

TROPHODYNAMICS OF *PLEUROBRACHIA PILEUS* (CTENOPHORA, CYDIPPIDA) AND CTENOPHORE SUMMER OCCURRENCE OFF THE NORWEGIAN NORTH-WEST COAST

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Stomach-content analyses and laboratory experiments on *Pleurobrachia pileus* (Cydippida) showed an average digestion time of 2.0 h at 12 °C and a high potential predation rate with highest daily ration in terms of prey carbon ingested as percent of predator body carbon for the calanoid copepod *Calanus finmarchicus*, the biggest prey tested. Predation rate increased almost linearly with increased prey abundance over the whole range tested (12-1043 l⁻¹ in start concentration) of mainly small-sized copepods. Tests of the importance of prey size showed an individual clearance rate of 6.1 l day⁻¹ with *Calanus* prey alone, which was depressed to 29 % of this when smaller prey was also present in high abundance. This is supposed to be an effect of handling time of prey in the feeding process. The laboratory results were used to estimate the impact of this species in Norwegian coastal waters. Abundance data were collected in summer from 56 stations between 63° and 69°N along a cruise track west of Norway. *P. pileus* was present in the southern part of the investigated area and was restricted to the uppermost 50 m throughout the day. It mainly occurred where its predator, the atentaculate ctenophore *Beroe* sp., was absent and its abundance was not correlated with the ambient prey biomass. Estimation of the predatory impact on the zooplankton stock in the area where *P. pileus* occurred, using experimentally determined daily ration, clearance rates, abundance and individual size of ctenophores, and zooplankton biomass in the field, revealed a rather low impact. Integrated over time and depth (down to 100 m) these calculations suggested that up to a few percent of the zooplankton stock could be removed daily by *P. pileus* predation, but in the surface water, where it was most abundant, it could be of considerable importance in controlling the zooplankton abundance.

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INTRODUCTION

Pleurobrachia pileus is considered an important planktivorous predator in coastal waters of the north-east Atlantic (e.g. FRASER 1970; FRANZ & GIESKES 1984; WILLIAMS & COLLINS 1985), the north-west Atlantic (FRANK 1986; SUTHERS & FRANK 1990) and the Black Sea (MUTLU & al. 1994). It is also reported to be a key predator in large experimental enclosures (HARRIS & al. 1982). *P. pileus* typically occurs in seasonal bloom concentrations in shallow areas, but peak abundance is reported both for early summer (YIP 1981; VAN DER VEER & SADÉE 1984; WILLIAMS & COLLINS 1985) and autumn (RUSSEL 1933; FRASER 1970). A survey over 16 years with high temporal resolution from the cooling water inlet of a power station in the Thames estuary near London showed regular summer occurrence (range 2×10^{-5} -

0.2 m^{-3}) occasionally combined with an autumn/winter occurrence (ATTRILL & THOMAS 1996). *P. pileus* also occurs in Norwegian fjords (RUNNSTRØM 1932) and data on the seasonal abundance from a land-locked fjord show that both spring and autumn maxima may occur (RISØEN 1983; STRAND 1983). Functionally, this species is an ambush, entangling predator (GREENE & al. 1986) and it has been previously indicated that cydippid and lobate ctenophores have a different functional response to prey concentration, as demonstrated for *P. bachei* and *Mnemiopsis mccradyi* by REEVE & al. (1978). Experimental studies based on a theoretical encounter model have also indicated a strong prey selectivity of *P. bachei* as a consequence of different swimming rate and susceptibility among different prey types (GREENE & al. 1986). This paper presents results on species composition of prey found in ctenophores from natural habi-

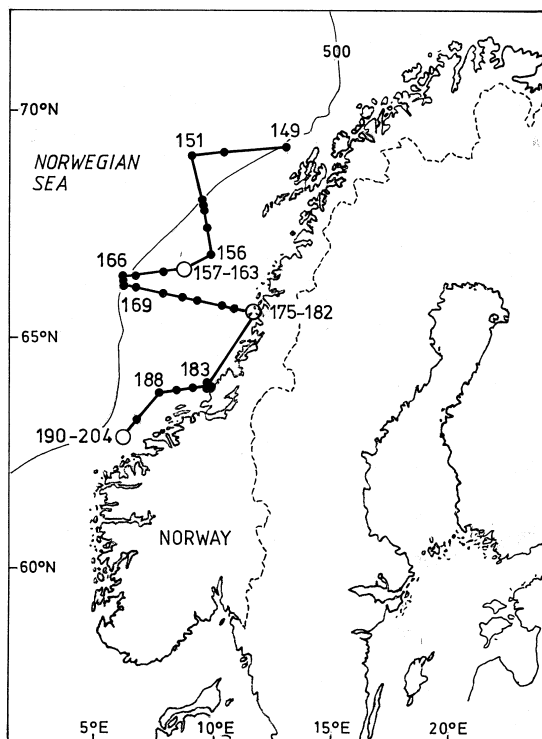


Fig. 1. Cruise track and position of sampling stations in the Norwegian Sea, starting on stn 149 on 19 June and ending on stn 204 on 3 July 1990. Three areas with closely spaced stations are shown as single circles only.

tats, together with the underlying predation rate, based on prey mass and a laboratory determined digestion rate. The laboratory experiments focused on the functional response at high prey abundance and the significance of prey size. The results are used along with field abundance data in order to estimate the predatory impact of *P. pileus* from the eastern part of the Norwegian Sea in a summer situation. Abundance data for gelatinous predators, including *P. pileus* and *Beroe* sp., were collected from 56 stations by using a 1 m² MOCNESS gear (WIEBE & al. 1985). Since this gear does not give good quantitative data for organisms with an abundance of $<< 0.01 \text{ m}^{-3}$, a Harstad trawl with 20×20 m opening during operation (NEDREAAS & SMEDSTAD 1987) was also used to sample larger and less abundant species. These samples showed patchy occurrence of the sennaeostome scyphomedusa *Cyanea capillata* and the coronate scyphomedusa *Periphylla periphylla*, but the non-quantitative sampling did not provide abundance data. The results in this paper is therefore restricted to the two ctenophore species that were quantitatively sampled by the MOCNESS gear.

