Predation impact of age-0 fish on a copepod population in a Baltic Sea inlet as estimated by two bioenergetics models

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Abstract. Decreasing spring abundances of the copepod Eurytemora affinis, in a shallow brackish inlet of the Baltic Sea, were compared with calculated consumption of age-0 fish [dominant species herring (Clupea harengus) and perch (Perca fluviatilis)] as determined by two bioenergetics models. Fish and zooplankton populations were sampled at three stations along a salinity gradient of 0.3-8.1‰ maximum range. Larvae and juveniles of both fish species preferred to prey on adults and developmental stages of E. affinis. Although there were substantial variations in fish density and copepod production across the salinity range, consumption of zooplankton by age-0 fish was never high enough to be a major source of copepod mortality. This finding is an independent confirmation of previous results obtained by direct food-intake measurements in the same region. The low impact of fish predation may be a function of the low individual fish biomass in spring, the increased copepod production and the dominance of the less planktivorous perch, rather than herring, in the less saline waters of the Barther Strom inlet.

Introduction

Large filter-feeding cladocerans (mainly Daphnia spp.) show bimodal density development with peaks in spring and autumn, and low numbers during summer in many freshwater lakes (Sommer et al., 1986). In late spring, there is often a rapid population decline within only a few weeks. The reason for this succession has been assumed to be primarily food limitation (DeMott, 1989), but predation by young fish may be important (Threlkeld, 1979; Gliwicz and Pijanowska, 1989). Newly hatched fish mainly prey on zooplankton (Hartmann, 1986). With increasing mouth gape width, they are rapidly able to ingest even the largest zooplankton species available. During the first weeks after hatching, larvae and juveniles have higher specific metabolic demands in comparison to older fish (Brett, 1979), and occur in extraordinarily high densities. Consequently, predation by young-of-the-year fish may potentially impact zooplankton population dynamics.

In waters where salinity is >2‰, calanoid copepods of the genera Eurytemora and Acartia are often the dominant zooplankton species (Jepesseen et al., 1994). Similar to population development in Daphnia, it has been observed that the population density of copepods in several waters also regularly decreases at the end of spring. This decline is followed by a period of low numbers and a subsequent second peak later in the year (Landry, 1978; Irvine et al., 1993; Heerkloss and Schnese, 1995). Since copepods and their nauplii form part of the diet of larval and juvenile fish (Checkley, 1982; Mills et al., 1984), substantial intake of copepod prey can be assumed during the first weeks after the mass hatch of fish in spring and early summer (Cushing, 1983). However, few studies exist in which the
feeding influence of age-0 fish on zooplankton communities has been calculated
during that time (Mills et al., 1987; Wu and Culver, 1994; Thiel, 1996).

This may also be attributed to difficulties in estimating the consumption of age-
0 fish. Direct field estimates of the daily rations of fish require high sampling effort
(Elliott and Persson, 1978; Ney, 1990). The quantity of food consumed per fish can
vary up to 16% on consecutive days (Trudel and Boisclair, 1993) and, due to vari-
ation in zooplankton abundance over time, consumption estimates cannot be
interpolated over periods of >3–4 weeks. The scope of variation may be even more
pronounced in small age-0 fish, since fast weight increments change the specific
metabolic demands within short periods. On the other hand, growth and food
supply are strongly coupled in fish (Brett, 1979). Therefore, if reliable growth and
density data of fish can be obtained, they can serve as a good predictor of food
consumption by fish populations during longer periods than are available with
24 h sampling programs alone (Rice and Cochran, 1984; Bartell et al., 1986).
Simple (Vinberg, 1956) or more complex bioenergetics models (Kitchell et al.,
1977) have been used to estimate food consumption from growth, even based on
data from age-0 juvenile fish (Rudstam, 1988; Post, 1990; Rudstam et al., 1992;
Madon and Culver, 1993). However, the transferability of data for age-0 juveniles
to fish larvae is questionable and requires evaluation by different methods due to
difficulties in calculating precisely the activity costs of fish (Boisclair and Leggett,
1989).

