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New Approaches to Mesozooplankton Production Estimates against the Background of Food Web Considerations for the Bornholm Basin (Southern Baltic Proper)

key words: mesozooplankton, catch efficiency, production, trophic structure, Baltic Sea

Abstract

Mesozooplankton production was estimated by using a new sampling technique and two alternative calculation methods. In essence, production estimates are based on significantly higher abundances. The contribution of juvenile stages to copepod and fish dynamics was generally low, so that the omission of juvenile stages in budgets will result in a small error. The situations reported in this study present a unique food web szenario, which in detail, however, was strongly dependent on methodology. Furthermore, relations between trophic levels were considered with respect to vertical distribution.

1. Introduction

This article presents an estimate of the seasonal status of mesozooplankton production in an area of the Baltic Proper. In contrast to LINDAHL (1977) spatial (i.e. vertical) variability of the mesozooplankton biomass is considered. The production estimates presented are based on studies of vertical distribution by DAHMEN (1995).

The chosen site is of particular significance for Baltic cod *(Gadus morhua callarias)* especially in recent years. Because of the bad oxygen conditions in the Gdansk deep, the Slupsk furrow and the Gotland Basin, the Bornholm deep became the only spawning ground for the eastern Baltic cod (PLIKSHS *et al.,* 1993). A strong decrease in the reproductive success of cod since 1980 led to a stock decline to 10% of the original size, accompanied by a corresponding decrease of catches since 1983 (HELCOM, 1996; KÖSTER, 1994). This led to a case study on the recruitment of cod in the central Baltic since 1987. A number of fishery studies already exist concerning the distribution of cod eggs and larvae and the egg mortality (for example GRØNKJÆR and WIELAND, 1997; LENZ *et al.,* 1995; WIELAND, 1995). Furthermore the predation on juvenile stages by potential spawn predators (KÖSTER, 1994; KÖSTER and SCHNACK, 1994) has been investigated.

Consideration of the vertical distribution and feeding ecology of cod larvae raises the question, whether there is enough food for them. The presented investigation was intended to complement the fishery study in this respect. On the other hand estimates from fixed samples from the fishery cruises and from further data sources are used to create a szenario as complete as possible with regard to the zooplankton. From the point of view of zooplanktologists the question is, whether the mesozooplankton dynamics is determined by predators or by primary production in the situations studied and whether the answer is strongly dependent on methodological variation.

2. Methods

2.1. *Sampling Tests*

The net introduced for this study had never been used before and needed to be tested. It was a small 47 µm auxiliary net with an opening diameter of 4 cm, which was hanging in the center of the opening of a 335 µm net with an opening diameter of 1 m^2. This kind of net construction is especially exposed to the danger of net avoidance because the great pressure wave caused by the great net is also preceeding the opening of the small net. Additionally, the towing speed was 3 kn. The abundances of both nets were counted.

A further comparison was carried out with 30-l Niskin samplers. Five sampling stations were distributed equally over the towing distance of about 280 m of the horizontal net to obtain the overlapping of the water volumes sampled by the two techniques. The individual numbers of the sampling stations were averaged. Copepods of different size classes were counted.

2.2. *Zooplankton*

The sampling stations (21 and D) in the Bornholm Basin (ICES subdivision 25) lie just north of the Polish fishery zone (Fig. 1) at a water depth of nearly 90 m. The mesozooplankton sampling was carried out using 47 µm horizontal nets and was carried out on fishery surveys, so that only three sampling dates, each in a different year and season, could be analyzed. These observations may be seen as snapshots and not necessarily as representative for a season. Therefore they will not be extrapolated to construct an annual cycle. For more details see DAHMEN (1995).

The potential copepod production was calculated using a holistic approach (HUNTLEY and LOPEZ, 1992; HUNTLEY, 1996) and additionally by summarizing the production values of single species and their developmental stages (EDMONDSON and WINBERG, 1971).