MATERIAL AND METHODS

Predation studies

These studies were performed at Tjärnö Marine Biological Laboratory, Sweden, in 1983/84. Ctenophores for stomach content analyses were collected near the laboratory in short (< 5 min.), gentle, vertical hauls in the surface water using a WP2 net, and preserved immediately in 4 % formaldehyde/seawater solution. A separate test showed no indication of regurgitation of stomach contents of *P. pileus* when preserved. The short duration of the hauls is assumed to minimize any cod-end feeding. A zooplankton sample from a vertical haul (50-0 m) with a WP2 net, taken in May 1984 in Kosterfjorden, was microscopically analysed in order to give an indication of the natural prey composition. After a few weeks preservation the oral-aboral length of *P. pileus* was measured to the nearest 0.1 mm under a dissection microscope and stomach contents removed, identified to the highest possible taxon and counted. I used a shrinkage factor of 20 %, according to the findings by OORTHUYSEN & SADÉE (1982) cited by VAN DER VEER & SADÉE (1984). The same calculations as described above were used to estimate the amount of ctenophore body carbon. Total prey carbon was estimated by using standard values for each prey item, irrespective of developmental stage. These values were taken from measurements on freshly collected zooplankton material either from Askim Bay, south of Gothenburg, Sweden, in 1972 (own unpublished results) or from material used as prey in the present study. Live specimens were sorted out using a spoon made of plankton netting and transferred to a filtering tube and the procedure for AFDW determination was followed (see below). Carbon content of a few of seldom occurring prey types were estimated from their size and a comparison with similar sized and measured types. The predation rate ($\mu\text{g C hour}^{-1}$) was calculated by multiplying the stomach content ($\mu\text{g C}$) with the digestion rate (hour^{-1}). Eleven individual ctenophores were used to estimate the digestion rate. These animals were fed in the laboratory at 12 °C and visually examined under a dissection microscope every 15 minutes. This procedure revealed the relative stomach fullness over time, and time to complete emptiness was defined as the digestion time. Because of the definition of the digestion time, prey items that were partly digested were counted as whole prey items in field collected ctenophores.

In the predation experiments I used either ctenophores collected by slow horizontal hauls in the surface water with a net equipped with a large non-filtering cod end, or ctenophores collected in plastic jars by scuba divers. The collected animals were quickly transported to the laboratory and held in large tanks in a constant-temperature room at 12 °C.

Darkness was used in all experiments in order to avoid any phototactic stimuli that could cause prey aggregation in the experimental jars. Since both predator and prey are non-visual feeders, any effect due to differences in light condition between the experiments and the field is supposed to be small.

The first type of experiment was performed in 2-litre jars with three small (< 10 mm) ctenophores per jar and were focused on the functional predation response with high prey concentrations, in order to detect any saturation level within realistic natural concentrations. I used approximately the same

size of experimental animals for all experiments. Two replicate jars and two controls (jars with prey only) were run for each prey concentration. The ctenophores were offered a mixture of the copepods *Temora longicornis*, *Acartia clausi*, *Paracalanus parvus* and *Pseudocalanus* sp. in decreasing dominance and some barnacle nauplii, in concentrations ranging from ca. 10 to more than 1000 prey litre⁻¹ in the start concentration. The functional prey concentration was defined as the arithmetic mean from the start and end of the experiment. The experimental animals were first held without food for 24 hours and the predation experiment proceeded then for another 24 hours. The whole procedure was performed at 12 °C. Remaining prey were enumerated after termination of the experiment and the difference between each experimental jar and the mean prey number of the two controls was defined as ingested prey.

The other type of experiments were focused primarily on the significance of prey size for predation, but in combination with both variable prey concentration (range 12 to 111 prey litre⁻¹ in start concentration) and ctenophore size. I used 5-litre plastic buckets with two ctenophores of the same size in each and two controls with prey only. Prey material was collected the previous day with a 90 µm meshed WP2 net in surface water. The fraction > 200 µm contained in decreasing order of abundance the copepods *Acartia longiremis*,

Centropages hamatus, *Acartia clausi*, cladocerans, the copepod *Pseudocalanus* sp. and some barnacle nauplii. The measured average individual dry weight was 5.0 µg and estimated carbon content 2.04 µg. The fraction < 200 µm contained almost exclusively rotifers of the genus *Synchaeta*, with an average individual dry weight of 0.67 µg and estimated carbon content of 0.27 µg. I also used copepodids stage V and VI of *Calanus finmarchicus* that were sorted out from material collected with a 180 µm WP2 net. These had an average dry weight of 200 µg and a carbon weight of 80 µg. All experiments were run for 12-24 hours in darkness at 12-13 °C. The difference between the average of the two controls and each experimental vessel was defined as ingested prey.

Spatial distribution study

Sampling was performed through stratified hauls with a MOCNESS (WIEBE & al. 1985) sampling unit with multiple nets of 1 m² opening area, 333 µm mesh and non-filtering cod-ends of ca 2 litre volume, along a cruise track starting on 19 June west of Lofoten and ending on 3 July 1990 west for Sandesjøen (Fig. 1). Salinity and temperature profiles were given from CTD probes mounted on the sampling gear, whereas the vertical distribution of chlorophyll was given from separate casts with an *in situ* fluorometer (Q-instruments, Denmark). These results are only presented as relative units

Table 1. List of prey found in the stomach contents of 91 specimens of *Pleurobrachia pileus*, sampled between February 1983 and May 1984 in Kosterfjorden, western Sweden.

Prey type	Body mass (µg C ind ⁻¹)	Total number	Maximum per <i>Pleurobrachia</i>	Number of <i>Pleurobrachia</i>	Total prey mass (µg C)
Copepoda					
<i>Calanus finmarchicus</i>	80	24	4	18	1920
<i>Paracalanus parvus</i>	5	40	5	20	200
<i>Pseudocalanus</i> sp.	8	60	26	24	480
<i>Acartia</i> sp.	4	11	3	9	44
<i>Metridia longa</i>	50	2	2	1	100
<i>Temora longicornis</i>	15	54	28	11	810
<i>Centropages</i> sp.	10	2	1	2	20
<i>Oithona similis</i>	1	74	9	29	74
Harpacticoid copepod	2	1	1	1	2
Copepod remains	20	12	3	8	240
Copepod nauplii	0.2	24	6	13	4.8
Cladocera					
<i>Evadne normanni</i>	1	59	50	2	59
<i>Evadne spinifera</i>	1	5	2	4	5
<i>Podon</i> sp.	1	6	2	4	6
Unidentified	2	2	2	1	4
Others					
Ostracods	2	20	12	6	40
Barnacle nauplius	0.5	48	16	13	24
Metanauplius larva	1	1	1	1	1
Zoea larva	10	4	3	2	40
Calyptopis larva	10	1	1	1	10
Foraminifera	5	1	1	1	5
<i>Oikopleura</i> sp.	1	2	1	2	2
<i>Sagitta</i> sp.	10	1	1	1	10
<i>Pleurobrachia</i> egg	0.4	9	9	1	3.2
Spionid larva	1	2	1	2	2

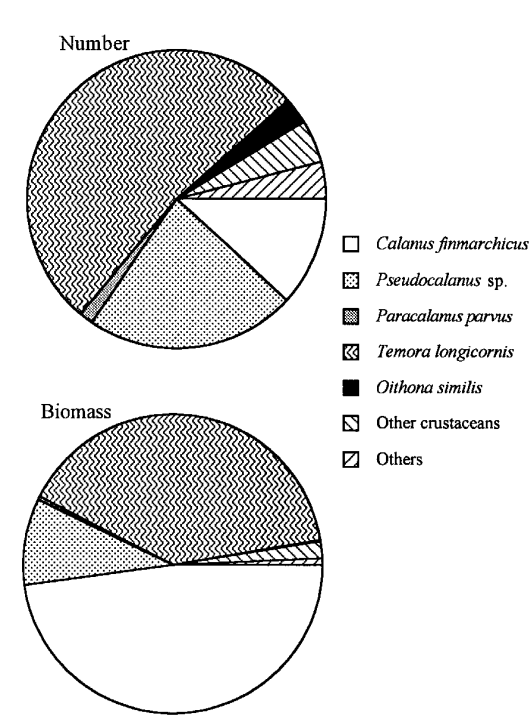


Fig. 2. Relative composition of zooplankton (50-0 m) number and biomass in Kosterfjorden, Sweden, May 1984.

