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Studies of a larval herring (*Clupea harengus* L.) patch in the Buchan area. IV. Zooplankton distribution and productivity in relation to hydrographic features

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Abstract

The distribution and activity of zooplankton were recorded across a temperature front and in relation to phytoplankton distribution in the Buchan area during the last half of September. Egg laying rates of the copepods *Acartia tonsa* and *Temora longicornis*, determined in shipboard experiments, closely followed the concentration of chlorophyll$_a$ and varied between 0 and an equivalent of 5-8 % body C · d^{-1}. The rates peaked in mixed and particularly frontal water and decreased with increasing intensity of temperature stratification. Copepod egg production rates of three copepod species, inferred from the ratio of egg to female biomass in the water column showed the same magnitude and pattern of variation. Accordingly, the abundance of copepod eggs was highest in mixed and transitional water and declined in stratified water. The distribution of successively older copepod stages showed decreasingly interpretable relationships to hydrography and abundance of phytoplankton. Copepod production in absolute terms showed a similar relation to hydrography as did the specific (egg) production rates, and varied between ca. 200-300 $\mu g\ C \cdot m^{-3} \cdot d^{-1}$ in mixed and frontal water and between 50-150 $\mu g\ C \cdot m^{-3} \cdot d^{-1}$ in stratified water. Total copepod biomass showed a different relation to hydrography than did production, viz. it was higher in stratified than in mixed and transitional water. However, biomass peaks were evident in transitional water for small sized (30-200 μm) copepods, and in the course of the study an additional peak of total copepod biomass evolved in transitional water. It is suggested that in the Buchan area frontal water may provide the best longterm average feeding conditions for herring larvae, even though the conditions at any specific point in time may be somewhat different.

Introduction

Herring autumn spawning grounds in the Western North Sea (and in the North Atlantic) apparently occur in the vicinity of temperature fronts (Iles & Sinclair 1982). Even though the physical-biological interactions in fronts are not well understood, these regions have been implicated as areas where, at least intermittently, there occur elevated phytoplankton abundance (e.g. Loder & Platt 1985). They may potentially, therefore, support high production and biomass of phytoplankton suspension feeding zooplankters. Since zooplankton, in particular copepod nauplii, constitute the main food for herring larvae (e.g. Marshall *et al.* 1937, Checkley 1982), the juxtaposition of herring spawning grounds and frontal regions may have relevance with respect to food availability for the larvae.

The few studies that have considered zooplankton distribution in relation to fronts are, however, equivocal. One study showed peak abundance of copepods along a front in Liverpool Bay (Floodgate *et al.* 1981). Two studies in the Ushant and the North Sea/Kattegat-Skagerrak fronts (Moal *et al.* 1985 and Richardson 1985, respectively) showed the abundance of zooplankton to be much higher in stratified than in mixed water with only minor additional peaks at the front. On the other hand Holligan *et al.* (1984) found a minimum abundance of mesozooplankton at a temperature front in the English Channel. They suggested that the presence of the dinoflagellate *Gyrodineum aureolum* in the frontal region caused the copepods to avoid this area at the time of their study. Finally, Kahru *et al.* (1984) reported zooplankton biomass to peak well away from a salinity front in the Baltic.

One possible reason for the lack of emergence of a consistent pattern in zooplankton studies carried out in frontal regions is the dynamic (transient) nature of fronts. The position of temperature fronts may change according to prevailing wind (mixing) and insolation (heating) conditions on a time scale of days. In comparison, the generation times of zooplankters within the size range relevant to a feeding herring larvae are in the order of weeks to months. The crucical question, therefore, is whether the frontal system under consideration is sufficiently persistent in time to allow the development of elevated zooplankton abundance.

In September 1984 we located a patch of recently hatched herring larvae in the Aberdeen Bank area (Munk *et al.* 1986). The larvae were concentrated along a thermal front running approximately north-south between 0 and 1°W, and coincided with a peak in phytoplankton abundance at the front (Richardson *et al.* 1986a, b). The purpose of the present study was 1) to describe the distribution and activity of zooplankton in relation to hydrographic features and phytoplankton distribution in the Aberdeen Bank area, and 2) to assess the region as a herring larval nursary ground.