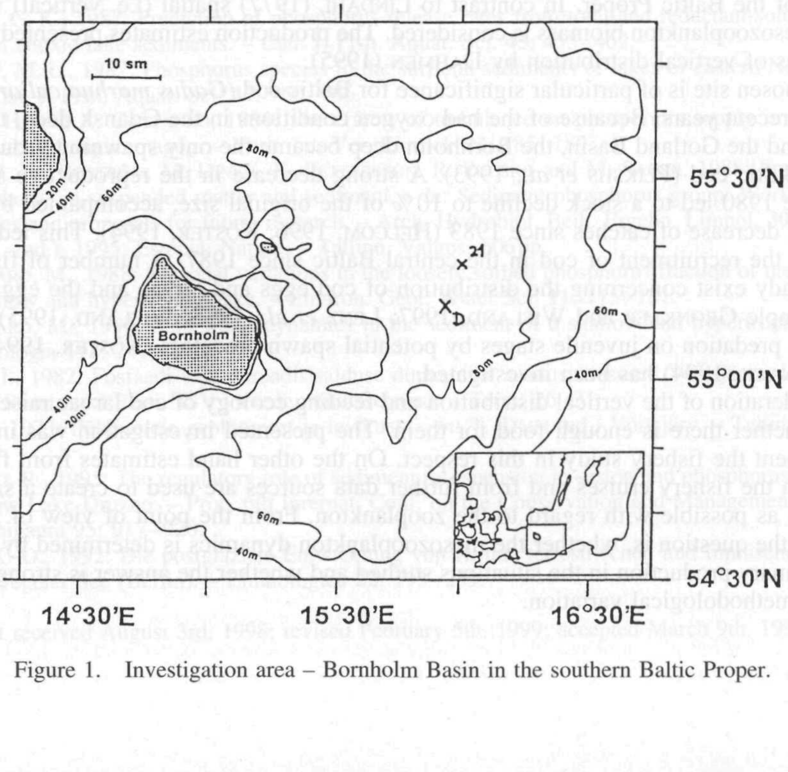

Figure 1. Investigation area – Bornholm Basin in the southern Baltic Proper.

Table 1. C/Chl *a* values determined from BMP data.

month	C/Chl *a*
26th July 1991	94.8
12th Aug. 1992	46.8
[31st Oct. 1988	6.3]
4th Nov. 1992	29.9

$$P = B \cdot g, \text{ where } g = 0.0445 \cdot e^{0.111T}$$ (Huntley and Lopez, 1992)

P = daily potential copepod production, B = biomass per area, g = weight specific growth rate per day, T = temperature in the respective depth.

$$P = N_i \cdot \Delta w_i / D_i$$ (Edmondson and Winberg, 1971)

N_i = individual number of stage i, Δw_i = weight increase of stage i, D_i = development time of stage i in days, i = {NI-VI, CI-V, females}.

The production of cladocerans was calculated with an equation derived for *Bosmina coregoni* (Kankaala *et al.*, 1984). For appendicularians a P/B value of 0.27 d^{-1} (rounded) for *Fritillaria pellucida* at 13.5°C (Fenaux, 1976) was adapted to other temperatures with a Q_{10} value of 2 (Ikeda, 1985). The production was calculated for each depth seperately according to the variation of T, D_i or P/B respectively with depth and integrated over the water column.

The consumption of copepods was determined by gross growth efficiency $K_1 = 0.245$, an average of a number of literature values with a standard deviation = 0.071. A value for *Fritillaria* has not been given so far, but according to Brafield and Llewellyn (1982) a higher value than 0.3 is not a realistic assumption. The consumption of cladocerans was negligible because of their low abundances at the sampling dates.

The food demand for basic metabolism is given by respiration. The amount of excretion is not marked compared with respiration (Omori and Ikeda, 1984). The respiration was calculated according to Ikeda (1985) with a respiratory quotient of 0.85.

$$\ln R = a_0 + a_1 \cdot \ln X_1 + a_2 \cdot X_2, \text{ where R in } \mu l\ O_2\ \text{Ind.}^{-1}\ h^{-1}$$ (Ikeda, 1985)

a_x = regression coefficients ($a_0 = 0.5254$, $a_1 = 0.8354$, $a_2 = 0.0601$), X_1 = individual weight in mg C, X_2 = temperature in °C.

2.3. *Phytoplankton*

The phytoplankton biomass in April 1992 was determined in the Baltic Monitoring Programme (BMP) using the Utermöhl technique. For July 1991 and October 1988 chlorophyll *a* concentrations (Dahmen, 1997a) were converted to biomasses. The C/Chl *a* ratios of various years calculated from corresponding BMP data (Table 1) proved to be very different both in summer and in autumn, so that for each season two C/Chl *a* ratios were used resulting in two alternative phytoplankton biomasses (Table 6). The C/Chl *a* value calculated for October 1988 was considered unrealistic according to Meyerhöfer (1994).

2.4. *Evaluation of Fishery Data*

Biomass and production of herring and sprat older than 12 months were calculated from numbers and individual weights (Köster, unpubl., taken from Dahmen, 1995). The production was calculated by the increment summation method, such as applied by Thurow (1984). Biomass and production of the larvae of cod and sprat resulted from individual numbers from Zuzarte (unpubl.) and Grønkjær (unpubl.), which refer to the same nets, in which the 47 μm inserts for this study were hung. The daily potential production was obtained by the specific growth rate (SGR) given by Munk (1993) for sprat and by Folkvord *et al.* (1994) and Gamble and Houde (1984) for cod.

The daily consumption of herring and sprat on single zooplankton groups was given by KÖSTER (unpubl., taken from DAHMEN, 1995) for April and July. The consumption for April refers to 1991, but was taken also for 1992 because of similar fish stocks. For the larvae of sprat and cod the consumption was calculated by a K_1 value of 0.3 (HOUDE, 1989; ARRHENIUS and HANSSON 1993) and for fish in October 1988 by a K_1 value of 0.25 (ELMGREN, 1984).