(mV readings from an analog plotter) since we did not calibrate the instrument against results from chlorophyll analyses. MOCNESS zooplankton samples were taken from eight depth strata from the surface down to 200-300 m, with the average opening/closing depth at 2-15-30-50-100-150-200-250-300 m. Sampling stations were all in open waters except one divergence to a sheltered area (stns 175-182). During the latter part of the cruise (stns 189-204) sampling was performed with 4-hour intervals over three days in order to study diel variability in vertical distribution of *Pleurobrachia pileus*.

Table 2. Digestion time of *Pleurobrachia pileus* at 12 °C, defined as the time from transfer to filtered water to time of total emptiness of stomach. Average digestion time = 2.0 hours (SD = 0.79).

Time feeding (hours)	Fullness (relative)	Digestion time (hours)
1.0	0.8	1.3
1.5	0.5	1
1.5	0.5	1.5
1.5	0.5	1.5
1.5	0.5	1.5
3.0	1.0	1.6
3.0	1.0	2.5
3.0	1.0	3
3.0	1.0	3
3.0	1.0	3

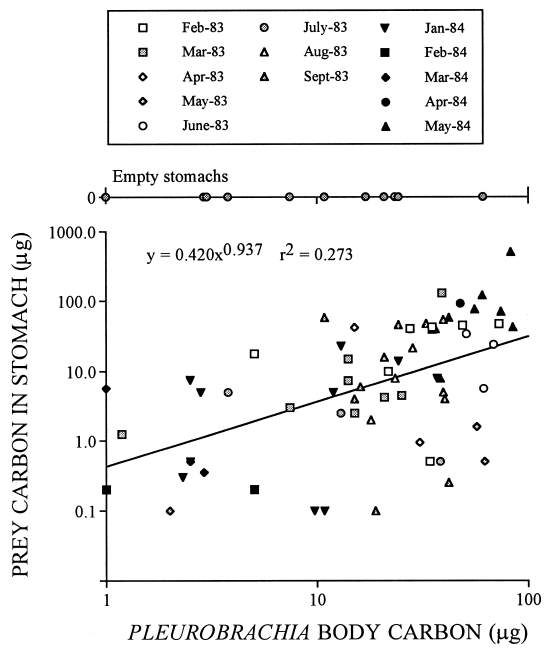


Fig. 3. Calculated prey mass in stomach contents of *Pleurobrachia pileus* collected in Kosterfjorden, Sweden, at different times of the year. The size distribution of the 14 individuals that had empty stomachs are displayed on a zero line.

The contents of the nets were poured into sorting trays and all medusae and ctenophores were sorted out, identified and enumerated. All specimens of *Pleurobrachia pileus* were transferred to separate glasses containing 4 % formaldehyde/seawater solution. In order to estimate the degree of shrinkage of *P. pileus* due to the preservation, I first measured the oral-aboral length (nearest mm) of 215 live ctenophores from 11 samples before the preservative was added. The oral-aboral length of all preserved ctenophores was measured to ± 0.5 mm in the laboratory one year after collection and the average shrinkage factor from this investigation, 31 %, was applied on the total material, in order to get an unbiased size distribution for the population. I did not discriminate between different size classes in the measurements.

The remaining zooplankton material was split in two aliquots with a Folsom splitter. One part was preserved in 4 % formaldehyde/seawater solution and the other transferred to a filtering tube with seawater and a pre-combusted (500 °C) and pre-weighed GF/C glass fibre filter in the bottom. The water was evacuated and the filter was quickly rinsed in distilled water and dried to constant weight at 70 °C and then incinerated at 500 °C for 24 hours and the weight loss was defined as the ash-free dry weight (AFDW). I used the conversion factor 0.5 from AFDW to organic carbon, as the samples were strongly dominated by copepods which typically have 90 % AFDW of DW and 40-50 % of DW as organic carbon (BÄRMSTEDT 1986).

In the calculations of body content of organic carbon and daily ration for *P. pileus* (DR%, food carbon ingested over

24 hours as percent of predator body carbon) I used a length/dry-weight relationship derived for *P. bachei* by REEVE & WALTER (1976): $\log DW \text{ (mg)} = 2.65 \times \log_{10} L \text{ (mm)}$, and 3.4 % organic C of DW, given for *P. pileus* by HOEGER (1983).

RESULTS

Predation studies in Kosterfjorden, Sweden

Prey caught by *P. pileus*. Prey identified from the stomach contents of 91 field collected *P. pileus* from Kosterfjorden, western Sweden, are listed in Table 1, together with their specific carbon content. The average frequency of occurrence in the stomach contents ranged from 0.011 (several prey types) to 0.822 (*Oithona similis*). The total prey carbon for each specific prey type should give an indication of its importance as a food source for *P. pileus* in the natural environment. *Calanus finmarchicus* was by far the most important, contributing 2.5 times more than the second, *Temora longicornis*. Copepods were overall the only important food source, and of the total stomach content (4107 $\mu\text{g C}$) only 5 % came from other prey types. The natural composition of zooplankton sampled in May 1984 is shown in Fig. 2 for a comparison. Copepods were the dominant group, with other crustaceans making up 3.1 % and non-crustacean organisms making up 3.4 % on a numeric basis, even less on a biomass basis. *Temora longicornis* was numerically dominant among copepods, but second on a biomass basis, with *Calanus finmarchicus* as the dominant one (Fig. 2).

Estimates of predation rate from stomach contents. The digestion time of the 11 studied ctenophores ranged from 1.0 to 3.0 h (Table 2), giving a mean value of 2.0 h, which is the figure I have used in the calculations for field predation rates.

