

Dynamics of planktivory in a coastal area of the northern Baltic Sea

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ABSTRACT: We studied the seasonal dynamics of zooplanktivory by the major zooplanktivores (sprat *Sprattus sprattus*, herring *Clupea harengus* and the mysid shrimp *Mysis mixta*) in 3 coastal areas of the northern Baltic Sea proper from the beginning of July through the end of October, 1985. The 3 areas are within 30 km of each other and differ in nutrient loading and primary productivity. Consumption rates were obtained by combining abundance estimates of the planktivores (from Bongo nets, gill nets and acoustics) with diet analysis and bioenergetics models. Both the dominating planktivore groups and total planktivory rates changed over the study period. Sprat and yearling herring were the major zooplanktivores in July and August whereas young-of-year herring and *M. mixta* were more important in September and October. Planktivory rates increased from low levels at the beginning of July to a peak in August coinciding with a late summer decline in crustacean zooplankton biomass. Planktivory rates were lower than estimated zooplankton production rates in July and early August when zooplankton biomass was increasing and similar to or higher than production in the autumn when zooplankton biomass declined. Both clupeids and mysids consistently selected prey in the order cladocerans (*Bosmina longispina maritima* and *Pleopis polyphemoides*) > *Eurytemora affinis hirundoides* copepods > *Acartia* copepods. The selected species represented a smaller proportion of total zooplankton biomass and decreased earlier in the season in the least productive area, indicating a larger and earlier effect of planktivory in that area compared to the most productive area.

INTRODUCTION

It is well established that fish and invertebrate predators affect the species composition and size structure of zooplankton in lakes (Hrbacek et al. 1961, Brooks & Dodson 1965, Dodson 1974). Planktivores may also indirectly affect phytoplankton and primary production (Carpenter et al. 1985). Although such top-down regulation has been given less attention in marine and estuarine environments, several authors have suggested that predation from invertebrates regulates seasonal zooplankton cycles and causes changes in zooplankton species composition (Möller 1979, Lonsdale 1981, Deason & Smayda 1982, Davis 1984, Ohman 1986, Horsted et al. 1988, Roff et al. 1988, Suthers & Frank 1990; but see Kuipers et al. 1990). Fish are generally not considered important zooplankton predators in oceanic and coastal areas (but see Landry 1978, Fulton 1985, Kimmerer & McKinnon 1989, Hansson et al. 1990a). However, fish yield per unit of primary production is higher in coastal areas, including the

Baltic Sea, than in lakes (Nixon 1982), and there is therefore no reason to expect weaker top-down effects of planktivorous fish in coastal marine environments than in freshwater.

In this paper we analyze the dynamics of zooplanktivory by both fish and invertebrates in 3 coastal areas of the northern Baltic proper from the beginning of July through the end of October, 1985. The 3 study areas are all within 30 km of the Askö field station on the east coast of Sweden but differ in nutrient loading, primary production and summer chlorophyll levels. We combined abundance estimates from field samples with diet analyses and bioenergetics models to create an integrated picture of the changes in zooplanktivory over time in the 3 areas. Seasonal patterns of planktivory are then compared with the seasonal development of zooplankton abundance and species composition. Specifically we will address the following questions: (1) Which predators are the dominating planktivores and do they change spatially and seasonally? (2) Are there seasonal changes in planktivory that correlate with seasonal changes in zooplankton abundances? (3) Are differences in zooplankton community structure among the 3 study areas predictable from differences in planktivory?

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METHODS AND MATERIALS

Study area. The differences in nutrient loading between the 3 areas are the result of nutrient discharge from a municipal sewage treatment plant in the inner part of Himmerfjärd Bay (Fig. 1). The 3 areas were the inner basin of this bay (Inner Bay), an outer basin of the same bay (Outer Bay) and a nearby reference area (Askö area) which is not measurably affected by the nutrient discharge. Water circulation in the Bay is driven by winds and freshwater runoff as the Baltic lacks tides (Wilmot et al. 1985). The zooplankton seasonal dynamics has been studied in these areas since 1977 as part of a research project on eutrophication in the Baltic Sea (Elmgren & Larsson 1987). In this project, nutrients (N and P), oxygen, salinity, temperature, chlorophyll *a*, and phytoplankton primary production have been measured (Table 1). The higher nutrient levels in the Bay are associated with 50 to 100 % higher annual primary production than in the Askö area. Estimated annual zooplankton production is also on average about 100 % higher in the Bay, primarily due to higher production of cladocerans (*Bosmina longispina maritima* E. Müller and *Pleopsis polyphemoides* Leuckart) and rotifers. The copepods are dominated by *Eurytemora affinis hirundoides* (Nordquist) in the Bay and by *Acartia* spp. in the Askö area. This shift in species dominance has been observed in all years studied (1977 to 1988). Our previous experience suggests that herring *Clupea harengus* and the mysid shrimp *Mysis mixta* (Liljeborg) are the most important planktivores and that estimates of planktivory are high compared with estimates of zooplankton production (Aneer 1980, Rudstam et al. 1986, Hansson et al. 1990a).

Field sampling and sample processing. Zooplankton larger than 90 µm were sampled during the day at every 5 m depth from surface to bottom with a 1.5 m high closable zooplankton trap (volume 25.8 l), pooled over the whole water column, and preserved in 4 % disodium-tetraborate buffered formaldehyde. Total volume sampled varied between 130 l (Inner Bay, Stn 5) and 205 l (Outer Bay). A similar plankton trap was found to be more efficient than traditional vertical net tows (WP-2 net) for plankton in the Baltic (Kankaala 1984). Samples were taken at 2 wk intervals at Stns 1 (Askö area) and 4 (Inner Bay) with the exception of the middle of August (equipment problem), and monthly at Stns 3 (Outer Bay) and 5 (Inner Bay). At least a quarter of the sample or 400 specimens were counted and identified to species (stage for copepods), and converted to biomass (Table 2).

Mysids and fish larvae were sampled in the water column at night on 5 occasions from July 3 to October 24 in the Outer Bay and the Askö area using oblique Bongo net tows. Bottom depth varied between 28 and