In this study, an attempt is made to evaluate whether the population dynamics
of a copepod species are directly influenced by age-0 fish predation. This was
carried out in a shallow inlet of the Baltic Sea on the northern German coast. In
this region, a substantial feeding influence of age-0 fish on the dynamics of the
copepod population has been assumed, since spring declines in copepod abun-
dance coincide with peaks in abundance of age-0 fish (Arndt, 1989; Thiel, 1996).
The analysis is based on quantitative data of age-0 fish, their diet and of the zoo-
plankton community. By using the two bioenergetics models mentioned above,
estimates of food consumption by age-0 fish from the hatch until the end of spring
were compared with biomass production of the copepod population during the
same period.

Method

Study site

The study was conducted in Barther Strom, the broad mouth of the small River
Barthe, part of the Darss–Zingst inlet situated on Germany’s southern Baltic Sea
coast (Figure 1). The Barther Strom is ~5 km long and 400–900 m wide, and covers
a total area of 2.1 km². Water depth reaches 1.6 m on average and maximum values
of 2.5 m in central parts. The entire, tideless inlet is highly eutrophic (maximum
primary production in April is ~2000 mg C m⁻² day⁻¹; Heerkloss et al., 1984) and
polymictic. Secchi depth normally does not exceed 0.4 m. The bottom of the inlet
consists mainly of mud and silt, and is only sparsely vegetated with Potamogeton
and Chara up to a water depth of ~0.7 m. Water temperature varies from 2°C in
winter up to 25°C in littoral areas during summer. Salinity fluctuates due to
Predation impact of age-0 fish on copepods

freshwater inflow from the Barthe and the inflow of brackish water (6–12% salinity) from outer regions of the Darss–Zingst inlet which are directly connected with the Baltic Sea (Figure 1).

Sampling

Sampling was performed at three different stations along the salinity gradient of the investigational area, since it was expected to find differences in the community composition of zooplankton and fish across the salinity range. Station 1 was situated in the inner part of Barther Strom, whereas stations 2 and 3 were chosen closer to the central part of the Darss–Zingst inlet (Figure 1). At each sampling point, water temperature in 0.5 m water depth (T, °C), pH and salinity (S, %) were measured. All samples were obtained during daylight between 10.00 a.m. and 4.00 p.m. Age-0 fish were caught at approximately weekly intervals between the middle of April and the middle of June of 1990 and 1991. A small (0.2 m diameter) double bongo net was used with 315 and 500 μm mesh size, respectively. The net was towed on the side of the boat in the middle of Barther Strom over a fixed distance of 350 m. Velocity was 1.2 m s⁻¹ and towing depth ~0.7–1.0 m. During one haul, ~11 m³ of water were filtered. The larval and juvenile fish were fixed in a 4% formaldehyde solution immediately after having been caught. In the laboratory,
Fish species were determined according to the keys by Kazanova (1953) and Kobličkaya (1981). Individuals were numbered, measured and grouped into length classes of 1 mm width. From this, mean total length (TL) was estimated. All fish of one length class were weighed together and mean wet body mass (wbm) was calculated from all fish caught during one haul. Fish population density and biomass were calculated from the filtered water volume corrected for a slightly lower filtration efficiency of the 315 μm net (B. Ladwig, Rostock University, unpublished results). Diet compositions were determined from at least 10 specimens of each fish species, from each station and sampling date. Prey species in the digestive tracts were identified under a stereomicroscope, and subsequently counted and measured. Reconstruction of prey biomass composition per fish was performed by means of length-weight regressions (Bottrell et al., 1976).