The total data on stomach content from field collected *P. pileus* are displayed in Fig. 3, with the sizes of 14 empty ctenophores given on a separate axis. The scatter is rather large, with only 27 % of the variability explained by the regression line. This line indicates a somewhat decreasing stomach fullness with size (exponent < 1.0). By using a constant digestion time of 2.0 h, field predation rate (h^{-1}) can be estimated by dividing the stomach content by 2. For a small ctenophore of 10 μg body carbon DR% will on average be 392 %, whereas a big individual of 1000 μg body carbon has on average a DR% of 293 %. Maximum stomach contents seem also to increase with size of *P. pileus* and parallel the regression line for the mean at a level more than ten times higher (see Fig. 3). That means that the maximum DR% for a small ctenophore would exceed 4000 % and that for a big one would be at least 3000 %.

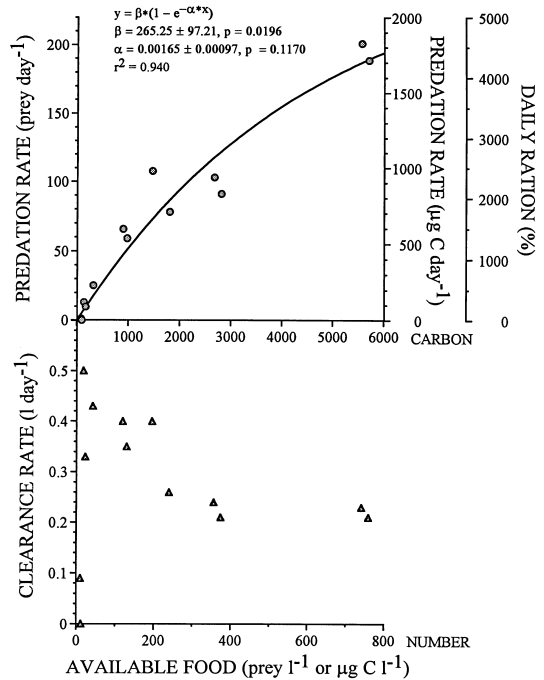


Fig. 4. Functional response of *Pleurobrachia pileus* on prey abundance. The predation rate, as prey ctenophore⁻¹ day⁻¹, was measured, whereas corresponding prey mass and DR% were calculated from average carbon content of prey and predator. The regression line shown represents an Ivlev function and its estimated parameters with \pm one SE are shown in the upper panel.

Laboratory determined predation rate. The functional response on prey concentration (Fig. 4, upper) showed an increase of the predation rate with increased prey abundance over the whole prey concentration tested. An Ivlev function that was fitted to the data indicated a maximum of 265 prey day⁻¹, reached at prey concentrations 4–5 times higher than I tested. The very low α -value, not significantly different from zero, thus indicates that the predation rate increased approximately linearly, without any saturation level within naturally occurring prey concentrations. Clearance rate showed a very sharp increase at low prey concentration, indicating a possible feeding threshold, with a gradual decrease thereafter (Fig. 4, lower).

Experiments with different sizes of prey (Fig. 5) showed that a single prey type gave clearance rates in a range from 6.1 l day⁻¹ for *Calanus* to around 1.7 l day⁻¹ for both > 200 μm and < 200 μm fractions. An addition of the > 200 μm fraction to *Calanus* prey (50 prey l⁻¹ together with 11 *Calanus* l⁻¹) dramatically reduced the clearance rate on *Calanus* to 29 % of that with *Calanus* only. The clearance rate on the > 200 μm fraction in this

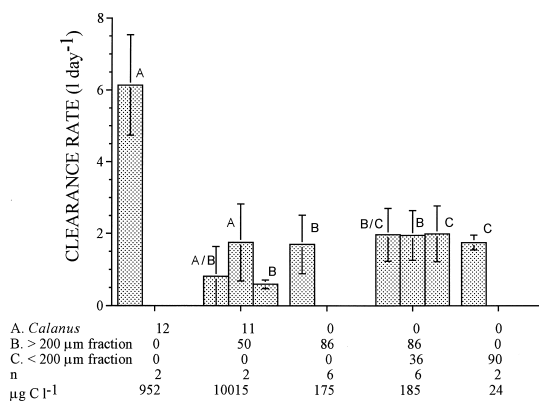


Fig. 5. Clearance rate of *Pleurobrachia pileus* in food environments with either a single prey type (A, B, C) or a combination of two types (A/B or B/C). Below the baseline are shown the start values of prey number, prey biomass and number of experiments. Bars denote 95 % confidence intervals.

combination was reduced to 35 % of that with this prey type only. The weighed clearance, calculated as $(F_1 \times n_1 + F_2 \times n_2) / (n_1 + n_2)$, where F and n represent the clearance

rate and start concentration, respectively, of the two prey types, was also lower than for any single-prey experiment or the combination of the two small prey (Fig. 5). The mixing of the two different size fractions did not show any effect on the clearance rate compared with that for the single prey type. However, it should be emphasised that the prey concentrations were similar (ca 350 prey l⁻¹) in these experiments but not in those where *Calanus* was involved.

The daily ration (DR%) normalises somewhat the effect of different sizes of the predator and in Fig. 10 upper right it is shown that DR% was closely related to the total prey carbon available, when using a log/log plot. Results from the combinations of the three different prey sizes are displayed in the two other panels and clearly show that the DR% of *P. pileus* decreased from *Calanus* prey (around 300 %) to prey fraction > 200 µm (11-32 %) and down to prey fraction < 200 µm (3-7 %). It is also shown that the smaller prey usually had a lower DR% in combination with a bigger prey than when offered alone. Within the size range of *P. pileus* used (10.5-16.0 mm length) there was no clear effect of size of the ctenophore (Fig. 6).