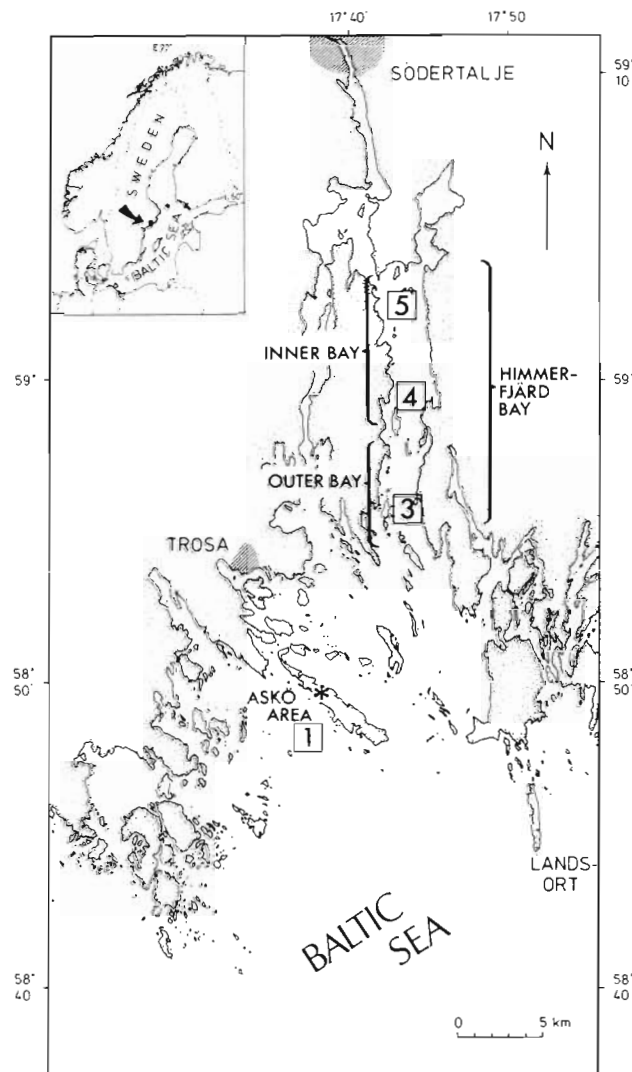


Fig. 1. Study area. Sampling stations for collections of zooplankton and of water for chemical analysis are indicated with a numbered symbol. Station numbers are identical to those used in other publications concerning this area. More detailed maps with acoustic and Bongo net transects can be found in Hansson et al. (1987) and Rudstam et al. (1986)

36 m. Duplicate samples were collected except in early July in both areas and at the beginning of August in the Askö area. Nocturnal sampling was necessary because mysids occur in the water column only at night (Rudstam et al. 1989a). Samples were preserved in 4 % buffered formaldehyde and all animals (excluding copepods and cladocerans) were counted. Total length of up to 20 clupeid larvae and mysid shrimps per sample was measured to the nearest mm and converted to biomass (Table 2). We did not identify clupeid larvae to species.

The pelagic fish populations were sampled in all 3 areas with five 3 m wide and 30 m deep monofilament

Table 1. Relevant environmental and biological data based on samples at ca 2 wk intervals during 1985 (from Larsson 1986, Larsson et al. 1991). The surface layer is the depths 0 to 20 m in the Askö area and 0 to 10 m in the Bay. The bottom layer is the depths from 20 m to the bottom in the Askö area and from 10 m to the bottom in the Bay. Oxygen concentrations at the bottom in 1985 was above 6 mg l⁻¹ in all areas. All years between 1977 and 1988 are included in the long-term averages for chlorophyll and primary production. All years except 1986 are included for zooplankton production for the Askö area and the Inner Bay and the years 1977, 1978, 1985–88 for the Outer Bay. The chlorophyll *a* values represent the average for samples taken between March 1 and November 30. Range of chlorophyll values observed between July 1 and October 30, 1985, are also included

	Askö	Outer Bay	Inner Bay
Water depth (m)	35	40	27
Mean temperature (May–October, °C)			
Surface layer	9.3	11.7	12.0
Bottom layer	5.0	6.0	7.2
Mean salinity (May–October, ‰)			
Surface layer	6.4	6.0	5.7
20–30 m depth	6.8	6.5	6.3
Winter total N (mg m ⁻³)	315	400	475
Winter total P (mg m ⁻³)	30	36	38
Chlorophyll <i>a</i> (mg chl m ⁻²)			
Average 1985	26	46	73
Range 1985	12–45	33–77	33–113
Average 1977–88	37	68	82
Range	28–49	32–78	58–104
Primary production (gC m ⁻² yr ⁻¹)			
1985	126	195	198
Average 1977–87	129	215	206
Range	97–161	165–286	150–278
Zooplankton production (gC m ⁻² yr ⁻¹)			
1985 Jun 15–Nov 15	1.7	8.6	5.0
1985 whole year	2.0	—	7.4
Average 1977–88	6.4	—	11.7
Range	2.0–9.7	—	7.4–16.2

vertical gill nets (Hansson 1988; mesh sizes 16, 24, 30, 33.2, and 37.6 mm stretch mesh). The nets were set at dusk in 28 to 30 m deep water and lifted 5 to 6 h later.

Fish were identified to species, measured and weight calculated from weight-length regressions (Table 2). Fish used for diet analysis were frozen within 1 to 3 h after lifting the nets. Catches were corrected for size selectivity of the nets (Rudstam et al. 1988).

Acoustic data from a 70 kHz single-beam echosounder (Simrad EY/M, half power beam width 11.2°, pulse length 0.6 ms, TVG of 40 log *R*) were recorded on cassette tapes at a ship speed of 1.5 to 2 m s⁻¹ at night when the fish were dispersed in the water column. Recordings were made for ca 40 min in the Askö area and in the Outer Bay and for 80 min in the Inner Bay. The same transects were used on each sampling occasion. Tapes were analyzed using an echo processor (Powell & Stanton 1983) and the deconvolution method (Rudstam et al. 1987). The proportion of fish in a limited number of size groups can be extracted from the echo peak distributions when fish size groups are sufficiently distinct, but this was not possible for all sampling occasions (Rudstam 1988). To be consistent, we used the proportions of different fish species and size groups in gill net catches to calculate abundances of different fish groups from total acoustic abundances. At low fish densities, acoustics and gill nets samples yielded similar size distributions (Rudstam et al. 1988, 1989b). We consider only targets larger than -56 dB (Fish larger than ca 5 cm; Rudstam et al. 1988) due to low signal-to-noise ratios for smaller fish sizes.

Zooplankton production. Species-specific zooplankton daily production was calculated from biomass estimates and temperature-dependent growth equations (Table 2). Egg production from adult females was assumed equal to specific somatic production of Copepodite V (Kiørboe et al. 1985) and adult males were assumed not to contribute to production. We used the mean temperature between surface and bottom for copepods and the mean temperature above the thermocline for copepod nauplii, cladocerans and rotifers (based on previous studies on diel vertical migrations in this area; Hansson et al. 1990a). Production

Table 2. Literature used for calculating biomass, energy density, production (prey) and consumption (predators)

Taxon	Biomass	Production/consumption
Prey		
<i>Eurytemora</i>	Hernroth (1985)	Vuorinen (1982)
Other copepods	Hernroth (1985)	McLaren (1978)
Cladocerans	Hernroth (1985)	Kankaala et al. (1984)
Rotifers	Hernroth (1985)	Pourriot & Deluzarches (1971)
Predators		
Herring and sprat	Rudstam et al. (1989b)	Rudstam (1989a)
Clupeid larvae	Checkley (1984)	Kiørboe & Munk (1986)
<i>Mysis mixta</i>	Rudstam (1989b), Wiktor & Szaniawska (1989)	Rudstam (1989b)

over the whole study period was obtained by linear interpolation between sampling dates (Kimmerer 1987). These production estimates do not account for differences in food availability between our study areas (see 'Discussion').

Diet analysis. Zooplankton parts (mandibles and second antennae) in *Mysis mixta* stomachs were identified and counted under 100 to 160 × magnifications (see Rudstam et al. 1989a). Between 5 to 25 % of the copepod mandibles could not be identified and were assigned to species in the same proportion as those identified. Stomach contents of sprat and 3 size groups of herring (young-of-year [YOY], yearling, and older fish) were first investigated under low magnification and the proportion by volume of major prey groups (zooplankton, mysids, fish, and insects) estimated. Up to 100 individual zooplankton prey per stomach were then identified and counted under an inverted microscope using whole zooplankton, tail ends and head capsules of cladocerans and furca of copepods. Due to taxonomic difficulties, the copepods were grouped as *Eurytemora/Temora* or as other species (primarily *Acartia* spp.).