The zooplankton community was analyzed in 1991 only, using the same stations set up for the fish sampling (1-3; Figure 1). Zooplankton were taken at roughly weekly intervals with a 5.2 l Friedinger sampler (Hydrobios, FRG) from 0.5 m deep water as a composite sample from both the start and the end point of each bongo catch. The sample was concentrated through 55 μm mesh and subsequently fixed in a 4% formaldehyde solution. Zooplankton were determined under a microscope to the lowest possible taxon; only cyclopoid and harpacticoid copepods were not differentiated further. After determining the species, calanoid copepods were additionally separated into adults and copepodids (hereafter referred to as copepods), and into nauplii. Biomass was calculated after measuring at least 50 specimens of each important zooplankton species using the same length-weight regressions as in the dietary analysis of fish. Daily production of the main copepod species, *Eurytemora affinis*, was estimated according to temperature-dependent daily production/biomass ratios (*P/B*, day⁻¹) as:

\[ P/B = 0.0137 \times \text{temperature (°C)} + 0.00124 \ (n = 92, R = 0.925) \]

(H. Arndt, Greifswald University, Institute of Ecology, Hiddensee, personal communication). The copepod production had been calculated by the cumulative growth method (Uye, 1982) and temperature-dependent regressions for developmental time (Arndt, 1989). These values had been compared with the copepod biomasses and the water temperatures during similar conditions from the same area in previous years (inlet south of the Darss-Zingst peninsula; Figure 1).

**Consumption estimates**

Daily food consumption of age-0 fish was calculated using (i) the complex generalized bioenergetics model originally developed by Kitchell et al. (1977; hereafter referred to as the Kitchell model; summarized in Hewett and Johnson, 1992) and (ii) the more simple model of Vinberg (1956).

The Kitchell model accounts for the energy use and intake of fish as follows:

\[ C = (R + S) + (F + U) + (\Delta B) \]

(1)
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where $C$ is consumption, $R$ is respiration, $S$ is energy accounted for by specific dynamic action ($SDA$), $F$ is egestion, $U$ is excretion and $\Delta B$ is the energetic equivalent of growth. The parameters are calculated on a daily basis as functions of fish weight ($W$) and water temperature ($T$) using the following formulae:

$$C = C_{\text{max}} + P \cdot f(T)$$

$$C_{\text{max}} = a \cdot W^b$$

where $P$ is a proportionality constant reflecting the relative amount of daily consumption in comparison to the maximum consumption under optimum temperature conditions, $C_{\text{max}}$.

$$R = a \cdot W^b \cdot f(T) \cdot A$$

where $A$ is a proportionality constant for activity.

Egestion ($F$) and excretion ($U$) are computed as constant proportions of consumption, and

$$S = SDA \cdot (C - F)$$

The Kitchell model is sensitive to the incorrect use of the allometric equations for consumption and respiration. However, the sensitivity to the activity multiplier of basal energy requirement ($A$) is rather low (Bartell et al., 1986). Consequently, species-specific intercepts ($a, \alpha$), slopes ($b, \beta$), type of temperature dependence of consumption and respiration, and proportions of $A, F, U$ and $SDA$ were chosen for age-0 perch according to Post (1990). For herring, parameter values described for age-0 herring by Rudstam (1988) were used.

The bioenergetics model of Vinberg (1956; summarized in Ney, 1990) estimates daily rations of fish according to:

$$C = 1.25 \cdot (A \cdot SMR + \Delta B)$$

where $A$ is the fixed activity multiplier of standard metabolic rate ($SMR$), this product together accounts for basal oxygen consumption and activity costs of fish; $\Delta B$ is the energetic equivalent of somatic growth during the preceding period. SMR rates for larval fish were taken from the studies of Kudrinskaya (1969; for perch) and Almatar (1984; for herring). The sensitivity of the Vinberg model to the activity multiplier is higher than that of the Kitchell model. Consequently, the same multipliers of activity as in the Kitchell model were chosen (4.4 in perch, 3.9 in herring). To compare the results obtained by both models, the differences in median daily consumption rates were statistically tested by the Wilcoxon signed rank test for paired samples.

Energy densities of small age-0 fish and zooplankton prey were assumed to be equal (2500–2800 J g$^{-1}$ wet wt, Post, 1990; Arrhenius and Hansson, 1993). Individual daily consumption rates, age-0 fish biomass and diet composition of fish
### Table I. Summary of data for salinity (S, %o) and data obtained from herring measurements 1990/1991

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<td>wbm</td>
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TL = total length in mm; SE = standard error of mean TL; wbm = wet body mass in mg; n.s., not sampled.