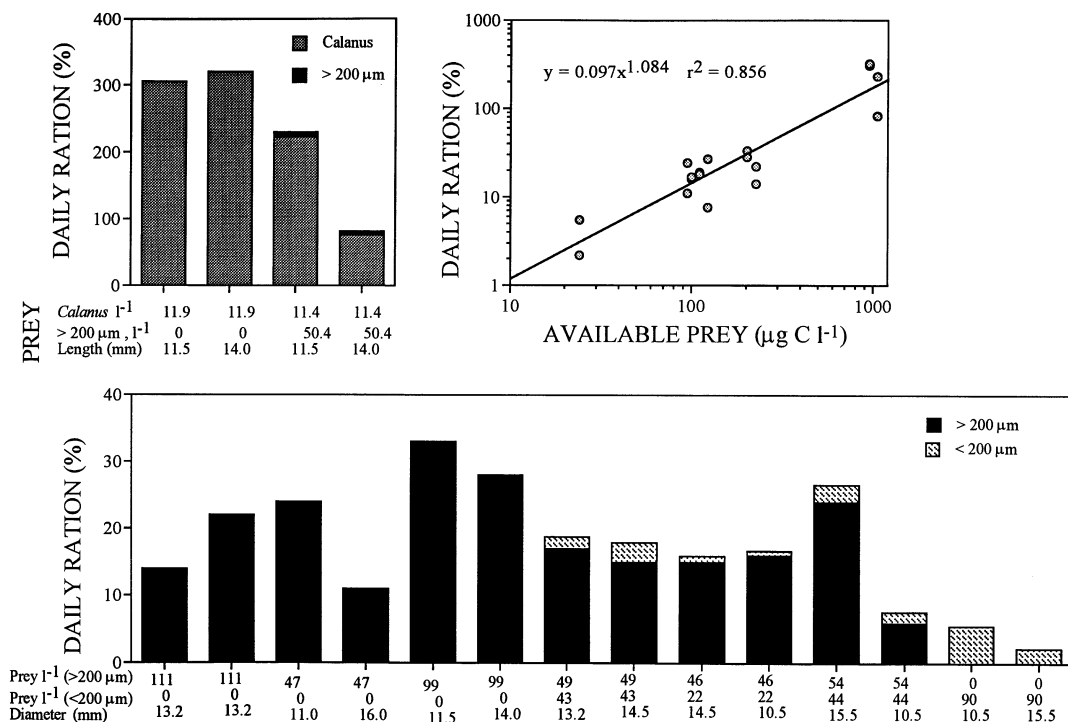


Fig. 6. Calculated daily ration of *Pleurobrachia pileus* in experiments where three different prey sizes were used. Upper left shows the results where *Calanus finmarchicus* was involved, lower panel shows the results where only the two other prey sizes were involved. Upper right shows the DR% plotted against the total prey mass in each experiment. In the bar histograms is also shown abundance (prey l⁻¹) of prey and oral-aboral length of predator. Same experiments as in Fig. 5.

Field study in the Norwegian Sea

Hydrography and chlorophyll. The hydrographical data from the cruise revealed three characteristic environments in the area covered (Fig. 7A-C). Stations far away from the coast (stns 155-171) had relatively warm (11-12 °C) and saline (34-35 psu) surface water whereas the more inshore stations (stns 172-188) were colder (ca 10 °C) at the surface and quite cold (6-7 °C) below 30 m, with a strong halocline between the brackish surface water (<< 30 psu) and the deeper parts (34 psu). In the southern area (stns 189-204) water was usually warmer (> 11 °C at the surface and > 9 °C above 30 m) and more saline, with 30-34 psu in the surface and 35 psu at 60 m. The first area was characterised by low chlorophyll in the surface, but with a strong sub-surface maximum at ca 20 m (Fig. 7C). The inshore area showed very high chlorophyll in the surface, but the maximum below, between 6 and 18 m. Finally the southern area showed the lowest chlorophyll, but a strong sub-surface maximum at ca 25 m (Fig. 7C).

Ctenophore abundance and zooplankton biomass. *Beroe* sp. mainly occurred in the southernmost part of the track, as did *Pleurobrachia pileus*, although they only partly overlapped. The abundance of *P. pileus* was not correlated with the zooplankton biomass (excluding gelatinous zooplankton), showing a correlation coefficient of -0.051 ($n = 16$). When plotting abundance of *P. pileus* against that of *Beroe* sp., using all stations and depth strata where *P. pileus* occurred, it was shown that they seldom co-occurred. *P. pileus* was present in totally 30 stations/depth strata in the area and in only two of them did *Beroe* sp. co-occur (Fig. 8).

Pleurobrachia pileus was abundant in the southernmost area investigated (stns 189-204, Fig. 1). Outside this area it was absent, except at stns 168, 183 and 184, where it was present in low or moderate abundance. The results from the former area represented 16 sampling stations taken at different times of the day over 91 hours. These have been plotted on a 24-hour time axis in Fig. 9, which shows that *P. pileus* had a mainly shallow distribution but showed no trend in vertical distribution with time of the day. The average number of individuals per m² was 12.4 ($n = 14$, SD = 1.75) in the

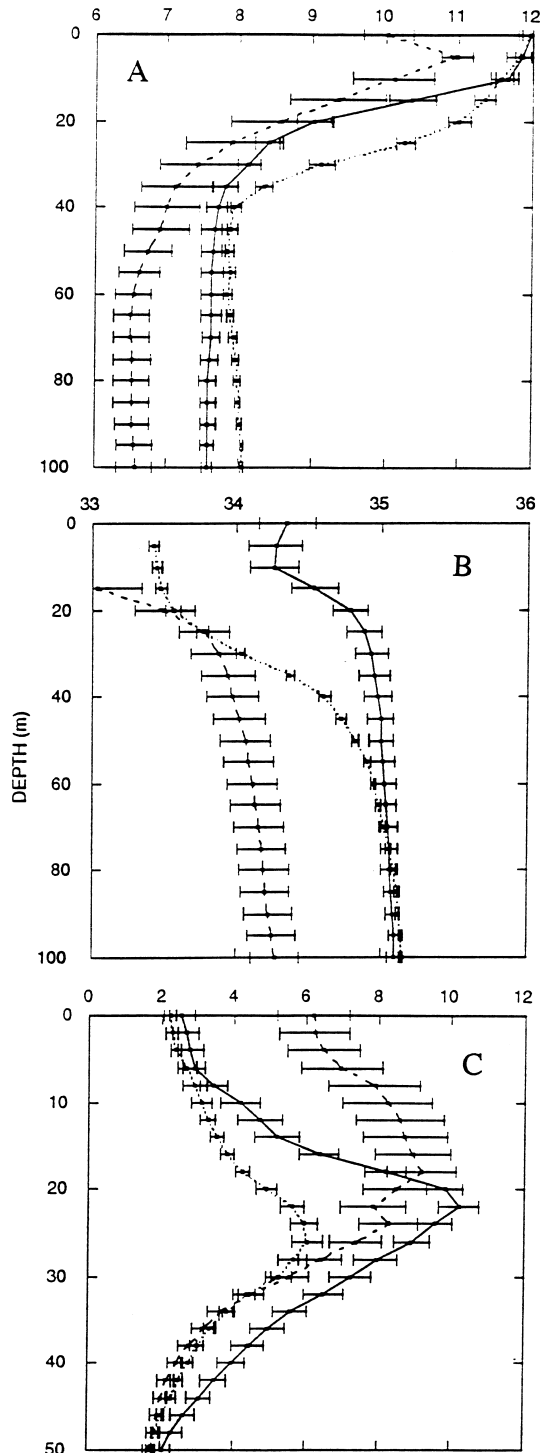


Fig. 7. The Norwegian Sea. Temperature (A, in °C), salinity (B, psu) and relative chlorophyll (C) profiles in the outermost area from the coast (stns 155-171, continuous line), the more inshore area (stns 172-188, broken line) and the southern area (stns 189-204, hatched line). The lines denote the average values and the horizontal bars \pm one standard error for the stations included in the respective areas.