Proportions of different zooplankton in mysid and fish diets were calculated as the average of the proportions by number (for selectivity calculations) and by weight (for calculations of consumption rates) in individual stomachs (excluding stomachs with less than 5 identified prey items). Numbers were converted to wet weight assuming a weight of 20 µg for copepods, 10 µg for cladocerans, 1 µg for nauplii, 0.2 µg for rotifers and 0.02 µg for tintinnids (from Hernroth 1985).

Consumption rates. Zooplanktivory by clupeid larvae was calculated from maximum growth rates observed in the laboratory and experimentally derived relationships between growth and ingestion for Baltic herring (Kjørboe & Munk 1986). We consider this relationship to represent upper bounds for larval consumption. For older fish and mysids, we used bioenergetics models developed by Rudstam (1989a, 1989b) and the computer program by Hewett & Johnson (1987). These models calculate food consumption from observed growth, occupied temperatures and the energy density of prey and predator. We used monthly weight changes to estimate consumption for young herring, sprat and *Mysis mixta*. Since we could not follow growth of individual age classes of older herring, we used a specific consumption rate for older herring derived from an annual growth period (Rudstam 1989a). For modeling purposes we consider sprat to be a yearling herring. The thermal histories of clupeids and mysids were obtained from the vertical distributions observed in gill nets, acoustics and Bongo nets (Rudstam 1988, Rudstam et al. 1989a). Energy density of the predators were assumed to vary seasonally between 5120 and 5940 J

g⁻¹ wet wt for herring (Aneer 1975) and to increase from 3230 J g⁻¹ wet wt in juvenile mysids to 3720 J g⁻¹ wet wt in adult mysids (Wiktor & Szaniawska 1989). Prey were assumed to have a constant energy density of 2850 J g⁻¹ wet wt (Laurence 1976, Vijverberg & Frank 1976). These models yield consumption rates in wet weight. Individual perturbation of the parameters in the models with ± 10 % of their nominal value resulted in at most a similar change in predicted daily consumption rates.

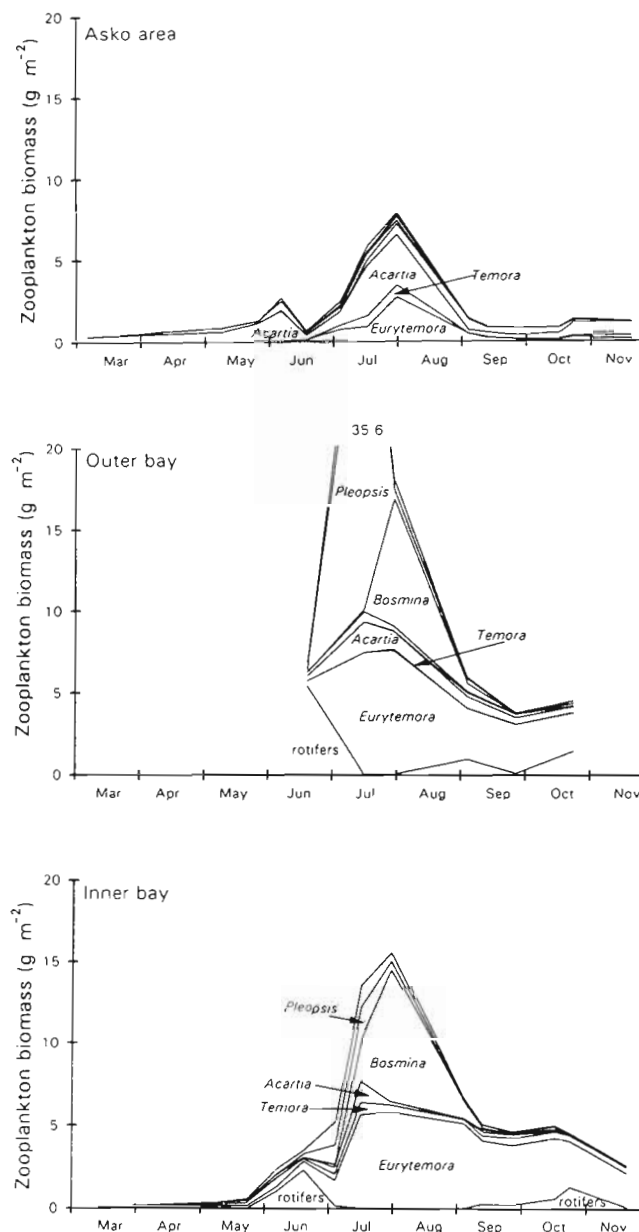


Fig. 2. Seasonal development of zooplankton biomass in 1985 in the Inner Bay (average of Stns 4 & 5), in the Outer Bay (Stn 3) and in the Askö area (Stn 1). Total biomass is divided in the major taxonomic groups discussed in the paper

RESULTS

Distribution and abundance

Zooplankton. The increase in zooplankton biomass during the summer was primarily caused by an increase of the copepods *Eurytemora* and *Acartia* spp. in the Askö area and of *Eurytemora* and cladocerans (*Bosmina longispina maritima* and *Pleopsis polyphemoides*) in the Bay (Fig. 2). Soft-bodied rotifers of the genus *Synchaeta* were common in early spring and late autumn in the Bay. There was a general decline in zooplankton biomass in late summer. The seasonal development and species composition in the different areas were similar to observations from 1977 to 1988 (Johansson 1983, Larsson et al. 1991). Annual production was low in 1985 compared to other years, especially in the Askö area, due primarily to low abundances of cladocerans and rotifers (Table 1).

Macro-invertebrates. Mysids were the dominating group in Bongo net samples. They constituted 58 to 96 % of the catch by number, except in the early July samples when few mysids and comparatively large numbers of clupeid larvae and of the normally benthic amphipod *Pontoporeia* spp. were caught. The dominant mysid was *Mysis mixta* which increased in water column abundances over the summer (Table 3). Small *Neomysis integer* (Leach) (5 to 7 mm) were also common in the Bay in August and September (20 to 60 ind. m⁻²). *M. mixta* produces one generation per year which is released in the spring and growth of the juveniles

can be followed throughout the year (Rudstam & Hansson 1990). Their growth was faster in the Bay than in the Askö area (Table 4; Hansson et al. 1990b).