### Table II. Mean water temperature in 0.5 m water depth (T, °C; pooled for all stations), and pH values and data obtained from perch measurements separated for the stations 1990/1991

<table>
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TL = total length in mm; SE = standard error of mean TL; wbm = wet body mass in mg; n.s., not sampled.
(**prey biomass**) were multiplied to obtain the daily intake of certain zooplankton species on the sampling dates, and were compared with the daily copepod production.

**Results**

**Abiotic conditions**

Salinity was substantially lower in 1991 than in 1990 and showed significant differences between sampling stations in both years (ANOVA, 1990: $F = 10.90$, d.f. = 25, $P < 0.001$; 1991: $F = 8.44$, d.f. = 26, $P < 0.005$, Table I). The highest salinity was recorded at station 3 on 6 June 1990 (8.1‰) and the lowest value was measured at station 1 on 14 May 1991 (0.3‰). Water temperature did not differ significantly between the three stations either in 1990 or in 1991 (Kruskal–Wallis test, 1990: $P = 0.57$; 1991: $P = 0.46$); consequently, mean daily temperatures for each sampling date were calculated (Table II). Temperature did differ between years, however.
Fig. 3. Biomass of age-0 fish (mg wbm m\(^{-3}\)) in Barther Strom during spring 1991.

The mean temperature rose rapidly from 12°C on 26 April to 20°C on 10 May 1990. In contrast, in 1991 the mean temperature remained below 11°C until the end of May, but later also increased to 16°C within 5 days (28 May 1991, Table II). pH values were in general slightly higher at station 3 than at stations 1 and 2, and increased to the highest values (10.7 in 1990, 9.4 in 1991) at around the end of May in both years (Table II). Available nutrient concentrations were measured as 71 μmol NO\(_3\)-l\(^{-1}\) and 0.4 μmol PO\(_4\)-l\(^{-1}\) (23 April 1991), and 0.4 μmol NO\(_3\)-l\(^{-1}\), 2.05 μmol NH\(_4\)+ l\(^{-1}\) and 0.5 μmol PO\(_4\)-l\(^{-1}\), respectively (11 June 1991; H. Baudler, Rostock University, personal communication).

**Numbers and biomasses of age-0 fish**

Altogether, nearly 9500 age-0 fish were caught in 1990 and 1991, the total number being about equal in each year. Most of the fish were herring (*Clupea* 1330
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Fig. 4. Diet composition (relative frequency of prey biomass) of age-0 herring and age-0 perch from Barther Strom during spring 1990. Fish from station 1–3 have been pooled. The number of fish stomachs analyzed is indicated above the bars.

harengus L., 57.9% of total catch) and European perch (Perca fluviatilis L., 33.4%). Gobies [Pomatoschistus minutus (Pallas) and P. microps (Krøyer); species not separated] contributed to 8.4% of the total catch, while roach [Rutilus rutilus (L.)] and three-spined stickleback (Gasterosteus aculeatus (L.)) contributed only 0.4 and <0.1%, respectively. In both years, more perch were caught at station 1 than at stations 2 and 3, whereas the opposite distribution was observed for herring and gobies.

Biomass values fluctuated at all stations, during both years (Figures 2 and 3). The largest fish biomasses occurred at station 2 on 3 May 1990 (~650 mg wbm m⁻³; Figure 2) and at station 3 on 23 May 1991 (~1000 mg wbm m⁻³; Figure 3). For herring, biomasses differed significantly between stations and years (Kruskal–Wallis test, \( P < 0.005 \)), but not for perch (Kruskal–Wallis test, \( P = 0.076 \)). The biomasses of gobies, roach and stickleback were always very low and never exceeded 15 mg wbm m⁻³. Consequently, these species were excluded from further considerations.
Fig. 5. Diet composition (relative frequency of prey biomass) of age-0 herring and age-0 perch from Barther Strom during spring 1991. Fish from station 1–3 have been pooled. The number of fish stomachs analyzed is indicated above the bars.