3. Results

3.1. Results of Method Control

The 335 µm net proved not to be suitable for testing, because the catch efficiency of this net even for the adult copepods was extremely lower than that of the 47 µm insert (Table 2). The results of the comparison between 47 µm insert and Niskin sampler are given in table 3. The relation between body size and catch efficiency was not clear, because trends were opposite in the two sampled depths. The great difference of the abundance quotients for nauplii between both depths was probably due to a small counting volume (nauplii: 0.47–2.88 l, copepodites: 3.75–7.5 l) and not only to the variability *in situ*. The average relation shows that the suspicion, that big copepods avoided the insert opening with its diameter of only 4 cm, cannot be confirmed by comparison with the Niskin sampler. However big copepods avoid this sampler, too (pers. comm.).

Table 2. Quotient of abundances obtained from the 47 µm and 335 µm nets. C = copepodite stage. </> means, that less than 20 individuals were counted for one net, so that a precise factor would not be realistic. For each copepodite stage two catches were counted. If one of the two resulting factors was unnecessary because of the </> information of one factor, only the other factor was given.

	A_{47}/A_{335}
Pseudocalanus minutus CIV	>62
Acartia longiremis CVI (1st sample)	134
Acartia longiremis CVI (2nd sample)	155
Acartia bifilosa CVI	>112
Temora longicornis CV	>104
Temora longicornis CVI (1st sample)	37.3
Temora longicornis CVI (2nd sample)	30.0
Centropages hamatus CVI (1st sample)	8.94
Centropages hamatus CVI (2nd sample)	<10
Evadne nordmanni	<30
Fritillaria borealis	>2600

Table 3. Quotient of abundances obtained from the NISKIN sampler (A_S) and the 47 µm insert (A_{47}). CL = cephalothorax length.

	A_S/A_{47} (10 m depth)	A_S/A_{47} (20 m depth)	Ø A_S/A_{47}
nauplii	0.442	1.490	0.967
0.2–0.36 mm CL	0.640	1.080	0.859
0.38–0.5 mm CL	0.749	0.844	0.797
>0.52 mm CL	0.763	0.481	0.622

3.2. Results of Calculations

3.2.1. Zooplankton Production

Zooplankton production was calculated from depth-dependent seasonal abundances and temperature profiles presented in full by DAHMEN (1995). In April 1992 the minimum temperature of 3.7 °C was above the halocline and below it ranged from 5.8–6.9 °C. In July the temperature was 17 °C at the surface and 4.1–6.9 °C below the halocline. In October 1988

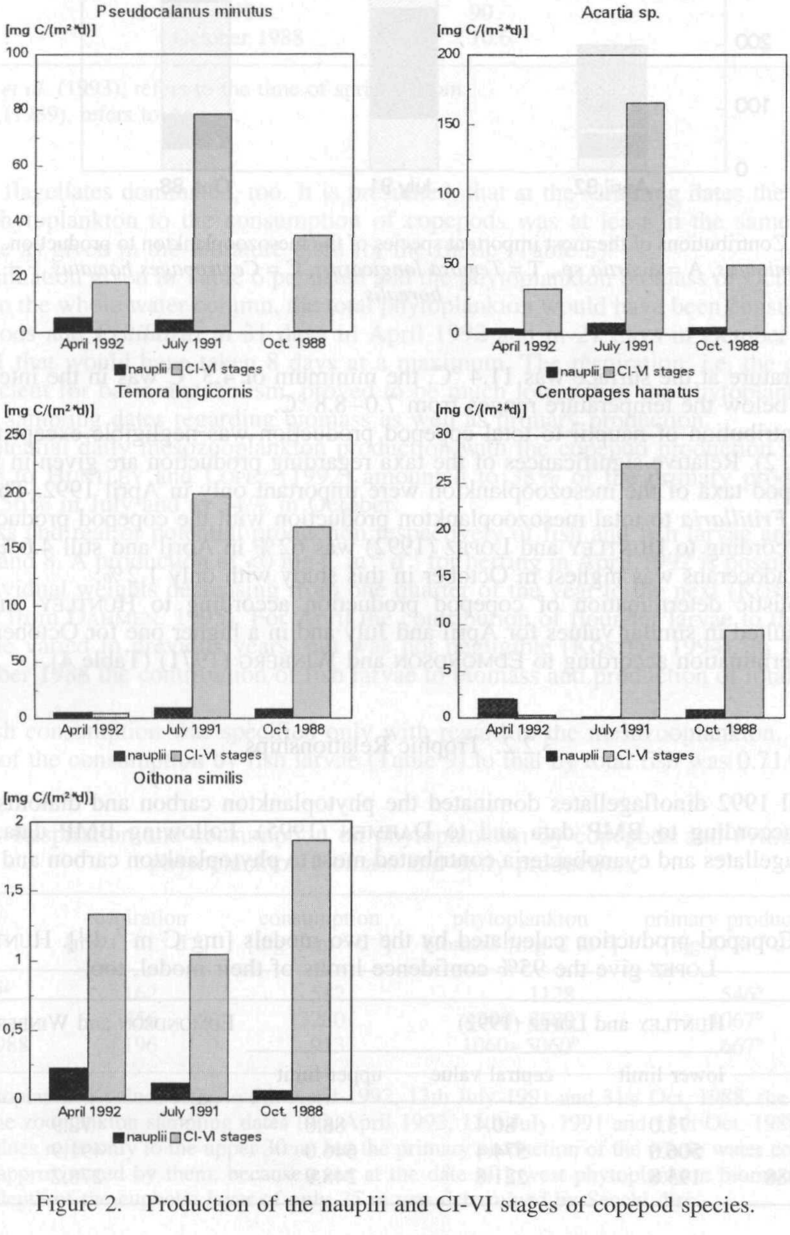

Figure 2. Production of the nauplii and CI-VI stages of copepod species.