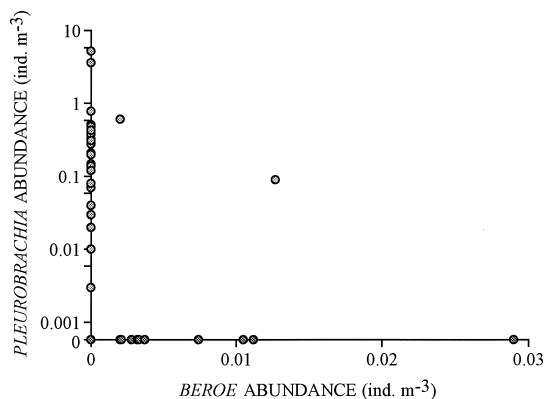


Fig. 8. The Norwegian Sea. The abundance of *Pleurobrachia pileus* plotted against the abundance of *Beroe* sp. in all samples from the southern area (stns 189-204) where at least one of them occurred. Each plot represents a sample from a given depth interval in a given station. Number of samples with *P. pileus* present = 30. Number of samples with *Beroe* sp. present = 17.

stations where it occurred. Highest number was recorded for stn. 191, with 111 m^{-2} , sampled at 10 hours.

The vertical distribution of *P. pileus*, *Beroe* sp. and zooplankton biomass (Fig. 10) indicated that *P. pileus* mainly occurred in the food-rich upper part of the water column, whereas *Beroe* sp. stayed below. There was a high variability in abundance of *P. pileus* between stations, with highest values (5.2 m^{-3}) recorded for stn 191.

The size distribution of *P. pileus* sampled with MOCNESS showed an arithmetic mean of 10.47 mm (SD = 2.76, $n = 1561$) and with some asymmetry towards large size (Fig. 11, skewness = 0.785).

DISCUSSION

Trophodynamics of *Pleurobrachia pileus*

Digestion rate. Recent studies on another gelatinous predator, the scyphomedusa *Aurelia aurita*, have shown that the digestion time is highly variable over time around an average value. The degree of variability is individually dependent, but the average value is rather constant between individual medusae, given that food and other conditions are the same (own unpublished results). In the present study the control of stomach fullness was done with rather low frequency (15 min.), thus probably contributing to the variability. But this should only decrease the precision. When comparing the presently found digestion time of 2.0 h with previously published results for *Pleurobrachia* there is

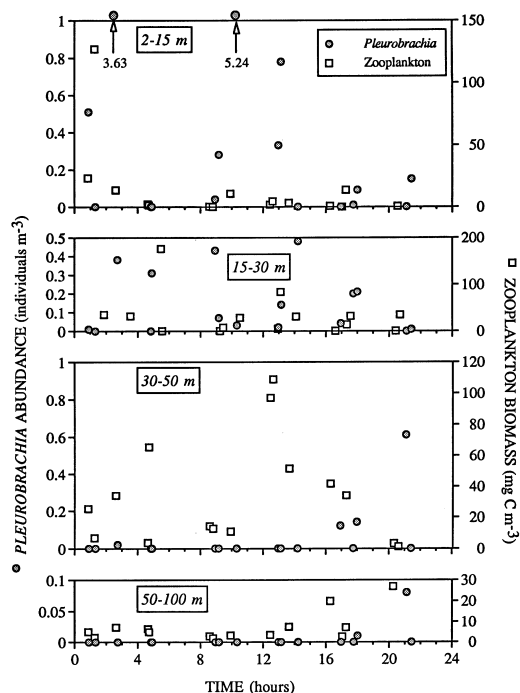


Fig. 9. The Norwegian Sea. Abundance of *Pleurobrachia pileus* and biomass of zooplankton, excluding gelatinous forms, in four vertical depth intervals, plotted along a 24-hour time axis. Each plot in a depth interval represents one sampling station from the southern area (stns 189-204), taken over a period of 91 hours.

a good agreement with that reported by ANDERSON (1974). He used copepods of the genera *Temora*, *Pseudocalanus* and *Acartia* and obtained a digestion time of 2.3 h for *P. pileus*. SULLIVAN & REEVE (1982) measured a digestion time for *P. bachei* of 1.7 h when given one prey item, 2.2 h when given more than one, and LARSON (1987) reported digestion times of the same species in the range 3.4-4.2 h. We have recently recorded the digestion time at 10°C of *Bolinopsis infundibulum* and with food dominated by the copepod *Calanus finmarchicus* the average digestion time was 2.3 h (own unpublished results).

Predation rate, clearance rate and daily ration. The calculations based on the stomach contents of field collected animals revealed very high predation rates as prey carbon. Overestimation could be caused by using too short digestion time, by an overestimate of the prey carbon in the stomach content, or a combination of the two. As argued above, the first alternative is not probable. My estimates of prey carbon of the different copepods were given for adults or late

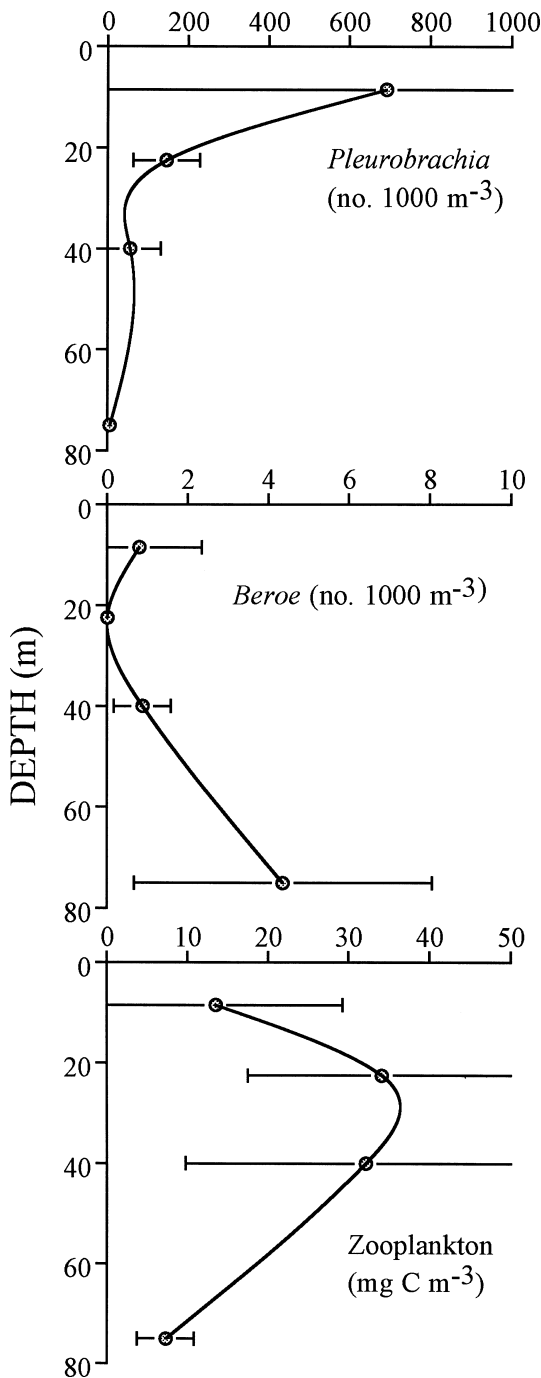


Fig. 10. The Norwegian Sea. Average vertical distribution of *Pleurobrachia pileus*, *Beroe* sp. and zooplankton biomass. Results based on MOCNESS samples from stn 189-204, sampled in the intervals 2-15, 15-30, 30-50, and 50-100 m. Bars = 95 % confidence intervals.