**Diet composition of fish and zooplankton composition**

Since diet composition was very similar at the three stations in both years, both in herring and in perch (Mehner, 1993), a mean composition of prey biomass was calculated for each sampling date. In 1990, perch and herring fed almost exclusively on copepodids and adult *E. affinis*. Nauplii played an important role as prey only at the end of April. Other species comprised a minor fraction of diet biomass (Figure 4). The same diet composition was found for herring in 1991 (Figure 5). By contrast, age-0 perch preferred to prey on rotifers (mainly *Brachionus calyciflorus*) in April and May, 1991. Later *E. affinis* and their nauplii also dominated the diet of this species (Figure 5).

Zooplankton were investigated in 1991 only. The calanoid copepod *E. affinis* dominated at all stations. Maximum biomasses of $>5$ mg wet weight l$^{-1}$ could be observed at station 1 and 2 until a population decline at the end of May (Figure 6). In June, rotifers (*B. calyciflorus*, *B. quadridentatus*, *B. plicatilis*, *Keratella* spp., *...
Flinia longiseta) occurred in extraordinarily high densities at all stations (>8000 ind. l⁻¹), whereas E. affinis was present only in maximum biomasses of ~0.3 mg wet wt l⁻¹.

**Daily rations and consumption estimates of fish**

The mean wet body mass of herring larvae and small juveniles did not increase regularly during the spring of both 1990 and 1991. A break occurred at all stations between 30 May and 6 June 1990, substantially reducing mean length and biomass (Table I). Similar patterns were observed in age-0 herring between 23 and 28 May 1991 (Table I), but not in perch (Table II). These breaks were attributed to the occurrence of a second spawning cohort. Therefore, growth in age-0 herring was calculated separately for the two periods before and after the break.

Individual daily rations in age-0 perch estimated using the Vinberg model were in general slightly higher than those calculated using the Kitchell model, but
Fig. 7. Comparison of individual relative daily consumption rates in age-0 herring and age-0 perch (g food g\(^{-1}\) fish day\(^{-1}\), wet wt basis) at stations 1-3 in spring of 1990 and 1991, calculated using the Kitchell and Vinberg models. Significant differences are indicated by an asterisk. Median values, 25th and 75th percentiles (box lines), 10th and 90th percentiles (capped bars), and data outside (circles) are shown.

The Wilcoxon test for differences in daily rations resulted in significantly higher relative consumption rates calculated using the Vinberg model at stations 1 and 2 only in 1990. The differences at station 3 in 1990, and at all stations in 1991, were insignificant (Figure 7). Consequently, there were only slight differences in consumption estimates by using the different bioenergetics models, but significant differences were obtained between the 2 years. Integrated consumption of age-0 perch and herring on copepods and nauplii was about seven times higher at stations 1 and 2 in spring 1990 (2.5–4.8 g wet wt m\(^{-3}\); Table III) than in spring 1991 (0.4–0.57 g wet wt m\(^{-3}\)). By contrast, higher consumption was calculated at station 3 in 1991 (~2.8 g wet wt m\(^{-3}\)) than during the same period in 1990 (~1.7 g wet wt m\(^{-3}\); Table III).
Daily copepod consumption by fish was always at least one magnitude lower than daily copepod production at stations 1 and 2 during the sampling period in 1991 (Figure 8). Only at station 3 did the predation on copepods exceed the daily copepod production for a short period. The maximum was found between 7 and 14 May 1991, when age-0 fish ingested 142% (Vinberg model) and 159% (Kitchell model), respectively, of the *E. affinis* production (Figure 8).

**Discussion**

In this study, zooplankton consumption by age-0 fish and copepod production were compared in a shallow Baltic Sea inlet during spring. Fish biomass, zooplankton consumption and copepod production varied substantially across the salinity gradient and with the course of time. Nevertheless, the population of the dominant copepod species *E. affinis* declined at all stations around the end of May, a dynamic which seems to be typical for this region (Heerkloss and Schnese, 1995). This decline could not be accounted for by the consumption of age-0 fish alone. Thus, these findings based on bioenergetics models are an independent confirmation of previous results obtained by direct food intake measurements in the same area (Mehner and Heerkloss, 1994).