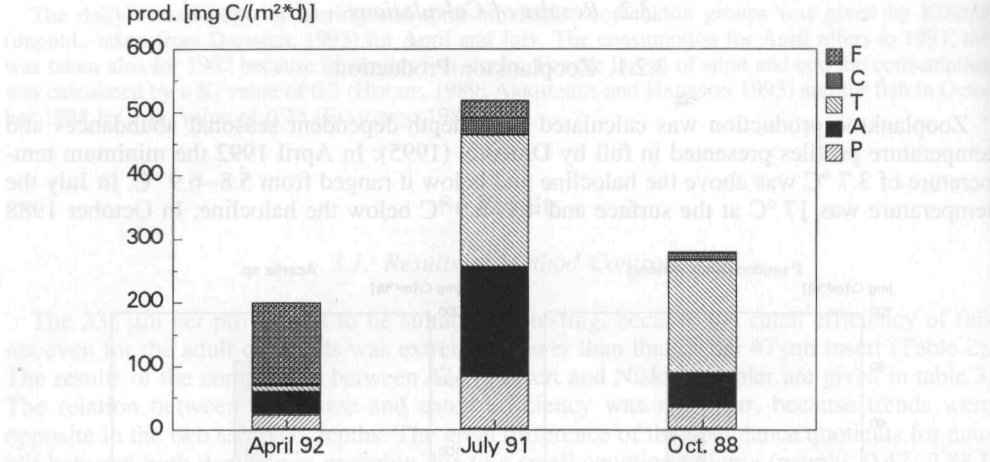

Figure 3. Contributions of the most important species of the mesozooplankton to production. P = *Pseudocalanus minutus*, A = *Acartia* sp., T = *Temora longicornis*, C = *Centropages hamatus*, F = *Fritillaria borealis*.

the temperature at the surface was 11.4 °C, the minimum of 4.3 °C was in the intermediate layer and below the temperature ranges from 7.0–8.8 °C.

The contribution of nauplii to total copepod production was negligible except for April 1992 (Fig. 2). Relative significances of the taxa regarding production are given in Figure 3. Non-copepod taxa of the mesozooplankton were important only in April 1992. The contribution of *Fritillaria* to total mesozooplankton production with the copepod production calculated according to HUNTLEY and LOPEZ (1992) was 62% in April and still 4.6% in July. That of cladocerans was highest in October in this study with only 1.2%.

The holistic determination of copepod production according to HUNTLEY and LOPEZ (1992) resulted in similar values for April and July and in a higher one for October compared to determination according to EDMONDSON and WINBERG (1971) (Table 4).

3.2.2. Trophic Relationships

In April 1992 dinoflagellates dominated the phytoplankton carbon and diatoms the cell number, according to BMP data and to DAHMEN (1995). Following BMP data, in July 1991 μ-flagellates and cyanobacteria contributed most to phytoplankton carbon and in Octo-

Table 4. Copepod production calculated by the two models [mg C m^{-2} d^{-1}]. HUNTLEY and LOPEZ give the 95% confidence limits of their model, too.

	HUNTLEY and LOPEZ (1992)			EDMONDSON and WINBERG (1971)
month	lower limit	central value	upper limit	
April 1992	73.0	80.4	88.0	72.9
July 1991	506.0	574.4	646.0	491.9
October 1988	195.8	221.8	248.9	278.2

Table 5. Total consumption by mesozooplankton groups.

taxon	month	consumption [mg C m^{-2} d^{-1}]	remarks
copepods	April 1992	325 (152)	(less heterotrophs)[a]
	July 1991	2330 (2190)	(less ciliates)[b]
	October 1988	902	
Fritillaria	April 1992	430	
	July 1991	90	
	October 1988	10.6	

[a] LIGNELL *et al.* (1993), refers to the time of spring bloom.
[b] TISELIUS (1989), refers to August.

ber 1988 flagellates dominated, too. It is presumed, that at the sampling dates the contribution of phytoplankton to the consumption of copepods was at least in the same order of magnitude as given in the literature cited for the Baltic (Table 5).

If the situation given in Table 6 persisted and the phytoplankton biomass of October 1988 referred to the whole water column, the total phytoplankton would have been consumed only by copepods and *Fritillaria* in 31 days in April 1992 and in 21 days in October 1988. In July 1991 that would have taken 8 days at a maximum. The respiration, i.e. the consumption sufficient for basic metabolism, proved to be much lower than the phytoplankton supply at all sampling dates regarding biomass as well as primary production.