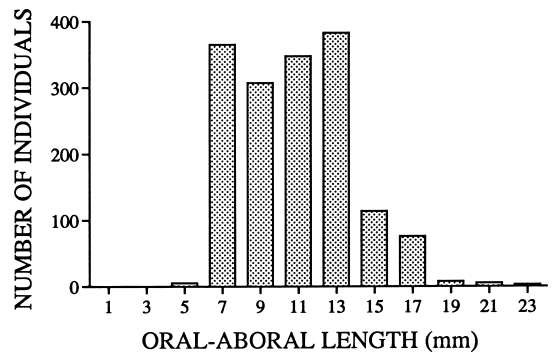


Fig. 11. The Norwegian Sea. The size distribution (oral-aboral length, compensated for 31 % shrinkage due to preservation) of *Pleurobrachia pileus* ($n = 1561$) sampled with MOCNESS in the southern area (stns 189-204).

copepodid stages, and since copepods made up on average 95 % of the prey carbon, incorrect carbon values could cause a considerable bias in the estimates of predation rate. However, I reached similar predation levels in experiments with *Calanus finmarchicus* as prey, and a closer look on the data of the field collected ctenophores with highest stomach content revealed a dominance of *C. finmarchicus*. Thus, *C. finmarchicus* might have a special position as prey by providing exceptionally high predation rates for *P. pileus*. However, the stomach content of *P. pileus* is highly variable, as shown by the > 100 fold range in all size classes (Fig. 6). Since the regression equation in Fig. 6 is calculated from the log-transformed data, the regression line will also systematically overestimate the predation rate, compared with an arithmetic mean value. If a linear regression model is applied to the data the predicted DR% of a small ($10 \mu\text{g C}$) ctenophore is 195 % compared 392 % when using a power function. Similarly, DR% is reduced from 293 % with the power function to 147 % with the linear function for a big ($1000 \mu\text{g C}$) ctenophore.

The functional response shown in Fig. 4 emphasises the potential ability of *P. pileus* to reduce prey populations, and within a range in concentration of 10-1000 prey l^{-1} , predation increased almost linearly. REEVE & al. (1978) showed the same linear increase with *P. bachei* and *Acartia* sp. as prey, but this levelled off at ca. 200 prey l^{-1} . My results do not indicate any saturation level and because the experiments were run for a full 24-hour period, they are not an effect of an extrapolation of short-term incubations. The ctenophore body carbon was estimated from empirical relationships (see Material and methods) and it has been shown that the carbon percentage may vary considerably in ctenophores (REEVE & al. 1989). Prey carbon was also indirectly

estimated, based on samples of dry weight of a mixture of prey organisms. However, even if these factors bias in the same direction it remains that the predation rate and daily ration can increase more or less linearly over extremely high food concentrations.

There were two striking results from the experiments with different prey types worth of discussing. First, these experiments showed that the largest prey gave three times higher clearance rate and 10–100 times higher daily ration than the other two prey types gave. Secondly, an addition of smaller prey to the *Calanus* prey dramatically reduced the clearance rate. However, the high daily ration produced from the *Calanus* experiments did not diverge from the trend shown when DR% was plotted against available prey (Fig. 6, upper right), and the high DR% can thus be explained solely as an effect of available prey biomass. The explanation of reduced clearance rate in the *Calanus* combination experiments is not so obvious, but probably includes a behavioural component. When catching a prey, *P. pileus* contracts its tentacles and rotates to manoeuvre the prey to the mouth. During this procedure it is unable to take another prey (REEVE & WALTER 1978). Although there is no time-budget study on this process for different prey types it is reasonable to assume that the difference in handling time between a big *Calanus* and a smaller prey is small. *P. pileus* is an ambush predator and the prey encounter is defined by the abundance and swimming speed of the prey (GREENE & al. 1986). Therefore, if there is not much difference in swimming speed between two prey types their encounter frequency with *P. pileus* will be directly proportional to their abundance. In an experiment like that with *Calanus* and the $> 200 \mu\text{m}$ fraction it is thus expected that *P. pileus* will encounter the small prey more frequently than the large. If *P. pileus* is an unselective predator it will have less time available for catching and handling *Calanus*. The experiments also showed that there is the prey number and not the prey biomass that governs this, since the two experiments with *Calanus*

had about the same prey biomass but contrasting prey number (cf. Fig. 5).

The choice of volume for the experimental vessel has been shown to be critical for an unbiased clearance rate. In a statistical evaluation of clearance data for *P. pileus*, GIBBONS & PAINTING (1992) showed that 81 % of the variability in clearance rate was explained by the variable volume of the vessel used (up to 100 l) whereas the size of the ctenophore only explained another 5 %. The effect of using small vessels seems to be exponentially increasing with the size of the ctenophore and rather small effects of vessel volume are expected for ctenophores around 10 mm oral-aboral diameter or less (cf. fig. 2, GIBBONS & PAINTING 1992). A summary of the clearance rates from the present experiments, standardised to litres day⁻¹ g⁻¹ wet weight, is given in Table 3. A comparison of literature data (see table VIII in MILLER & DAAN 1989) reveals that the range given from the present study (1.0–15 l day⁻¹ g⁻¹ wet weight) covers most of the range from the cited review (0.6–32 l day⁻¹ g⁻¹ wet weight). In opposite to the findings by GIBBONS & PAINTING (1992), MILLER & DAAN (1989) could not detect any effect of incubation volume, in the range 4 to 16 l, whereas there was a difference for prey type with late copepodids giving higher clearance rate (mean 4.4 l day⁻¹ g⁻¹ wet weight) than copepod nauplii (mean 1.0 l day⁻¹ g⁻¹ wet weight).

Abundance and distribution of ctenophores

The two ctenophores sampled here represent a classical predator-prey relation (GREVE 1970) and our data indicate that *Beroe* sp. more or less excluded *Pleurobrachia pileus*. The results for both *Beroe* sp. and *P. pileus* is supposed to be quantitative, because (1) both species are sufficiently robust to withstand the net stress and (2) they both were sampled well with the MOCNESS in vertically stratified hauls, thus making a direct comparison between them possible. I therefore think that the restriction of *P. pileus* almost completely to sam-

Table 3. *Pleurobrachia pileus*. Clearance rate as l g⁻¹ wet weight day⁻¹ from the different experiments with various food sources. The wet weight is calculated from the ctenophore length and the dry-weight relationship of REEVE & WALTER (1976) and a dry-weight proportion of 3.95 % (HOEGER 1983). In the combined-prey experiments the clearance rate for the first prey type is given. *Average dry weight of one prey item is 19.6 μg .