In general, the highest predation impact by the age-0 fish populations may be expected only if the individual fish biomass exceeded a certain value. For zooplanktivorous freshwater fish, late July was determined as the critical period (Mills et al., 1987; T. Mehner, unpublished). Relationships between zooplankton population dynamics and predator consumption rates have also been observed in other coastal areas of the Baltic outside of spring (Hansson et al., 1990). Daily food intake of herring and the mysid shrimp *Mysis mixta* equaled or even exceeded the summer copepodid production in this region. Rudstam et al. (1992) estimated the planktivory rates to be lower than zooplankton production in July and August, but higher in autumn when zooplankton biomass declined in coastal areas. Using Rudstam’s (1988) bioenergetics model for herring, Arrhenius and Hansson (1993) calculated that the yearly zooplankton intake of larvae and age-0 juvenile herring and sprat (*Sprattus sprattus*) contributed to ~50% of the total zooplankton consumption in the Baltic Sea. In addition, they stated that the total annual
consumption estimates were now four times higher than previous estimates due to the inclusion of age-0 fish. Consequently, between 60 and 80% of zooplankton production was consumed by planktivores on an annual basis. Thiel (1996) found a substantial predatory influence of small fish (including age-0) on copepod population development in adjacent Barther Bodden (Figure 1). Using the Vinberg model, he calculated that, on an annual basis, the *E.affinis* population dynamics were possibly influenced by the copepod intake of small fish in a year with an unusually low zooplankton biomass. However, in years with higher zooplankton production, predation by age-0 fish contributed only marginally to the total copepod mortality.

All the studies cited above have also included fish older than age-0, and were
undertaken in coastal and open regions of the Baltic Sea in which clupeids (herring and sprat) are dominating. The diet of herring and sprat older than age-0 also consisted predominantly of copepods, and these age groups may contribute to 50% of total zooplankton consumption (Rudstam et al., 1992; Arrhenius and Hansson, 1993). Additional predation by older herring is also possible in Barther Strom, but should be low at station 1, since a mass occurrence of adult herring during the spawning period was never observed in the low-salinity regions of Darss-Zingst inlet (H.Winkler, Rostock University, personal communication). In contrast, perch dominated in the low-salinity regions of Barther Strom, possibly excluded from the outer regions due to high mortality of perch larvae in water of >5‰ salinity (Bein and Ribi, 1994). Older perch do not feed exclusively on zooplankton in the inlet (Thiel, 1996). Therefore, the total feeding influence of perch populations on copepods might be comparably low in the majority of the regions of the Baltic Sea. Invertebrate predators (*M. mixta, Neomysis integer*) also feed on copepods, and their predation can account for nearly 50% of total zooplankton consumption during certain periods in the Baltic (Hansson et al., 1990; Rudstam et al., 1992). Unfortunately, mysids were not collected in the Barther Strom in this study. However, Thiel (1996) calculated that in the adjacent Barther Bodden, *N. integer* ingested approximately the same amount of zooplankton as all zooplanktivorous fish of age groups 0–2. Even by doubling the daily predation impact due to additional intake of copepods by mysids, the direct influence on copepod dynamics remains negligible, at least in the inner regions of Barther Strom.

This low predation influence may also be attributed to variability in zooplankton densities along the salinity gradient. At least 10 times higher copepod biomasses were found at stations 1 and 2 of Barther Strom 1991 (Figure 6), in comparison with values described from open Baltic regions and coastal areas (Hansson et al., 1990). Only at station 3 was the copepod biomass in the same lower range as had been reported from other parts of the Darss-Zingst inlet by Heerkloss and Schnese (1995) and Thiel (1996). Thus, the density of *E. affinis* appears to decrease with increasing salinity, although Bernat et al. (1994) have found the opposite to be true during tidal cycles in the Elbe estuary.