Material and methods

The study was carried out onboard the RV *Dana* during 16-29 September 1984 in the square between 56 to 58°N and 02°W to 02°E. Water depth in the study area varied between ca. 60 and 100 m, surface temperatures were between 12 and 13 °C, bottom water temperatures between 9 and 12 °C. Further details on cruise area and hydrography can be found in Richardson *et al.* (1986a).

Zooplankton distribution

Zooplankton were sampled at 20 stations situated along two transects running perpendicular to and across the front, and through the herring larvae patch. The first transect (57°10′N; 00°18′E to 57°10′N; 01°10′W) was sampled on September 17, the second (56°55′N; 01°20′W to 56°55′N; 00°20′E) on September 24. The stations were spaced at 5 nm intervals along the transects. Depth integrated samples were taken by means of a submersible pump (170 l · min^{-1}) that was raised through the water column (20 m · min^{-1}) from 60-70 m depth to the surface. The

water was pumped on deck via a 2 inch diameter hose and successively filtered on 200, 100 and 30 μm mesh sieves. Samples were preserved in 4% buffered formaline. Zooplankters in the samples (or subsamples for the finer fractions) were later counted, identified to species (or genus) and in the case of copepods (except *Oithona* sp. and Harpacticoids) aged and sexed (i.e. egg, NI-III, NIV-VI, CI-III, CIV-V and adult male or female). Abundance data for copepods were converted to biomass by using weights of nauplii and copepodite stages adopted from Klein Breteler *et al.* (1982) and Paffenhöfer (1971). The natural logarithm of the ratio of abundance in 30-100 μm and 100-200 μm fractions was regressed against body weights for species and stages of known weight. This regression was then used to estimate the approximate weights of *Oithona* sp. and harpacticoids from their size distribution, since these species were not staged. Data on temperature and chlorophyll$_a$ distributions along the transect are from Richardson *et al.* (1986a).

Copepod egg production

On 19 stations scattered over the entire study area (Table 1) adult female copepods were collected for measurement of their rates of egg production by the method of Kiørboe *et al.* (1985a). The stations included 4 locations with totally mixed water (bottom to surface temperature difference, $\Delta t \sim 0$), 7 with significant temperature stratification ($\Delta t > 1.5$) and 8 transitional or frontal stations ($0 < \Delta t < 1.5$). Egg production rates were measured in six species, viz. *Acartia tonsa, Temora longicornis, Calanus finmarchicus, Pseudocalanus* sp., *Centropages typicus* and *Metridia lucens*. Only the three first species were caught in sufficient numbers to allow

Table 1. Positions and dates of stations where copepods were collected for egg-production measurements. Δt: Surface to bottom water temperature difference.

Station no.	Date	Position	Δt °C
1	15/9	57°47'N, 10°25'E	7.7
6	16/9	56°55'N, 00°50'W	1.0
29	17/9	57°15'N, 00°03'E	2.6
35	17/9	57°10'N, 00°30'W	1.3
53	18/9	57°00'N, 00°20'W	3.0
93	19/9	57°16'N, 00°30'W	1.4
98	20/9	57°06'N, 00°42'W	1.1
109	21/9	56°59'N, 00°38'W	0.7
116	22/9	57°01'N, 00°41'W	0.8
120	22/9	57°01'N, 01°10'W	0.0
137	23/9	56°35'N, 00°40'W	1.6
162	24/9	56°55'N, 00°20'E	4.1
166	26/9	56°55'N, 01°49'W	0.0
178	27/9	57°55'N, 01°31'W	0.1
189	27/9	57°15'N, 01°30'W	0.0
207	28/9	56°20'N, 00°50'W	0.6
246	29/9	56°45'N, 01°29'W	0.0
261	30/9	56°57'N, 00°20'E	5.2
262	30/9	56°58'N, 00°30'E	4.7

Table 2. Measurements of egg production rates in six species of planktonic copepods: number of stations, no. of determinations (bottles), average no. of females per bottle, average no. of females incubated per station and average female body dry weight.