The potential daily mesozooplankton production with the copepod production calculated according to HUNTLEY and LOPEZ (1992) amounted to 38% of the primary production in April, to 56% in July and to 34% in October.

Biomass and real or potential production respectively of fish and fish larvae are given in Tables 7 and 8. A production of <0 mg C m^{-2} d^{-1} for herring in April 1992 is possible because of individual weights decreasing from one quarter of the year to the next (KÖSTER unpubl., taken from DAHMEN, 1995). For April the contribution of flounder larvae to the total of fish larvae varied in previous years, but was not negligible (KÖSTER, 1994). In July 1991 and October 1988 the contribution of fish larvae to biomass and production of total fish was low.

The fish consumption was specified only with regard to the mesozooplankton. The contribution of the consumption by fish larvae (Table 9) to that by total fish was 0.71% in July

Table 6. Respiration and consumption on phytoplankton by copepods and *Fritillaria* and phytoplankton biomass and daily production.

	respiration [mg C m^{-2} d^{-1}]	consumption [mg C m^{-2} d^{-1}]	phytoplankton biomass [mg C m^{-2}]	primary production [mg C m^{-2} d^{-1}]
April 1992[a]	162	582	1128	546[b]
July 1991	456	2280	4390–8880	1067[b]
October 1988	196	913	1060–5060[b]	667[b]

[a] The phytoplankton values refer to 5th April 1992, 13th July 1991 and 31st Oct. 1988, the consumption to the zooplankton sampling dates (9th April 1992, 13th July 1991 and 13th Oct. 1988).
[b] These values refer only to the upper 30 m, but the primary production of the whole water column may be well approximated by them, because even at the date of lowest phytoplankton biomass, in April 1992, a depth of the euphotic layer of only 25 m was determined by Secchi disc.

Table 7. Biomass and production of herring and sprat. Sum from age class 1 up.

species	month	biomass [mg C m^{-2}]	contribution to herring + sprat [%]	production [mg C m^{-2} d^{-1}]	contribution to herring + sprat [%]
herring	April 1992	28.5	3.29	–0.032	–34.41
	July 1991	534.3	62.07	1.028	48.20
	October 1988	667.2	79.69	0.078	31.45
sprat	April 1992	837.7	96.71	0.125	134.41
	July 1991	326.5	37.93	1.105	51.81
	October 1988	170.0	20.31	0.170	68.55
herring + sprat	April 1992	866.2		0.093	
	July 1991	860.8		2.133	
	October 1988	837.2		0.248	

Table 8. Biomass and potential production of larvae of sprat and cod.

species	month	biomass [mg C m^{-2}]	contribution to all fish larvae [%]	production [mg C m^{-2} d^{-1}]	contribution to all fish larvae [%]
cod	April 1988/1989	0.008/0.009		$9 \cdot 10^{-4}$/0.001	
	July 1991	0.010	2.54	0.001	1.89
	October 1988	$3 \cdot 10^{-4}$	0.94	$3 \cdot 10^{-5}$	0.75
sprat	April 1988/1989	0.073/4.655		0.001/0.629	
	July 1991	0.384	97.46	0.052	98.11
	October 1988	0.032	99.06	0.004	99.25
cod + sprat	July 1991	0.394		0.053	
	October 1988	0.032		0.004	

Table 9. Consumption by fish larvae.

species	month	consumption [mg C m^{-2} d^{-1}]
cod	April 1988/1989	0.003/0.004
	July 1991	0.004
	October 1988	10^{-4}
sprat	April 1988/1989	0.033/2.097
	July 1991	0.173
	October 1988	0.015
cod + sprat	April 1988/1989	0.036/2.101
	July 1991	0.177
	October 1988	0.015

1991 disregarding the unknown consumption of age class 0. For the other two months a percentage cannot be given.

The biomass and production of medusae is given for the time of mass occurrence, i.e. for October, as mean value of the years 1983–1991 following JANAS and WITEK (1993). They amounted to 71.1 mg C m^{-2} and 0.765 mg C m^{-2} d^{-1} respectively. The potential production of medusae was in the same order of magnitude as the real production of herring and sprat

Table 10. Predation on mesozooplankton relative to its biomass and production.

	consumption [mg C m^{-2} d^{-1}]	zooplankton biomass [mg C m^{-2}]	zooplankton production [mg C m^{-2} d^{-1}]
April 1992[a]	7.26/9.32	2040 (268)[b]	202 (29)[b]
July 1991	24.89	5180 (786)	523 (70)
October 1988	3.83[c](3.90)	1920 (813)	284 (95)

[a] The consumption of all fish in that month refers to other years, for fish from age class 1 onwards (herring and sprat) generally to 1991, for fish larvae (sprat and cod) of 1988/ 1989.

[b] The values in brackets refer to the part of the water column from 50 m downwards. Concerning production that of copepods was determined according to Edmondson and Winberg (1971).