Table 4. Length (mm) of planktivores in 1985. *Mysis mixta* and clupeid larvae were caught with Bongo nets. Sprat and 3 size classes of herring are from gill net samples corrected for the size selectivity of the nets (see Rudstam et al. 1988)

Date	<i>Mysis mixta</i> juveniles	Clupeid larvae	YOY	Herring Age 1+	Older	Sprat
Askö area (Stn 1)						
Jul 4	8.6	8.2	NA	95	234	95
Aug 1	11.2	15.4	NA	113	188	97
Aug 28	13.6	12.5	82	121	223	106
Sep 24	16.2	NA	89	125	209	98
Oct 23	16.4	12.8	88	NA	202	125
Outer Bay (Stn 3)						
Jul 4	8.3	11.7	NA	85	187	85
Aug 1	12.1	16.5	30 ^a	115	183	96
Aug 28	15.3	17.8	70/37 ^a	128	168	116
Sep 24	17.9	22.1	76/65 ^a	NA	190	111
Oct 23	18.6	19.0	76/67 ^a	135	185	131/60 ^b
Inner Bay (Stn 5)						
Jul 4	NA	NA	NA	88	183	102
Aug 1	NA	NA	NA	117	193	98
Aug 28	NA	NA	66	128	165	107
Sep 24	NA	NA	74	131	174	NA
Oct 23	NA	NA	76	131	181	115

^a From Bongo nets; ^b YOY sprat

Table 3. Seasonal changes in abundance (ind. m⁻²) of *Mysis mixta*, sprat *Sprattus sprattus* and 3 size classes of herring *Clupea harengus* in the 3 study areas in 1985. Abundances are from Bongo net catches (mysids and clupeid larvae at Stns 1 and 3) and from a combination of acoustics and gill net samples for metamorphosed fish (see text). The range of abundances from duplicate Bongo tows are in parenthesis. NA: not available

Date	<i>Mysis mixta</i>		Clupeid larvae		YOY	Herring Age 1+	Older	Sprat
Askö area (Stn 1)								
Jul 4	5		7			0.001	0.046	0.002
Aug 1	28		5			0.051	0.013	0.032
Aug 28	47	(44–51)	0.3	(0.2–0.5)	0.042	0.087	0.016	0.087
Sep 24	65	(44–85)	0.1	(0–0.1)	0.070	0.019	0.013	0.012
Oct 23	76	(66–72)	0.3	(0.2–0.4)	0.032	0	0.071	0.063
Outer Bay (Stn 3)								
Jul 4	2		4			0.002	0.039	0.001
Aug 1	18	(17–18)	9	(9–9)		0.078	0.011	0.093
Aug 28	28	(27–29)	2	(2–2)	0.514	0.176	0.062	0.031
Sep 24	30	(25–34)	0.4	(0.3–0.5)	0.659	0.003	0.020	0.070
Oct 23	16	(12–20)	0.1	(0.1–0.2)	0.779	0.058	0.117	0.020
Inner Bay (Stns 4 & 5)								
Jul 4	NA		NA			0.004	0.073	0.031
Aug 1	NA		NA			0.319	0.076	0.383
Aug 28	NA		NA		1.21	0.136	0.072	0.755
Sep 24	NA		NA		2.00	0.055	0.034	0
Oct 23	NA		NA		1.54	0.117	0.160	0.017

Fish larvae. Clupeid larvae occurred primarily in the July 4, August 1 and August 28 samples and reached abundances of 9 ind. m^{-2} (Table 3). Herring spawn primarily in June in this area, but newly hatched clupeid larvae were found throughout the summer because sprat (which spawn in the open Baltic in the summer) or later-hatched herring recruited to the larval populations (Aneer 1985). Other fish larvae, primarily gobies, always numbered less than 1 ind. m^{-2} .

Fish. Herring (73 %), sprat (24 %), smelt *Osmerus eperlanus* L. (2 %) and roach *Rutilus rutilus* L. (1 %) constituted over 99 % of the fish caught in gill nets. Because of their dominance in gill net catches, we assumed that all acoustic targets were clupeids. Some smaller fish, primarily 2 to 3 cm sand goby *Pomatoschistus minutus* Pallas, were caught in the Bongo nets but these fish are too small to be included in the acoustic density estimates (Rudstam et al. 1988). YOY and juvenile herring can be separated using the length distributions of fish caught in gill nets and these distributions were used to calculate seasonal growth patterns for these age groups (Table 4). Sprat were probably of Age 1 and 2, but some YOY were caught in late October (Table 4). We expected the average length of YOY fish caught in the gill nets to be biased toward larger fish because of the mesh sizes used. Fish caught in gill nets were larger than fish caught in Bongo nets at the end of August, but differences were small in September and October (Table 3).

At both stations in the bay, hydroacoustic fish abundance increased from values around 0.05 fish m^{-2} at the beginning of July to between 0.7 and 1 fish m^{-2} in the Outer Bay and to between 1.5 and 2 fish m^{-2} in the Inner Bay in late August through October, primarily a result of increased abundances of YOY herring. The increase in

the Askö area was smaller, resulting in an order of magnitude higher autumn abundances in the Bay (Table 3). Sprat and yearling herring were common in the 1 August samples. Abundances of older herring varied less with time and among sampling areas.

Diet of major zooplanktivores

***Mysis mixta*.** We found 4 species of calanoid copepods, 2 species of cladocerans, rotifers (*Keratella* sp.) and tintinnids in *M. mixta* stomachs (Table 5). Stomach content of the mysids reflected prey availabil-

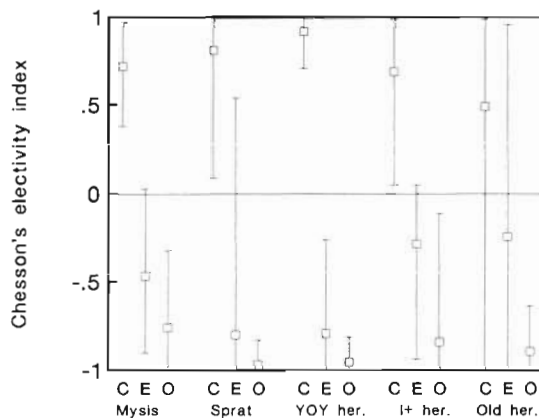


Fig. 3. Electivity indices (Chesson 1983) for the major planktivores between the end of July and the end of October for 3 prey groups: Cladocerans (C), copepodites and adults of *Eurytemora/Temora* (E) and of other copepods (O, primarily *Acartia* spp.). Electivities are based on zooplankton abundances in the whole water column. Symbol represent average values and line the range of values observed. Numbers of occasions included are 8 for *Mysis*, 10 for sprat, 8 for YOY herring, 9 for age I+ herring, and 13 for older herring

Table 5. Proportions by number (in %) of different prey groups identified in stomachs of *Mysis mixta* caught in the water column between 10 and 30 m depth at night in 1985. Length of mysids (mm), number of stomachs analyzed (N), number of empty stomachs (E) and total number of identified prey items are also given. Eur.: *Eurytemora*; Tem.: *Temora*; Aca.: *Acartia*; Pse.: *Pseudocalanus*; Bos.: *Bosmina*; Ple.: *Pleopsis*; Ker.: *Keratella*; Rot.: Rotatoria; Tint.: Tintinidae

Date	Stn	Mysid length \bar{x} (SD)	N	E	No. of identified prey	Copepoda				Cladocera		Rot.	Tint.
						Eur	Tem.	Aca.	Pse.	Bos.	Ple.		
Jul 4	1	6.7 (1.9)	9	6	3	100	0	0	0	0	0	0	0
	3	7.1 (1.1)	8	0	13	56	0	3	0	0	37	4	0
Aug 1	1	11.5 (2.0)	15	0	142	32	1	8	0	6	42	5	4
	3	12.3 (1.2)	15	0	205	22	0	2	0	56	11	7	2
Aug 28	1	13.6 (1.1)	15	1	335	19	2	9	<1	13	10	7	40
	3	15.6 (1.4)	15	0	234	34	0	7	0	26	2	21	10
Sep 24	1	16.2 (0.6)	10	0	161	26	<1	12	4	12	6	19	21
	3	16.9 (0.7)	10	0	391	60	<1	8	1	3	<1	23	3
Oct 23	1	14.5 (1.3)	16	0	137	27	3	13	0	4	2	4	47
	3	17.3 (1.5)	15	1	120	68	2	1	1	7	<1	13	7