Species	No. of stations	No. of determinations	Females per bottle	Females per station	Body dry weight μg
Temora longicornis	18	79	6.7	29	31
Acartia tonsa	16	63	10.1	40	8
Centropages typicus	13	21	3.0	5	40
Pseudocalanus sp.	16	47	7.7	23	13
Calanus finmarchicus	19	106	2.9	16	194
Metridia lucens	3	5	5.0	8	91

measurements at most stations, whereas observations in the last three species are more limited (cf. Table 2). Water column characteristics (temperature and *in situ* fluorescence) were recorded prior to zooplankton collection as described by Richardson *et al.* (1986b). Fluorescence was converted to chlorophyll$_a$ by the calibration formulae given by those authors. Live zooplankton were collected with an opening-closing 250 μm WP2 net (Tranter, 1968) at the depth of maximum *in situ* fluorescence and always above the thermocline. The cod end contents were immediately diluted in water pumped from the collection depth. Thereafter, adult, fertilized females were picked out, sorted to species and distributed in 1-10 600 or 1130 ml screw cap bottles per species containing water from the collection depth. The bottles were placed on a slowly rotating wheel (½ rpm) in a dimly lighted (12L:12D), temperature controlled room (± 1 °C of *in situ* temperature) for 24 h, whereupon spawned eggs were counted. In order to minimize egg cannibalism, the density of females was kept low, 1-5 $\cdot l^{-1}$ for large species and less than 20 $\cdot l^{-1}$ (normally 5-10) for small species. Egg cannibalism is mainly a problem in *C. finmarchicus* and *M. lucens*, since there are no visible remains of eaten eggs in these species; crumbled egg shells are left by the remaining species. To allow correction for eggs naturally occurring in the water, the bottles containing other species served as controls. The blank correction was always less than 5 %. Representative specimens were dried and weighed at the termination of incubations (cf. Table 2). Egg numbers were converted to carbon from data in Kiørboe *et al.* (1985a), and egg production rates were expressed as % body carbon $\cdot d^{-1}$ assuming a female carbon content of 40 % body dry weight (Parsons *et al.* 1977).

Results

Zooplankton distribution

Copepods dominated the zooplankton. Seven genera or species were found in significant numbers in the depth integrated samples, namely the six above mentioned species as well as *Oithona* sp. (mainly *O. similis*). *Pseudocalanus* sp., *Acartia* sp. and *Temora longicornis* (in decreasing order of female abundance) together

with *Oithona* sp. were the numerically dominating species/groups. However, the zooplankton pumps slightly underestimated densities of the old stages of the large species (i.e. *C. finmarchicus, M. lucens* and *C. typicus*) as revealed by a crude comparison with samples taken by a large (3 $m^3 \cdot min^{-1}$) submersible pump. Nevertheless, the numerical ranking remains the same when the underestimation is taken into consideration. *M. lucens* was found only in stratified water and the abundance of *C. finmarchicus* and *C. typicus* increased in an offshore direction. Thus, the zooplankton became increasingly oceanic in character in an offshore direction.

Fig. 1 shows the distribution of copepod eggs, nauplii and copepodites (excl. *Oithona* sp. and harpacticoids) along the two transects together with data on the surface to bottom temperature differences (indicative of water column stratification/mixing) and the concentration of $chlorophyll_a$ averaged over the upper 50 m. There is a general trend of lower abundances for all stages along the second transect. The distribution patterns are in both cases rather complicated. The distribution along the second transect is, however, the easiest to interpret and will, therefore, be dealt with first. The abundance of copepod eggs was highest in mixed ($\Delta t = 0$) and particularly frontal ($0 < \Delta t < 1.5$) waters, and declining density was recorded with increasing stratification (Fig. 1b). Averaged $chlorophyll_a$ showed a similar pattern. There was an additional minor peak of egg abundance at the easternmost station (no. 162) concurrent with an additional patch of elevated $chlorophyll_a$.