[c] Consumption only of medusae; total consumption in brackets. The fish consumption was estimated by a $K_1 = 25\%$ (Elmgren, 1984), given a mesozooplankton share in food of 80% for herring and of 100% for sprat following consumption values of August 1988 (Köster unpubl., taken from Dahmen, 1995).

in that month. The mean consumption of medusae of 3.83 mg C m^{-2} d^{-1} was calculated from respiration according to Janas and Witek (1993). The contribution of further predators to total consumption on mesozooplankton was negligible.

Referring to the whole water column, zooplankton biomass as food was 200 times as high as predation in April and July and production 20 times as high (Table 10). In October the corresponding factors with values of about 500 and 70 respectively were even higher. Considering the vertical distributions, the consumption-prey relations changed, because feeding by fish of the age class equal or greater than one took place primarily below the halocline. Then biomass of the mesozooplankton available for fish was about 30 times and mesozooplankton production 3 times as high as predation in April and July, bearing in mind that the interpolated depth intervals were greater below than above the halocline in these months. In October the greatest consumption was caused by medusae, which occurred predominantly above the halocline. That means that factors without and with considering the rough vertical distribution remain nearly the same, because the maxima of medusae and mesozooplankton were located in the same depth range. Summarizing, a food limitation didn't exist for mesozooplankton predators, even if the rough vertical distributions of predator and prey were considered.

The daily production of mesozooplankton predators without 0-group fish amounted to a minimum value of 0.05% of the mesozooplankton production in April with the copepod production calculated according to Huntley and Lopez (1992). The corresponding values for July and October were 0.42% and 0.09% respectively. The efficiencies are therefore much lower than those of the next lower trophic level.

4. Discussion

The method control can be supported by a theoretical approach. The filtration efficiency of the 47 μm insert was calculated to amount to 91.6% (Tranter, 1967; Wieghardt, 1953). The percentage will not have decreased during the towing distance because of clogging. The "open area" ratio was 31.8, while Tranter and Smith (1968) recommended values of >9 for smaller mesh sizes. A net comparable with the 47 μm insert was tested by Nichols and Thompson (1991). It had a mesh size of 61 μm, an opening diameter of 5 or 6.4 cm respectively and was towed at 4.5–5 kn. The "open area" ratio was 37 or 23 respectively and the filtration efficiency determined by a flowmeter was 87%.

Table 11. Daily mesozooplankton production [mg C m^{-2} d^{-1}] for the months investigated in this study.

Month	this study [a] Bornholm Sea	LINDAHL (1977) Eastern Gotland Sea	LINDAHL (1977) Åland Sea
April (1992/ 1976)	202 (210)	<10	20
July (1991/1976)	523 (606)	55	55–80
October (1988/1976)	284 (228)	30	40

[a] The part of the mesozooplankton production caused by copepods was calculated according to EDMONDSON and WINBERG, in brackets according to HUNTLEY and LOPEZ.

A further comparison of abundances was possible with values from the BMP obtained by WP–2 net catches (100 µm; DAHMEN, 1997b). The abundances compared refer to the whole water column. The WP–2 net samples were taken at nearly the same position in the Bornholm Basin with a time difference of two weeks in maximum relative to the 47 µm net catches. The abundances obtained by the 47 µm net were considerably higher both for nauplii and for copepodites at all sampling dates. The large differences between abundances obtained by the WP–2 net used in the BMP and the 47 µm inserts are assumed to be a result of the bad catching properties of the WP–2 net as established by POSTEL *et al.* (1991), KANKAALA (1984) and MØHLENBERG (1987).

With regard to the high abundances obtained a suction effect by the conus of the 47 µm net resulting in catch efficiencies greater than 100% may exist. Such an effect was observed for the "Nackthai" by SCHNACK (1992). It can be verified by comparison with the Niskin sampler only, if the catch efficiency of the sampler was 100%. According to SCHNACK (1992), however, the suction effect was 13% and therefore not very strong.

The growth model of HUNTLEY and LOPEZ (1992) for calculating the potential production with the constants used in this model is only suitable for copepod communities and not for single copepod species or other zooplankton groups. The growth rate of a community is said

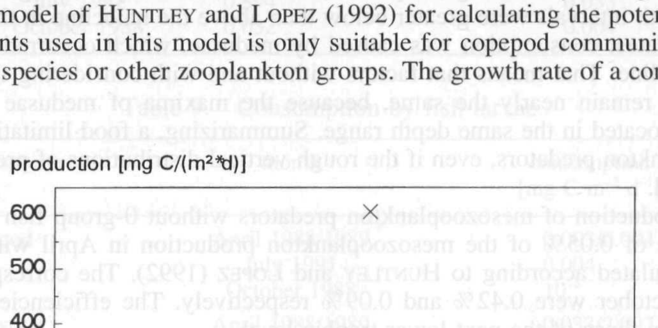

Figure 4. Annual course in mesozooplankton production from this study (crosses) and averaged over the years 1988–1992 (line, DAHMEN, 1997b) with bars indicating the standard deviation. The copepod production is calculated in both cases according to HUNTLEY and LOPEZ (1992).