Table 6. Estimated proportions of zooplankton in fish stomachs (% by volume) and proportions of identified zooplankton taxa (% by number). Proportions were calculated as the average of proportions in individual fish. Fish were caught in Bongo nets and gill nets at Stns 1, 3 & 5 in 1985. Length of fish (mm), number of stomachs analyzed (N), number of empty stomachs (E) and the total number of identified prey items are also given. Prop.: proportion; zoopl.: zooplankton; id.: identified; ad&cop.: adult and copepodites; E/T: *Eurytemora/Temora*; Unid.: unidentified; Bos.: *Bosmina*; Ple.: *Pleopsis*

Date	Stn	Fish length (mm) \bar{x}	(range)	N	E	Prop. zoopl. (%)	No. of identified prey	Copepoda (ad&cop.)			Cladocera		Other zoopl.
								E/T	Other ^a	Unid.	Bos.	Ple.	
Sprat													
Jul 4	1	88	(85–90)	4	2	100	18	0	0	0	0	100	0
	5	88	(82–110)	13	3	100	474	7	0	1	18	51	25 ^b
Aug 1	1	95	(84–142)	11	1	99	329	16	0	1	49	33	2
	3	94	(85–97)	10	0	100	1015	20	0	2	77	2	0
	5	90	(87–93)	10	1	100	633	30	0	1	69	1	0
Aug 28	1	115	(85–144)	15	5	100	729	1	0	0	93	6	0
	3	122	(120–124)	3	0	100	132	23	1	1	74	0	2
	5	108	(71–147)	5	0	100	500	0	0	0	100	0	0
Sep 24	1	108	(71–147)	5	2	100	57	25	0	2	57	17	0
Oct 23	1	120		1	0	100	100	36	25	15	0	24	0
	3	109	(60–142)	4	1	100	45	64	2	0	0	29	6
YOY herring													
Aug 28	1	80	(72–87)	10	0	100	705	12	0	0	84	4	0
	3	72	(62–83)	10	0	100	897	5	0	0	95	0	0
Sep 24	1	85	(81–90)	10	0	100	506	8	1	1	64	25	2
	3	65	(55–75)	11	0	95	332	25	0	2	23	40	14 ^c
	5	83	(73–90)	10	0	100	530	90	1	0	3	2	3
Oct 23	1	85	(84–86)	4	0	100	92	37	24	6	8	25	0
	3	66	(62–75)	11	0	100	431	7	7	14	5	21	46 ^d
	5	80	(64–93)	10	0	100	114	92	2	1	0	6	0
I+ herring													
Jul 4	5	91	(80–108)	3	0	100	228	22	1	0	10	17	50 ^b
Aug 1	1	107	(98–122)	11	3	100	252	36	0	2	47	12	2
	3	117	(93–133)	16	0	100	616	25	0	4	69	0	1
	5	113	(106–130)	5	0	100	500	7	0	0	93	0	0
Aug 28	1	125	(118–134)	9	2	100	300	41	0	0	58	1	0
	3	122	(115–134)	10	1	100	811	47	0	0	53	0	0
	5	124	(115–133)	9	0	100	900	2	0	0	98	0	0
Sep 24	1	122	(107–136)	10	2	97	162	41	0	0	57	2	1
	3	113		1	0	50	0				Only zooplankton eggs		
Oct 23	5	123	(118–131)	10	0	100	418	94	4	0	1	0	0
Older herring													
Jul 4	1	191	(137–249)	8	6	50	0				Only zooplankton eggs		
	5	196	(176–233)	8	4	98	377	30	0	0	2	58	10 ^b
Aug 1	1	199	(162–261)	9	3	100	5	60	0	0	40	0	0
	3	197	(178–217)	10	2	100	484	33	0	0	67	0	0
	5	198	(150–220)	7	1	100	308	4	0	0	93	3	0
Aug 28	1	185	(168–207)	9	0	90	87	27	0	2	70	0	0
	3	195	(183–207)	5	0	80	173	87	1	0	12	0	0
	5	153	(142–166)	7	0	86	408	2	0	0	98	0	0
Sep 24	1	174	(142–219)	9	4	79	15	39	6	31	0	0	25
	3	162	(148–178)	8	0	88	103	56	0	6	23	14	0
	5	163	(148–186)	10	0	100	909	99	1	0	0	0	0
Oct 23	1	188	(165–208)	7	1	5	3	67	0	0	33	0	0
	3	186	(150–250)	10	8	50	50	92	2	2	4	0	0
	5	169	(150–202)	10	2	88	117	95	0	0	5	0	0

^a Primarily *Acartia*

^b Primarily *Balanus nauplii*

^c Primarily *Keratella*

^d Primarily copepod nauplii

ity but there were consistent patterns of prey preference throughout the study period. The mysids selected cladocerans (*Bosmina longispina* and *Pleopsis polyphemoides*) over copepods, especially *Acartia* sp. (Fig. 3). Comparable values for rotifers and tintinnids were not calculated because they represented a small portion of the diet.

Fish. Sprat and young herring fed almost exclusively on zooplankton throughout the study period while older herring also fed on other food items (primarily mysids and fish) in early July and in October (Table 6). The zooplankton species in the diet of the clupeids reflected prey availability (Table 6, Fig. 2). Copepod nauplii were present in fish caught in October when the proportion of nauplii in the water was high. In early and late August, *Bosmina longispina* dominated the YOY herring and sprat diets and both *B. longispina* and copepods were found in older herring. *Pleopsis polyphemoides* was consumed in early summer and in the autumn when this was the most common cladoceran. Copepods were the dominant prey item in all clupeids in October (Table 6). Rotifers were rare and tintinnids absent. Clupeids, especially sprat and young herring, selected cladocerans over copepods and *Eurytemora/Temora* copepods over other copepod species (Fig. 3). These patterns of selectivity were consistent over the seasons and among sampling areas.

Consumption rates

Calculated specific consumption of *Mysis mixta* juveniles declined from 14 % d⁻¹ at the beginning of the summer to 4 % d⁻¹ at the end of October. Consumption per mysid was similar from August 1 to October 23 as lower specific consumption rates in the autumn were compensated by increased mysid size. Daily consumption was up to 50 % higher in the Bay than in the Askö area as the mysids grew faster in the Bay. Specific consumption rates of herring during the summer was 10 to 20 % of body weight d⁻¹ for YOY fish larger than 5 cm, 7 to 13 % d⁻¹ for I+ fish, and ca 4 to 5 % d⁻¹ for older age groups. These consumption rates declined to 2 to 4 % d⁻¹ by the end of October for all age classes. Similar specific consumption rates have been reported elsewhere from experiments and field estimates of daily food rations (mysids: Bowers & Vanderploeg 1982; YOY herring: Franek 1988).