The distribution of nauplii and immature copepodites showed similar patterns as for the eggs, with higher densities occurring in mixed water, peak abundances at the front and declining densities in stratified water. However, the additional peak at the easternmost station(s) is much more pronounced than in the case of eggs. This is particularly true when considering the copepodites, and may be indicative of a formerly high chlorophyll concentration and zooplankton productivity east of the front. This suggests that the present minor patch of elevated chlorophyll at station 162 is a remnant of a luxurious past time. The adults showed no interpretable distribution pattern.

The situation at the time/position of the first transect is not so obvious (Fig. 1a). No totally mixed water was included in the transect, and there were apparently two peaks in chlorophyll concentration along the transect (Fig. 1a). The occurrence of copepod eggs also suggests a bimodal distribution with, however, the highest densities occurring in frontal water ($0 < \Delta t < 1.5$) and lowest densities again occurring in the most stratified water. The bimodality can also be found in the distribution of nauplii and coeppodites but their occurrence showed no obvious relationship to either stratification or chlorophyll distribution.

The ratio of the biomass of copepod eggs to biomass of females in the water column is indicative of current female egg production. In Fig. 2, this ratio has been pooled for the three most common species and plotted for the two transects. In both cases there was a high ratio in mixed and stratified waters, and a declining ratio with increasing stratification. This trend becomes even more obvious in Fig. 3, where the ratio has been plotted against Δt ($r = 0.76$; $p^* < 0.1\%$). Thus, copepod