Type of prey	Prey l ⁻¹ at start	Oral-aboral length (mm)	Temp. (°C)	Volume (litre)	n	Clearance rate	
						Average	Range
<i>Calanus</i>	12	11.5–14.0	12	5	2	10.79	6.5–15
<i>Calanus</i> / $> 200 \mu\text{m}$	12	11.5–14.0	12	5	2	2.63	2.1–3.2
$> 200 \mu\text{m}$	47–111	10.5–15.5	12–13	5	6	2.60	1.0–4.9
$> 200 \mu\text{m}/\textit{Calanus}$	50	11.5–14.0	12	5	2	1.04	0.6–1.4
$> 200 \mu\text{m}/< 200 \mu\text{m}$	46–54	10.5–15.5	12–13	5	6	2.80	1.0–4.1
$< 200 \mu\text{m}$	90	10.5–15.5	13	5	2	3.15	2.0–4.3
$< 200 \mu\text{m}/> 200 \mu\text{m}$	22–44	10.5–15.5	12–13	5	6	2.92	1.2–5.0
Mainly copepods*	37–1047	8.5–10.0	12	2	11	0.99	1.0–1.5

ples where *Beroe* sp. was not present is explained by the strong predator-prey relationship.

The restricted data showed a patchy distribution of *P. pileus*, but because the ctenophore was almost continuously present from stn 189 throughout the cruise track I do not know the southward extent of its distribution. WILLIAMS & COLLINS (1985) and GREVE & REINERS (1988) have shown that *P. pileus* abundance proceeds as a wave through shallow coastal waters in the North Sea. My hydrographical data from the area of occurrence showed a deeper thermocline and halocline than the other two areas (Fig. 2) that might be explained by an intrusion of North Sea water. The vertical profile of chlorophyll also showed considerably lower level and somewhat deeper sub-surface maximum than those for the two other areas (Fig. 7), indicating a later post-bloom phytoplankton situation here.

The average abundance of 1 ctenophore m^{-3} in the surface water is within the range given for Scottish coastal waters (FRASER 1970) and waters outside south-western Nova Scotia (SUTHERS & FRANK 1990), but one or two orders less than reported from the Seine estuary at the French north-east coast (WANG & al. 1995) and the Wadden Sea (DE WOLF 1989). Both FRASER (1970) and GREVE & REINERS (1988) found large inter-annual variations; typical years with ctenophore blooms were followed by a year without a bloom. This species typically occurs with a maximum in abundance in the summer, and the reproduction causes a second maximum in the fall (WIBORG 1944; GREVE 1971; LENZ 1973). The abundance is heavily influenced by advective forces in shallow areas (SCHNEIDER 1987; WANG & al. 1995). The highest abundance in this study was mainly in the upper 15 m, above the pycnocline, and unlike the congener, *P. bachei*, which has been shown to migrate through the thermocline in deep water off California (HIROTA 1974), *P. pileus* did not show any tendency of vertical migration through the pycnocline. The same was shown by RISØEN (1983) and STRAND (1983) over several years for the local population in a land-locked fjord north of Bergen. It has been reported to undergo a diel vertical migration in a shallow (< 15 m depth) estuary (WANG & al. 1995). Although the vertical resolution in the sampling did not permit changes on a scale of a few meters, the light regime in my study at 63–64°N during the beginning of July, with short and light nights, may certainly be a factor that causes depression of a migration behaviour.

Predation impact in the Norwegian Sea

I can give a momentary picture of the effect of *P. pileus* predation from my data on abundance and predation ability. I do not know if the abundance I recorded is

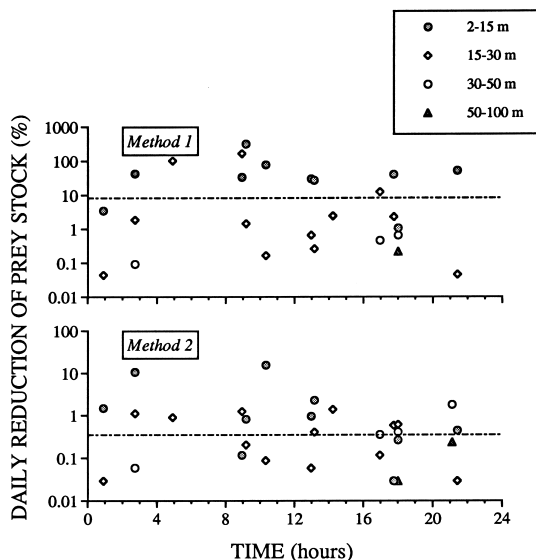


Fig. 12. The Norwegian Sea. Calculated predatory impact from *Pleurobrachia pileus* on the zooplankton stock in the area where *P. pileus* occurred most abundant (stns 189–204). Broken horizontal lines indicate the average (arithmetic mean) value, integrated over time and depth. Method 1 is based on a daily ration of 314 %, method 2 on an individual clearance rate of 10.8 l day^{-1} .

representative over larger areas and longer periods, but the abundance figures are comparable to those from an investigation off Nova Scotia, where this species has been suggested to be responsible for reduction in > 1050 μm zooplankton (SUTHERS & FRANK 1990). I have used two approaches, both assuming that *Calanus* was the main prey in the area. This assumption has been confirmed from the microscopic analyses of the zooplankton samples. The first method uses the DR% I obtained with *Calanus* prey alone, i.e. 392 %, whereas the second method uses the clearance rate found for the same prey, i.e. 10.8 l day^{-1} g^{-1} wet weight. Data on the abundance of *P. pileus* and the zooplankton biomass are taken from Fig. 9 and the size distribution of *P. pileus* displayed in Fig. 11 is used in both cases. The first method gives the highest figures (Fig. 12). An integration over depth and time gives 8.4 % daily reduction in prey mass with the first method and 0.4 % with the second method. It is also shown that the impact in the surface layer is a factor of ten or more higher, solely dependent on the vertical distribution of *P. pileus* (cf. Fig. 9). Calculations based on the results for the other types of prey used in the experiments reduces these figures significantly. A prey concentration of 11.9 *Calanus* l^{-1} , used in my experiments, is also unnaturally high and a lower prey concentration will certainly give a lower DR%. The true impact on the zooplankton

community from predation by *P. pileus* in a situation described for the Norwegian north-west coast is probably therefore a daily reduction of a few percent at the highest. This species therefore seems to be considerably more important in shallow, estuarine areas (DE WOLF 1989; WANG & al. 1995) and in e.g. the Black Sea (MUTLU & al. 1994) where it occurs in much higher abundance than in a more open-water planktonic system.

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