Abundances of different planktivores were combined with their calculated daily consumption rates to yield an estimate of total consumption of zooplankton. Planktivory by fish increased from early July to a maximum in August (Fig. 4). Consumption rates declined in the autumn although fish abundance increased. This is the result of smaller average fish sizes, slow growth and

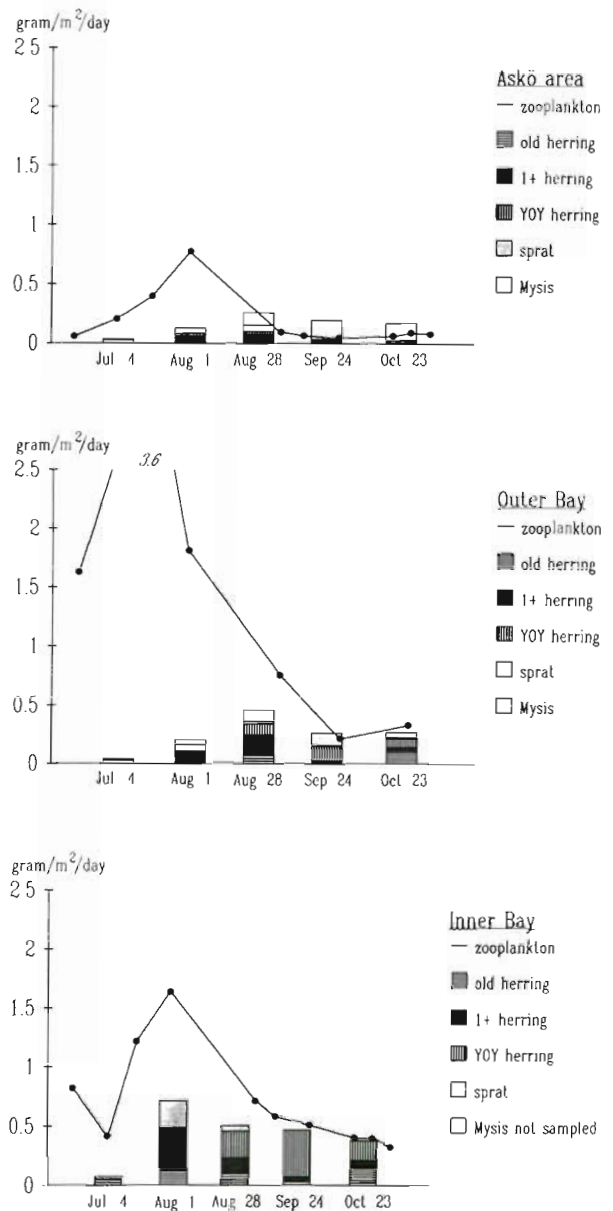


Fig. 4. Estimated zooplanktivory rates and zooplankton production rates (in g wet wt m⁻² d⁻¹) in the Inner Bay, the Outer Bay and the Askö area. Zooplanktivory rates (bars) show the contributions from different predators on 5 occasions from July 4 to October 23, 1985. Mysids and fish larvae are not included in the Inner Bay. Line: zooplankton production calculated using samples collected at shorter time intervals; (●) sampling dates. Production estimates for the Inner Bay are based on averages for samples collected at Stns 4 & 5

low temperatures. Sprat and yearling herring dominated during late summer (August 1 and 28). The contribution from YOY herring was high from the end of August through October. Older herring were less important planktivores and clupeid larvae contributed at the most 4 % of the total planktivory. *Mysis mixta*

was less important in the Outer Bay than in the Askö area, where it was the dominant planktivore in the autumn (Fig. 4).

Comparison of planktivory and zooplankton production

Zooplankton daily production increased through the summer, peaked in August and decreased thereafter (Fig. 4). This pattern was similar in all 3 areas. Production interpolated over the period 15 June to 15 November increased by a factor of 3 to 5 between the Askö area and the Bay (Table 7). Crustacean zooplankton production accounted for 85 to 97 % of total zooplankton production (larger than 90 µm; Table 7).

Consumption of zooplankton by planktivores was lower than zooplankton production on July 4 and August 1 and higher than or similar to zooplankton production on August 28, September 24 and October 23 (Fig. 4). The ratio between zooplanktivory and production of crustacean zooplankton interpolated from 15 June to 15 November was similar in the Inner Bay and in the Askö area (0.7) and lower in the Outer Bay (0.3).

The patterns for individual prey groups are similar to the observations for zooplankton in general with higher zooplanktivory relative to production in late August through October (Fig. 5). Planktivory rates on *Bosmina longispina maritima* peak earlier (early and late August) than planktivory on *Eurytemora/Temora* (late August through October) which is consistent with the earlier decrease of cladoceran (Fig. 2). The patterns are less clear for the 2 less abundant prey groups (*Pleopsis polyphemoides* and other copepods, primarily *Acartia* spp.) shown in Fig. 5.

DISCUSSION

Identification of major planktivores

Our calculations show that the dominant zooplanktivores in this area in 1985 were sprat, herring and *Mysis mixta*. The relative importance of these predators changed both seasonally and spatially. *M. mixta* was the major planktivore in the Askö area but not in the Outer Bay. Sprat and yearling herring were important in the summer and YOY herring in the autumn. The contribution from older herring was fairly similar over the sampling period and among areas. Unfortunately, we do not have information on mysids and fish larvae from the Inner Bay in 1985 but results from other years suggest lower abundances than in the Outer Bay (Rudstam et al. 1986, Rudstam & Hansson 1990).

Other planktivores contributed only marginally to

Table 7. Estimations of planktivory and zooplankton production for selected zooplankton groups for the period June 15 to November 15 1985. The estimates are based on interpolations between sampling dates. Planktivory by mysids is not included for the Inner Bay. The production value in parentheses for copepods excludes egg production. Zooplankton production not accounted for by crustaceans are primarily from rotifers (*Synchaeta* and *Keratella*)

Zooplankton group	Production (g wet wt m ⁻²)	Consumption (g wet wt m ⁻²)
Askö area		
All zooplankton	35	23
<i>Bosmina</i>	1	6
Other cladocerans	1	2
<i>Eurytemora/Temora</i>	15 (8)	11
Other copepods	18 (9)	4
Outer Bay		
All zooplankton	172	36
<i>Bosmina</i>	22	11
Other cladocerans	58	2
<i>Eurytemora/Temora</i>	46 (29)	21
Other copepods	11 (4)	2
Inner Bay		
All zooplankton	113	64
<i>Bosmina</i>	26	31
Other cladocerans	6	1
<i>Eurytemora/Temora</i>	59 (41)	31
Other copepods	6 (4)	1

the overall zooplankton consumption. Clupeid larvae accounted at the most for 4 % of the total zooplanktivory. Sand gobies did contain zooplankton, but because of their small size would contribute less than 3 % of total planktivory (given abundances derived from Bongo net catches, a specific consumption rate of 20 % and a diet of 100 % zooplankton). *Neomysis integer* do feed on zooplankton (Hansson et al. 1990a) but were mostly smaller than 7 mm and contributed less than 3 % of the total mysid biomass. There were no other potentially important invertebrate predators on crustacean zooplankton present. The coelenterate *Aurelia aurita*, considered an important planktivore in the southern Baltic (Möller 1979), was rare in 1985.