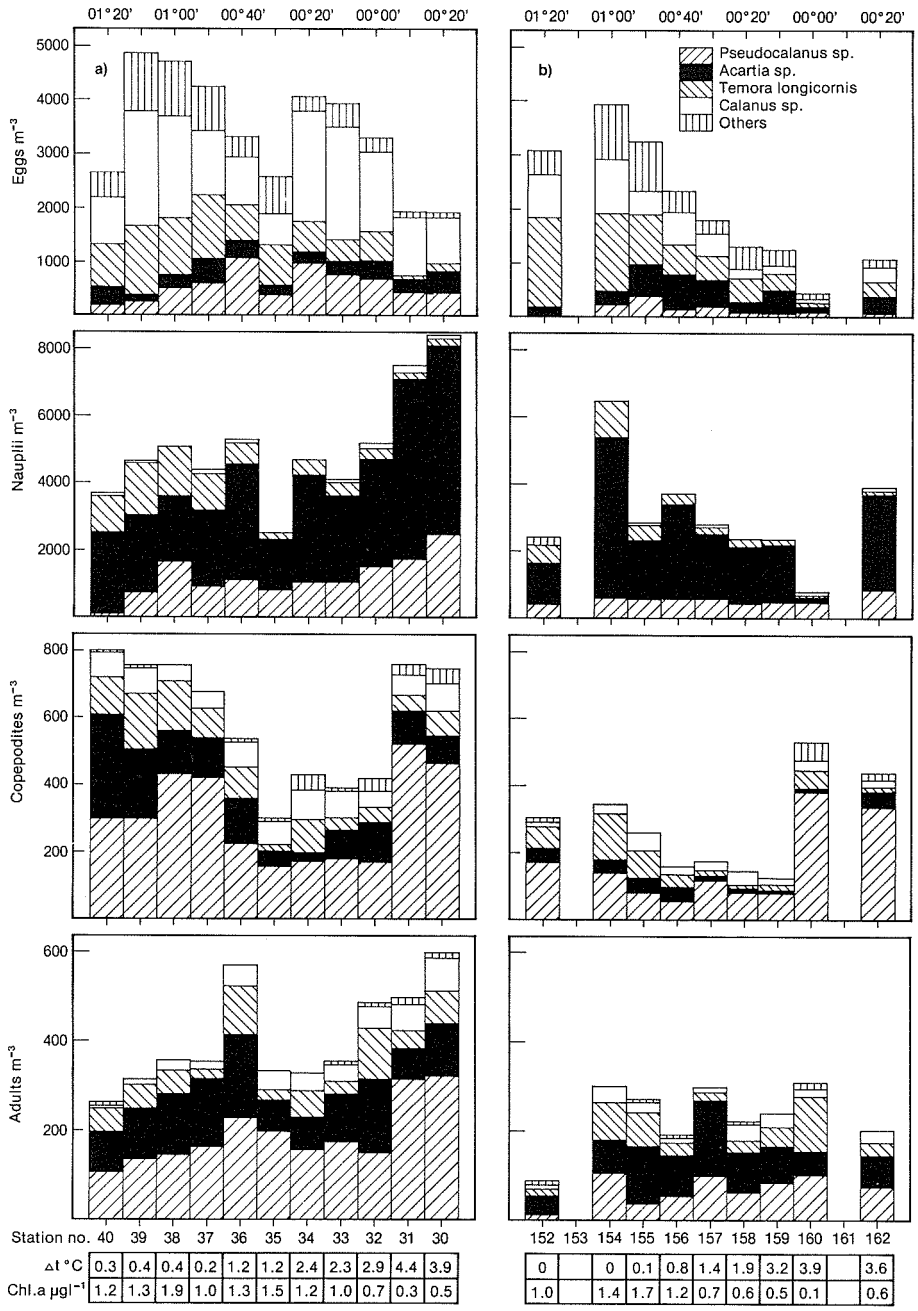

Fig. 1. Distribution of copepod eggs, nauplii, immature copepodites and adults (excl. *Oithona* sp. and harpacticoids) along the two transects. Figures represent numbers $\cdot m^{-3}$ in depth-integrated samples (60-70 m). Surface to bottom temperature of chlorophyll$_a$ are given for each station in the bottom of the figure. (a) 1. transect on 57°10'N on 17 September 1984, (b) 2. transect on 56°55'N on 24 September 1984.

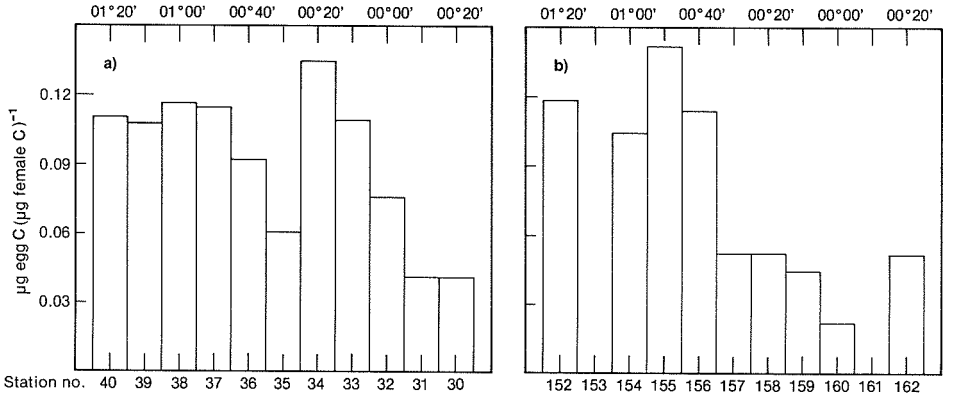

Fig. 2. Ratio of egg to female carbon in the depth-integrated samples pooled for *Pseudocalanus* sp., *Acartia* sp. and *Temora longicornis*. (a) 1. transect, (b) 2. transect.