Table 12. Production of *Pseudocalanus acuspes* and *P. acutus*.

month	*P. acuspes*	*P. minutus*
	[mg C m^{-2} d^{-1}]	
April 1992	28.5	23.2
July 1991	110.4	82.6
October 1988	47.8	34.9

not to be dependent on the species composition and the body size of copepods. Additionally the influence of temperature on growth rates of populations is assumed by Huntley and Lopez (1992) to override that of food availability in nature. The objections by Hay (1995) and Kleppel *et al.*, (1996), that not only temperature controls growth rate, were faced by Huntley (1996).

The potential production according to Edmondson and Winberg (1971) may refer to single species and even distinguish between nauplii and copepodites. This method was used also by Kankaala (1987) and Leppänen and Bruun (1988) for Baltic copepods. Two assumptions were made for obtaining the presented results. The first was isochronality for *Acartia*, *Oithona* and *Centropages*. The "isochronal rule" was introduced by Miller *et al.* (1977) and discussed for example by Klein-Breteler *et al.* (1994) and Van Den Bosch and Gabriel (1994). The second assumption was that of an unlimited food supply, which was apparently less the case at least for July 1991. Furthermore potential production excludes mortality. That mortality usually causes a significant difference between actual and potential production, was stressed for example by Ohman and Wood (1995).

Values of daily production in open areas of the Baltic Sea are given also by Lindahl (1977) for the Åland Sea and the Eastern Gotland Sea (Table 11). The great difference between the own results and those of Lindahl (1977) can sufficiently be explained by the following two reasons: 1) The production calculation was based on biomasses differing already by factors of 2.8 in October and 4.4 in April, because Lindahl (1977) used the WP–2 net (100 µm). The difference in production values (Fig. 4) from this study and from BMP recordings (Dahmen, 1997b) refers to the same fact (see also above, methodological discussion). 2) Hernroth and Ackefors (1979) noticed that the southern and the northern Baltic Sea differ in annual production by the factor of two.

The copepod species, which is called *Pseudocalanus minutus* in the BMP and also in this article, is thought to be actually *P. acuspes* according to Frost (1989) and Koszteyn (pers. comm.). According to McLaren *et al.* (1989) the productivity of *P. acuspes* is 27–37% higher than that of *P. minutus* under the seasonal conditions in the Bornholm Basin (Table 12).

The potential mesozooplankton production in July 1991 of 523 (606) mg C m^{-2} d^{-1} (Table 11) can be contrasted with a potential production of ciliates in the Bornholm Sea in July 1990 of 122 mg C m^{-2} d^{-1} in the upper 35 m (Auf Dem Venne, 1994).

The evaluation of the mesozooplankton production estimates and of the methods employed in this study will ultimately turn out badly with regard to the very high transfer efficiencies between phytoplankton and zooplankton in this study of nearly 40%. The maximum literature value was 21.4% for Kiel Bight, referring however to a whole year (Martens, 1976). Heerkloss *et al.* (1990) give values for single days, reaching from 2.5 to 16.4%. Two explanations can be offered: 1) The zooplankton abundances are too high. It is already shown that they are higher than results with the often used WP–2 net and it is also shown that just this net is likely to be deficient. 2) The phytoplankton production values are too low. Primary production was estimated by *in-situ* measurements, but with some days difference to mesozooplankton measurements. Realistic transfer efficiencies of 30% in maximum would require primary production values nearly one and a half times as high as estimated. Furthermore protozoa, rotifers and microbes as additional consumers and sedimentation especially of greater algae have to be considered (LIGNELL *et al.*, 1993; SMETACEK *et al.*, 1984). Especially in summer the contribution of autotrophic picoplankton, which is inaccessible for copepods, to primary production amounted to 18% in the inner Kiel fjord and at Boknis Eck to 60% (JOCHEM, 1990). On the other hand ciliates may play a significant role as food (POULET, 1983). The actual utilization of detritus including bacteria settling on it is not yet clarified (PAFFENHÖFER and VAN SANT, 1985). Summarizing, the primary production has to be at least two times as high to result in realistic transfer efficiencies. The solution of this problem is perhaps presented by PLATT *et al.* (1989), who showed the very high variability in the results of single primary production measurements. That means that the transfer efficiencies presented in this article are not realistic, because they refer only to such single highly variable values of primary production.

Regarding trophic relationships considerations about food availability may give an impression on the smaller scales of time and space. The question is whether phytoplankton concentrations in the water column were high enough to ensure individual survival in this depth and only at this moment and without regarding competition. According to HARRIS and PAFFENHÖFER (1976) copepod requirements usually amount to more than 200 mg C m^{-3}, and the lowest records found were 50 mg C $m^{-3.}$ Own maximum chlorophyll concentrations at the sampling dates (DAHMEN, 1997a) had to be converted to carbon values. In April 1992 a maximum carbon concentration of 297 mg C m^{-3} with a minimum C/Chl *a* ratio of 45 for dinoflagellates (MEYERHÖFER, 1994) could be found. For July 1991 and October 1988 C/Chl *a* ratios of 46.8 and 29.9 were used (Table 1) resulting in carbon concentrations of 114 and 132 mg C m^{-3}. Looking at the given concentrations, not only in July 1991, but also in October 1988 a moderate food availability even in the maximum layer may have made it difficult for individuals to meet patches with sufficiently high phytoplankton concentrations. However, this sight provides no conclusions on the survival chance of the population in future, as possible by consideration of phytoplankton and zooplankton production.