Seasonal changes in proportions of copepods and cladocerans consumed by both mysids and young clupeids reflected the seasonal changes in zooplankton species composition, but there were consistent patterns of prey selection by both groups. Cladocerans (*Bosmina longispina maritima* and *Pleopsis polyphemoides*) were selected over copepods and *Eurytemora/Temora* were selected over other copepod species. This is similar to earlier observations in this area (Hansson et al. 1990a), to results for mysids elsewhere (Lasenby & Fürst 1981, Murtaugh 1981), and to reports for Baltic herring and sprat (Sandström 1980, Shvetsov et al. 1983). *Eurytemora affinis hirundoides* is

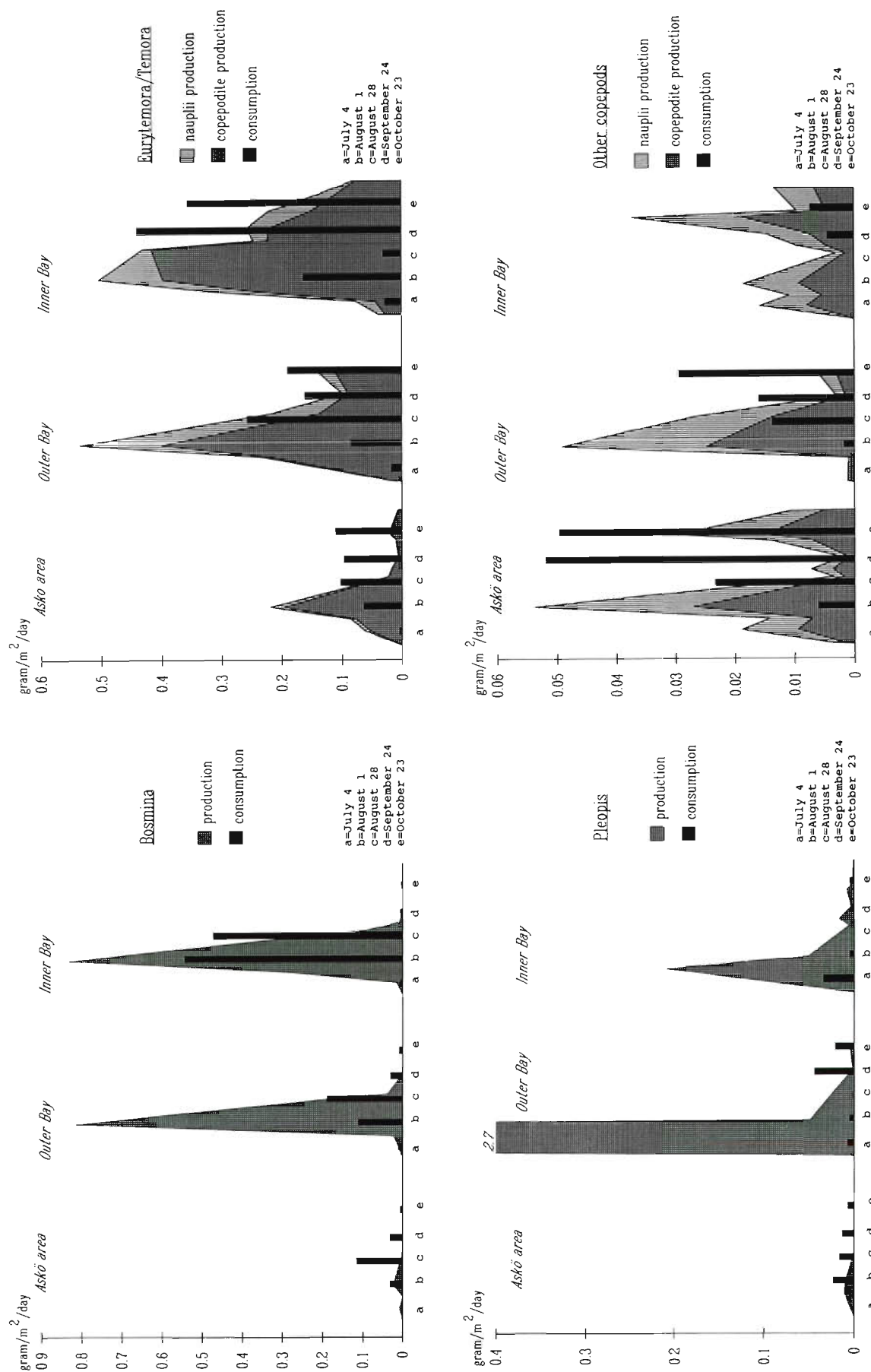


Fig. 5. Seasonal development of somatic zooplankton production (hatched area) and planktivory (black bars) for selected zooplankton groups (in $\text{mg wet wt m}^{-2} \text{d}^{-1}$) in the Inner Bay, the Outer Bay and the Askö area. Consumption by mysids is not included in the Inner Bay. Note difference in scale among groups

a more active copepod when observed in the laboratory and the high selectivity for this species compared to other copepods by all predators could reflect differences in encounter or detection rates. Fish often choose moving over non-moving prey (O'Brien et al. 1984).

Reliability of production and planktivory estimates

Except for the Inner Bay where we sampled 2 stations, we have no information on the spatial variation in zooplankton abundance for 1985. Later studies in the Askö area indicate a coefficient of variation of 40 to 50 % for dominating taxa (Johansson et al. unpubl.). Our data from the 2 stations in the Inner Bay gave similar results.

Our production estimates are based on temperature-dependent growth equations and daily production/biomass ratios and we did not consider differences in food availability. Cohort analysis based on field samples was not possible due to continuous reproduction of these species during the summer, a common problem with marine zooplankton (Kimmerer 1987). The equations used for copepods are based on experiments on populations that were not food limited and we consider these estimates to represent maximum potential consumption. Somatic production of coastal herbivorous copepods is often not food limited (Huntley & Boyd 1984) although egg production often is (Kjørboe et al. 1985). The assumptions made for *Eurytemora affinis hirundoides* are supported by experiments in large plastic bags conducted in July 1989. Generation time was estimated to 14 d at 17.5 °C both at chlorophyll concentrations typical of the Askö area and at those of the Inner Bay. (Johansson pers. obs.). This should be compared to the 15 d calculated from the equation used in this paper (Vuorinen 1982). However, egg production was only observed in the bags with higher chlorophyll concentrations. Thus, we believe that our copepod production estimates are reasonable in the Bay but may be high in the Askö area. Cladocerans generally respond to increased food availability by increased production (DeMott 1989) and we may therefore have underestimated the differences in cladoceran production between the Bay and the Askö area.

Mysid abundances are based on catches in Bongo nets, which are considered an effective sampling gear for the similarly sized euphausiids (Pearcy et al. 1980). Duplicate Bongo net samples gave results within 3 to 32 % of the mean for *Mysis mixta* (Table 3; see also Rudstam et al. 1986). Abundances are similar to those obtained in 1983, 1984 and 1986 in this area (Rudstam & Hansson 1990) and elsewhere in the Baltic (Salemaa et al. 1986). Our estimates are lower bounds for total mysid abundances because part of the population

occurs on the bottom at night, especially in the Askö area (Rudstam et al. 1989a). We will have underestimated planktivory by mysid shrimps if the mysids caught on the bottom also feed in the water column during part of the night.

Fish abundances are based on the species and size distribution in vertical gill net catches and the total abundances from acoustics. On 5 occasions in 1985, we recorded 3 or more repeated acoustic transects over a 24 h period in the Askö area and in the Bay. Coefficients of variation for the abundance of fish over 5 cm length ranged from 13 to 52 % (average 32 %). The gill nets used had very low selectivity for fish below 5 to 6 cm length and we may have underestimated the number of YOY clupeids in August. However, the small number of YOY herring caught in the Bongo net in August compared to September and October (when these fish are larger and better able to avoid the Bongo net) indicate that YOY herring were uncommon in August in our area. Urho & Hildén (1990) reported that small YOY herring stay close to shore in an archipelago area on the Finnish side of the Baltic Sea.