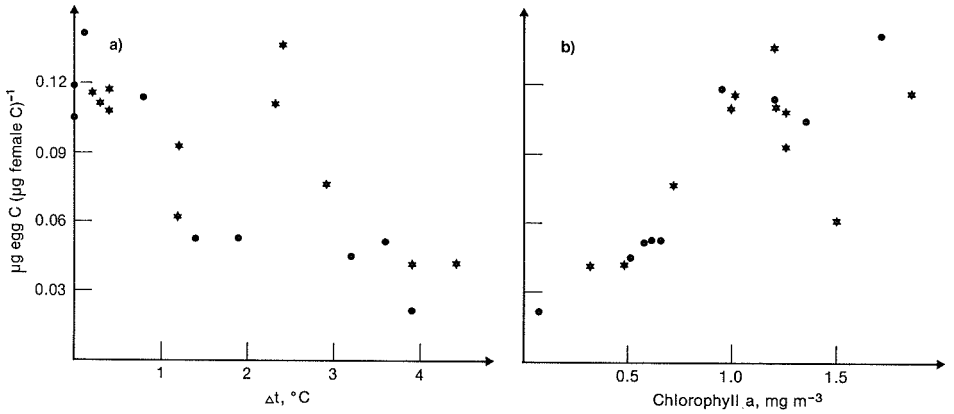

Fig. 3. Ratio of egg to female carbon plotted against (a) Δt and (b) depth-integrated concentration of chlorophyll$_a$. Stars: 1. transect; filled circles: 2. transect.

egg production decreases with increasing stratification and, as is apparent from Fig. 3b, increases with increasing concentration of chlorophyll$_a$ ($r = 0.80$; $p < 0.1\%$).

Fig. 4 shows the distribution of all other zooplankters (30-200 μm). As for the copepods, abundances were generally low along the second transect in comparison with the first. The abundance of lamellibranch larvae tended to decline in an offshore direction. There were no other obvious relationships to stratification or chlorophyll distribution.

The total biomass of copepods in the depth integrated samples varied between 5 and 15 mg C $\cdot$ m^{-3} in the first transect, and between 2.5 and 8 mg C $\cdot$ m^{-3} in the second (Fig. 5). The biomass can be split into size fraction 30-200 μm and >200 μm. The smaller fraction comprised 15-57% ($\bar{X} = 30\%$) of total biomass. For both transects, the total biomass was highest in stratified water, first of all owing

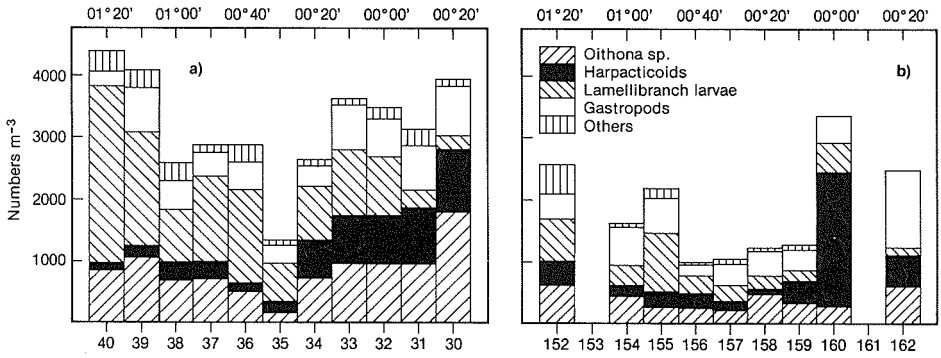

Fig. 4. Distribution of *Oithona* sp., harpacticoids and non-copepod zooplankters in size fraction 30-200 μm along the two transects. (a) 1. transect; (b) 2. transect.