The integrated consumption at stations 1 and 2 was higher in 1990 than in 1991. The higher water temperature in spring 1990 (Table II) increased the growth rates and thus the daily rations in fish (Figure 7). Consequently, the total consumption exceeded those values that were found in 1991 (Table III). In addition, more herring were caught at stations 1 and 2 in 1990 than in 1991 due to the higher salinity (Table I). Therefore, one can conclude that predation pressure by fish may influence copepod dynamics more strongly in areas with higher salinity (>5‰) than in the inner, low-salinity regions. This is attributed to both the decreased copepod biomass and production, and the increased herring biomass with higher salinity of the water. Corroborating this conclusion, essentially higher predation rates of age-0 fish (mainly herring) were found at station 3 compared to the results obtained at stations 1 and 2 in 1991 (Figure 8).

The reliability of these conclusions is strongly affected by the estimates of fish biomass and growth. Samples taken with a small bongo net may under-represent juvenile fish that are longer than ~25 mm TL due to decreased catch efficiency
(Thiel, 1996), but in 1991, all perch caught were smaller than 25 mm TL (Table II) and, also, the majority of herring did not exceed 25 mm TL until the end of May (Table I). In addition, the age-0 fish biomasses at stations 2 and 3 (Figures 2 and 3) were nearly identical to values obtained for the pelagic area of adjacent Barther Bodden in previous years (0.2-0.7 g wbm m⁻²; Thiel, 1996). In that study, a small-mesh otter trawl was also used to sample juvenile fish. Age-0 fish were not caught with another fishing equipment in the present study. Even if there were severe underestimations of densities of fish larger than 25 mm TL, this would have influenced mainly the estimates of food consumption at station 3 in 1991, and preferentially in June. During that time, copepod biomass had already declined to levels <1 mg wet wt l⁻¹ (Figure 6) and this decline was therefore not the result of fish predation.

Hansen et al. (1993) pointed out that bioenergetics models were seldom tested against in situ consumption estimates. In a previous study, we estimated daily rations of perch larvae and herring juveniles by direct consumption measurement in the same area during a 24 h period (Mehner and Heerkloss, 1994). The direct calculations were substantially lower (0.013 g g⁻¹ day⁻¹ in herring, 0.055 g g⁻¹ day⁻¹ in perch, mean water temperature 16°C) than our model calculations (median values 0.30–0.58 g g⁻¹ day⁻¹ in perch, 0.20–0.33 g g⁻¹ day⁻¹ in herring; Figure 7). Furthermore Arrhenius and Hansson (1994a,b) calculated only 0.13–0.17 g g⁻¹ day⁻¹ daily ration in herring 25–39 mm long, based on in situ investigations at ~17°C. These values are ~50% lower than estimates predicted by the bioenergetics model of Rudstam (1988). Houde and Zastrow (1993) calculated a weight-independent relationship between temperature and daily food ingestion for fish larvae across many species of both freshwater and marine origin. Using their formula, fish larvae ingested 0.34 g g⁻¹ day⁻¹ at 10°C and 0.64 g g⁻¹ day⁻¹ at 20°C. These estimates fit very well in our calculations of daily rations (Figure 7). All these comparisons indicate that in the present study underestimation of the daily rations of perch and herring larvae due to incorrect use of model parameters is unlikely. Instead, there is slight evidence that models developed for age-0 juvenile fish rather tend to estimate higher daily rations for fish larvae than are observed during in situ studies.

In summary, it is concluded that the spring decline of the E.affinis population in Barther Strom is not the exclusive consequence of predation by age-0 perch and age-0 herring. Besides predation by adult fish and invertebrates, other reasons must be responsible for that dynamic. Interspecific competition within the zooplankton community due to lowered food supply appeared to contribute in only a minor way to the observed fluctuations in copepod density (Heerkloss et al., 1984; Arndt, 1989). However, rapid changes in the water temperature and the pH during the spring phytoplankton blooms (as at the end of May, Table II), connected with high NH₄⁺ concentrations (see above), were shown to increase E.affinis mortality substantially (Ring et al., 1985).

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