adjustment for differences in body size. Abundance of copepods in Subdivision 25 was only slightly higher than in Subdivisions 26 and 28 (HELCOM, 1996). Thus, these differences are difficult to explain in terms of food limitation.

Investigations on the food consumption by planktivores in a coastal area of the Baltic have revealed a simultaneous increase in planktivory and decrease in zooplankton biomass in late summer (Rudstam *et al.*, 1992). Rudstam *et al.* (1994) inferred that planktivory by clupeids contributes to the decline in zooplankton in late summer, thus acting as a seasonal top-down force. Such a seasonal signal would seem to find support in our data, which show high daily rations of clupeids in late summer/early autumn (Table 1). However, daily rations of the two species combined followed the seasonal development of mesozooplankton standing stocks (Fig. 5a) and thus the influence of predation on zooplankton abundance is not obvious. In contrast with earlier studies, high daily rations were already observed in spring, when mesozooplankton biomass was still low (Fig. 5b), suggesting a substantial influence of herring and sprat on their prey populations at this time of year. However, a large part of the herring population stays on the coastal spawning grounds in spring (Aro, 1989) and does not contribute to predation in open sea areas. A rough calculation of the daily consumption by the herring and sprat populations in April, based on average daily rations and on estimated fractions of the populations remaining in open sea areas (Möllmann, 1996), indicated rates between $0.6\text{--}5.2 \cdot 10^3$ and $0.3\text{--}1.1 \cdot 10^3 \text{ t d}^{-1}$ in Subdivisions 26 and 28, respectively. Compared to a production of $0.7\text{--}1.3 \cdot 10^3$ and $0.4\text{--}0.7 \cdot 10^3 \text{ t d}^{-1}$, based on a secondary production of $4\text{--}7 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the Gotland Sea in April 1976 (Ackefors and

Lindahl, 1979), predation pressure would still be substantial.

The hypothesis of a major impact of predation by clupeids in April is supported by the data for the three most important copepod species (Fig. 5b). The mesozooplankton community in spring consists largely of *P. elongatus* that have survived the winter (Viitasaalo, 1994). These are apparently subjected to high predation pressure from both species (Fig. 6), which probably affects production rate, because reproductive females are actively selected (Flinkman *et al.*, 1992). During summer, daily rations of herring are reduced but still considerable, which, in combination with the aggregation of the population in the open sea feeding areas (Aro, 1989), may contribute to the decline in the *P. elongatus* population in autumn.

Vertical distributions change during summer (Starodub and Kondratjeva, 1988), when sprat is feeding mainly on *T. longicornis* at lesser depths than herring. When herring also switches to this species in late summer/early autumn (Fig. 6), predation pressure increases and biomass declines before clupeid consumption is reduced (Fig. 5b). This may be taken as an indication that predation contributed to the population decline, an effect that may be intensified by 0-group clupeids, which recruit at this time of year and which were not incorporated in the analysis.

Rudstam *et al.* (1994) could not find a negative correlation between zooplankton abundance and clupeid biomass in the Baltic, neither in coastal nor in open sea areas. They explained this partly by low predation pressure in spring and early summer (Arrhenius and Hansson, 1993), allowing the mesozooplankton populations to build up even in years when high predation pressure was observed in late summer and early autumn. In contrast, our data show high daily rations for both planktivores also in April, which might reduce production rates. However, time-series comparisons of consumption and copepod abundance indicate largely decoupled developments (Figs 7–9). Thus, there is no evidence for a strong top-down control of copepods. Alternatively, species composition and abundance of the mesozooplankton community may be controlled by bottom-up forces, such as the hydrographic environment and food resources. In the Northern Baltic, changes in the mesozooplankton community have been attributed to decreasing salinity (Vuorinen *et al.*, 1998) caused by the absence of significant salt water intrusions from the North Sea (Matthäus and Franck, 1992) and an increase in freshwater run-off (Bergström and Carlsson, 1994).

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