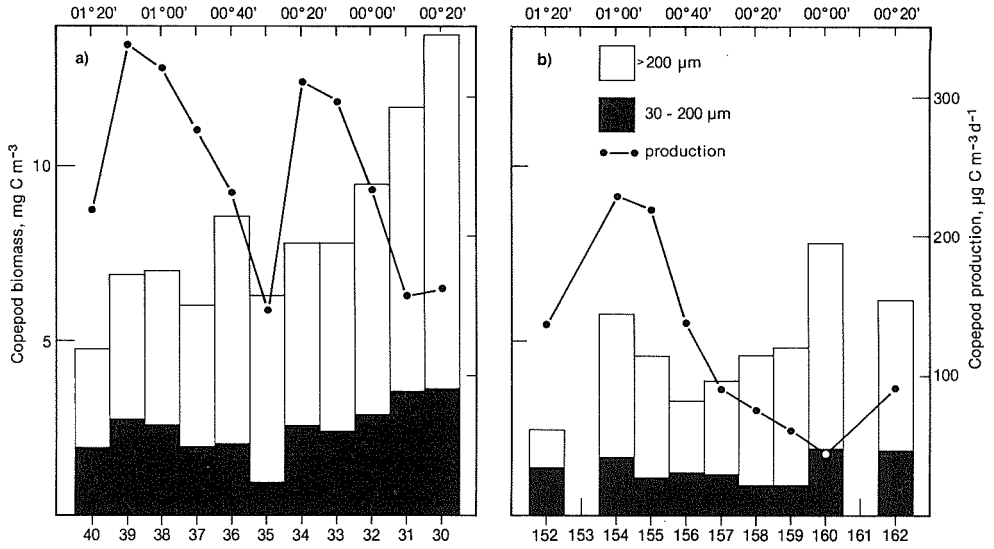

Fig. 5. Distribution of copepod biomass (incl. *Oithona* sp. and harpacticoids) along the two transects. The biomass has been split into two size fractions: 30-200 μm and >200 μm. The graph shows estimated current copepod production – see text. (a) 1. transect; (b) 2. transect.

to increasing density of large sized, oceanic species in offshore direction. For the smaller fraction, and also for the large fraction on the second transect an additional biomass peak is evident in tranitional water.

Copepod egg production rates

Table 3 summarizes the experimentally measured egg production rates for all species at all stations. Egg production rates in terms of numbers of eggs per female per day were low, averaging between 0.2 and 5.0. In terms of percentage of bodily carbon spawned as eggs per day, the two largest species (*C. finmarchicus* and *M. lucens*) exhibited the lowest rates, less than $0.5\% \cdot d^{-1}$ on average, whereas the

Table 3. Range and average (paranthesis) egg production rates in six species of planktonic copepods.

Species	Rate of egg production no. female$^{-1}\cdot d^{-1}$	% body C $\cdot d^{-1}$
Temora longicornis	0- 6.5 (2.2)	0-2.6 (0.9)
Acartia tonsa	0- 7.7 (1.3)	0-8.3 (1.4)
Centropages typicus	0-24.7 (5.0)	0-5.7 (1.2)
Pseudocalanus sp.	0- 2.0 (0.5)	0-5.5 (1.4)
Calanus finmarchicus	0- 5.0 (1.6)	0-1.4 (0.5)
Metridia lucens	0- 0.5 (0.2)	0-0.3 (0.1)

remaining species showed somewhat higher average rates, between 0.9-1.4% $\cdot d^{-1}$.

In Fig. 6, the experimentally measured egg production rates of *T. longicornis* have been plotted against depth integrated concentration (50 m) of chlorophyll$_a$. The descriptive model of Kiørboe *et al.* (1982) was fitted to the data:

$$A = A_{max} e^{-b/C}$$

where A is the egg production rate, A_{max} the maximum egg production rate, C is the concentration of chlorophyll$_a$ and b is a constant. The coefficient of determination of this fit (0.83) was highly significant ($p < 0.05\%$). Evident from Fig. 6 is a threshold concentration of chlorophyll$_a$ of about 0.5 $\mu g \cdot l^{-1}$ below which egg production vanishes. The egg production rate of *A. tonsa* showed a similar significant relationship ($p < 5\%$) to the concentration of chlorophyll$_a$ and a lower threshold of about 0.75 μg chlorophyll$_a \cdot l^{-1}$. No significant relationships could be established for the other species.

In Fig. 7a, the weight specific egg production rates of *T. longicornis* and *A. tonsa* have been plotted against Δt. In spite of the scatter, it is evident that the specific egg production rates peak in frontal water, are lower in mixed water, and decrease with increasing intensity of water column stratification. The scatter in Fig. 7a is, to a large extent, due to variation in the availability copepod food (cf. above). This is