It doesn't look, as if the decrease in zooplankton abundance in July 1991 as shown by the BMP data was induced by predators (Table 10). That means on the other hand that the predators seemed not to be limited by food. In the North Sea in summer MUNK and NIELSEN (1994) found a consumption by fish larvae, especially by sprat larvae, of less than 1% per day and a predation by scyphomedusae of 1.3% of the copepod biomass. The copepod production, however, was as great as consumption on copepods. MUNK and NIELSEN (1994) added, that only a certain part of the size spectrum of copepods is useful for fish larvae. Confining to this part in form of nauplii, the consumption by fish larvae (Table 9) relative to the biomass of nauplii (April – 467, July – 259, October – 267 mg C m^{-2}) was still very low in this study and didn't come near the production of nauplii either (April – 16, July – 21, October – 14 mg C m^{-2} d^{-1}). Other results show a comparison between annual values of zooplankton production and consumption by fish, according to which consumption amounts to 30% (MÖLLMANN and KÖSTER, 1996, only Gotland Sea), 50% (RUDSTAM *et al.*, 1994) or 93% (ARRHENIUS and HANSSON, 1993) of production. Even if annual results are more appropriate for generalizations, seasonal considerations can better be compared with own conclusions. MÖLLMANN and KÖSTER (1996) showed a significant predation pressure on zooplankton in the first quarter of the year and a decreasing predation impact in the further progress of the year. The decreasing trend was found in this investigation, too. MÖLLMANN and KÖSTER (1996), however, demonstrated a higher predation pressure during all seasons, mainly because they used the essentially lower seasonal zooplankton production values according to LINDAHL (1977). Further reasons for the difference in the magnitude of the predation impact may be the variability in the estimates of fish consumption and presumably less sea area-specific details.

According to ARRHENIUS and HANSSON (1993), the zooplanktivory peaked in late summer and autumn because of age-0 clupeids. Regarding age class 0, quantitative values couldn't be given in this study. KÖSTER (1994) observed from catches in the Bornholm Basin, that 0-group sprat appeared in August and 0-group cod in September for the first time. ARRHENIUS and HANSSON (1993) obtained 0-group predation values for July and October for herring of <10 and 50% of the predation of all age classes (for all prey types) and for sprat of 0 and 65% respectively. In April the age class 0 was not involved in consumption at all. In the presented investigation in October 1988 the greatest consumption was caused by medusae. The low fish consumption at that time will not result in significant changes of the predator-prey ratio found, even if the age class 0 is included by doubling consumption. The method of estimating fish consumption for October 1988 by a K_1 value may not be appropriate, as tested by a comparison of methods for the two other sampling dates, but that would not be significant anyway in this context.

The contribution of fish larvae to total fish consumption of 0.71% for July 1991 given in this study is not representative. According to ARRHENIUS and HANSSON (1993) in April and October the sprat larvae didn't participate in consumption at all, while in July their contribution to consumption was 50%. The critical point is either the difference in the abundance ratios of fish larvae to fish in both investigations at that time or the difference in the methods used by KÖSTER (1994) and ARRHENIUS and HANSSON (1993) to determine fish consumption. Concerning the abundance ratios of fish larvae to fish, the abundances used by ARRHENIUS and HANSSON (1993) are more representative, because they are averages of several years.

As done for the phytoplankton-zooplankton relationship, a look at small-scale conditions, i.e. the food availability in certain depths, completes the picture of the food web situation on this trophic level and the evaluation of zooplankton net data. The net construction used in this study was especially suitable for investigating this aspect, because it allowed the quantitative sampling of fish larvae and nauplii during the same haul (DAHMEN, 1997a). The food concentration required for first-feeding cod larvae at a given swimming speed, feeding success and catabolic energy demand is 40–90 nauplii per litre corresponding to the age of larvae (SOLBERG and TILSETH, 1984). During the day such conditions were not observed at any depth with greater abundance of cod larvae, but July 1991 was the only sampling date, for which data on the vertical distribution of cod larvae exist (GRØNKJÆR unpubl.). For example in 35 m the concentration of nauplii was 12 individuals per litre (DAHMEN, 1995). Only the maximum concentrations of nauplii in April 1992 and July 1991 in 10–30 m and 5–15 m respectively were in the range demanded by SOLBERG and TILSETH (1984). If according to ELLERTSEN *et al.* (1989) a minimum concentration of 5–10 nauplii per litre was relevant, the density of nauplii in the Bornholm Basin was sufficient for the first-feeding cod larvae at all sampling dates at least in the upper 40 m. KRAJEWSKA-SOLTYS and LINKOWSKI (1994) came to the same conclusion, except for March and April. Regarding food concentration, they combine nauplii and younger copepodites.

Ultimately, results about the zooplankton-fish relationship like those about the feeding situation for zooplankton need more complete data and methodological clearness to allow a better assessment of trophic situations.

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