Results from stomach analysis is potentially biased by differential gut passage times and digestibility, especially when prey items are very different in size (Bowen 1983). However, we are primarily using stomach contents to estimate proportions of similarly sized zooplankton species. Only older herring fed on larger prey items. Clupeids feed continuously throughout the day but not at night (Nellbring 1975, Shvetsov et al. 1983) and stomach content of fish caught in the first part of the night should reflect day time food intake. For mysids, Rybock (1978) found no significant differences between gut passage times for different zooplankton mandibles in mysid stomachs. Mysids feed during the night and the zooplankton were collected during the day, but zooplankton species composition and abundance from integrated water column samples for day and night are similar (Rudstam 1988, Hansson et al. 1990a).

Total planktivory is calculated as $\sum A_j \cdot C_j$, where A_j is the abundance of predator j , and C_j is its daily zooplankton consumption. The coefficients of variation associated with the abundance measures are ca 20 % for *Mysis mixta* and 30 % for fish (see above). The variance associated with the daily consumption rates are harder to estimate since they are based on non-linear models with many parameters. A coefficient of variation for the daily consumption estimated of 30 % may be reasonable. First-order error analysis (Carpenter 1984) yields estimate for the coefficient of variation for total planktivory rates ranging from 20 to 35 % for the different sampling occasions and areas. Thus, the observed order of magnitude changes in planktivory rates from low values in early July to high values in August are real.

Seasonal patterns of planktivory and zooplankton production

Zooplanktivory changed dramatically during the study period. Consumption of zooplankton was low in early July because clupeids were rare and because *Mysis mixta* were small and did not utilize the open water, possibly due to the high light levels around midsummer at these latitudes (Rudstam et al. 1989a). Planktivory peaked in late summer as a result of immigration of sprat and yearling herring, increased abundance of YOY herring (probably recruited from shallow water areas) and increased planktivory from *M. mixta* as the juveniles released in the spring grew in size and darker nights made the water column accessible for mysids. A peak in planktivory by YOY fish in late summer and autumn is also typical in temperate lakes (Mills et al. 1987, Hewett & Stewart 1989). Zooplanktivory declines in the autumn as a result of slower growth at lower temperatures, and a shift in diet of older herring to mysids and fish. The increase in planktivory follows the seasonal increase in zooplankton biomass with comparatively short time lags (about 1 mo in this area), which may be necessary for planktivores to control seasonal zooplankton cycles (Gliwicz & Pijanowska 1989, Luecke et al. 1990).

Because this seasonal dynamic in zooplanktivory is caused partly by ontogenetic changes in behavior and seasonal changes in light levels, it may be repeated each year. Year to year variation in absolute levels of planktivory may however be substantial due to notoriously variable year class strength of planktivores (Sissenwine 1984). Fish abundances in late summer – autumn varied by a factor of 4 in the Askö area and a factor of 5 in the Inner Bay for the years 1985 to 1988 (0.16 to 0.7 fish m⁻² in the Askö area and 1 to 5 fish m⁻² in the Inner Bay; Hansson & Rudstam 1990).

We suggest that the increase in planktivory caused the late summer – autumn decline in zooplankton abundances. Consumption of zooplankton was lower than zooplankton production in early summer when zooplankton biomass increased, and higher or similar to production in late summer and autumn when zooplankton biomass decreased in all 3 areas (Figs. 2 & 4). Alternatively, the decline could be the result of resting egg production or low food concentrations. However, previous studies in this area show that parthenogenetic females of *Bosmina longispina maritima* dominate at least through the middle of September (Kankaala 1983), indicating that resting egg production did not cause the August decline of this species. Unfortunately, we do not know when the copepods produce resting eggs. The autumn decrease in zooplankton abundances is probably not caused by food shortage. Chlorophyll levels in September and October were

similar to (Askö area) or higher than (Inner Bay) levels in July and August 1985 (Larsson et al. 1991).

Differences among the study areas

The planktivores were estimated to consume about 70 % of crustacean zooplankton production both in the Inner Bay and in the Askö area even though zooplankton production was 3 times higher in the Bay. This ratio was 30 % for the Outer Bay, but this is probably too low since zooplankton production in that area depended strongly on samples from one date (July 16) with unusually high abundances of the cladoceran *Pleopsis polyphemoides* (Fig. 2). The similarity between the independently derived consumption and production estimates indicate that most of the annual crustacean zooplankton production is consumed by the predators. For specific prey groups, the comparisons between estimates of production and consumption in the 3 areas are more variable, reflecting the increased uncertainties associated with including information from diet analysis in the estimates. The proportions of somatic production of *Eurytemora/Temora* consumed by planktivores were close to 1 in all areas even though the estimated production was 4 times higher in the Inner Bay than in the Askö area. Consumption of *Bosmina* was higher than production estimates in the Inner Bay and in the Askö area and lower in the Outer Bay (Fig. 5, Table 7; see also Hansson et al. 1990a).

The zooplankton seasonal dynamics and species composition show indications of larger effects of planktivory in the Askö area than in the Bay. The most selected species (cladoceran and *Eurytemora* copepods) were a smaller proportion of total zooplankton biomass and declined earlier in the season in the Askö area than in the Inner Bay. The high summer abundances of cladocerans in the Bay may actually delay an autumn decline in copepod biomass because YOY and juvenile clupeids selected cladocerans over copepods. Although the ratio between planktivory and zooplankton production was similar in the Inner Bay and the Askö area, these production estimates represent potential, not food limited, zooplankton production. Food limited zooplankton production is more likely in the Askö area than in the Bay. Predatory regulation of zooplankton dynamics will interact with food limited growth (Gliwicz & Pijanowska 1989) and this interaction probably produces the observed differences among our study areas.

Final remarks

The zooplankton assemblage present in this part of the Baltic Sea shows signs of being strongly affected by

predation. Both the cladoceran and copepod species present are comparatively small, the preferred copepods have marked diel vertical migrations (Hansson et al. 1990a) and most of the annual crustacean production is consumed (this study). Also, daphnids, which are sensitive to predation, were completely absent although they occur in comparable salinities in an eastern Baltic archipelago (Vuorinen & Ranta 1987). The abundances and biomass of planktivorous fish in the area (reaching 2 fish m^{-2} and 10 g m^{-2} in the Inner Bay in the autumn) are larger than the abundance of YOY perch *Perca flavescens* causing the disappearance of *Daphnia pulex* in Oneida Lake, New York, USA (1.4 fish m^{-2} or 2 to 4 g m^{-2} ; Mills et al. 1987) and the estimated biomass of alewife *Alosa pseudoharengus* in Lake Michigan in 1976 associated with low abundances of larger daphnids (1.3 g m^{-2} ; Scavia et al. 1988). We have shown here that planktivory varies substantially over the season and that the increase in planktivory in the late summer and autumn is correlated with the seasonal decline of the zooplankton populations. Thus, the importance of planktivory for regulating zooplankton populations in the Baltic Sea changes with season, as suggested by Roff et al. (1988) for the North Sea (see also Viitasalo et al. 1990).

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