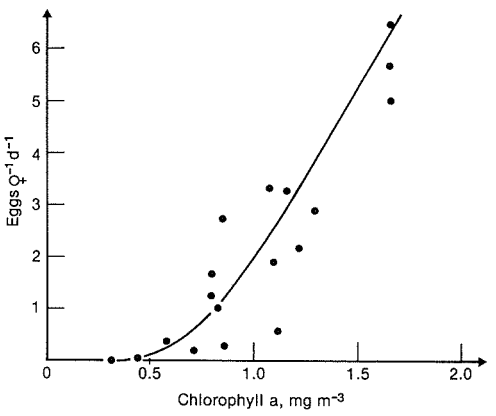

Fig. 6. *Temora longicornis*. Experimentally measured egg production rates (A, eggs $\cdot$ female$^{-1}\cdot d^{-1}$) as a function of depth-integrated (50 m) concentration of chlorophyll$_a$ (C, mg $\cdot m^{-3}$) at collection site. Fitted curve: $A = 37.8\, e^{-2.9/C}$.

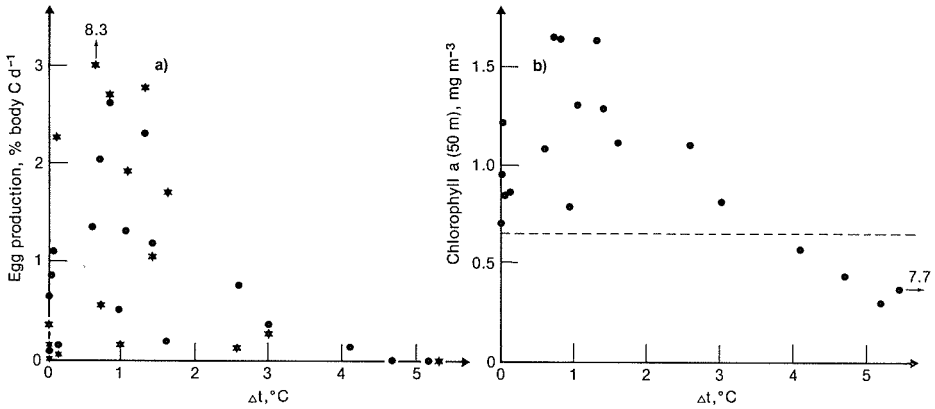

Fig. 7. (a). Experimentally measured specific egg production rates in *Temora longicornis* and *Acartia tonsa* plotted as a function of bottom to surface water temperature difference (Δt). Filled circles: *T. longicornis*; stars: *A. tonsa*. (b). Depth-integrated (50 m) concentration of chlorophyll$_a$ *versus* Δt. The dotted line represents the lower threshold concentration for copepod egg production.

also evident from Fig. 7b where depth integrated chlorophyll$_a$ has been plotted against Δt. If the zero axis in this plot is exchanged by a line $Y = 0.65$ μg chlorophyll$_a \cdot l^{-1}$, representing the lower threshold concentration for egg production, the plots in Fig. 7a and b show similar trends and similar variation.

Copepod production

It is possible to arrive at a crude estimate of current copepod production in absolute terms by assuming that the specific rate of egg production is a measure of the population production/biomass (P/B) ratio. Specific egg production rates may either be obtained from those measured experimentally or, more conveniently, estimated from the ratio of eggs to females in the water column, since we, then, obtain P/B estimates for individual stations. By noting that the hatching time for copepod eggs at 12 °C is about 2.5 days, irrespective of species and food concentration (*A. clausii*: 2.45 d, Landry 1978; *Pseudocalanus* sp.: 2.8 d, Corkett & McLaren 1970; *Temora stylifera*: 2.5 d, Abou Debs & Nival 1983), and by assuming that egg mortality is insignificant, then egg biomass/female biomass/2.5 is equal to specific egg production rate and, hence, P/B-ratio. Egg to female ratios are only available for the three commonest species, but by taking these as representative for all other copepod species, current production was calculated as the biomass of nauplii and copepodites (excl. adults but incl. *Oithona* sp. and harpacticoids) multiplied with the station specific P/B-estimates. Growth of and production by adult males is zero, and production by females is in the form of eggs/nauplii. This was calculated as egg density × weight of NI-stages/2.5, summed for all species and added to the above.

Estimated current production is indicated in Fig. 5. For the second transect it reaches a peak of 225 $\mu g\, C \cdot m^{-3} \cdot d^{-1}$ in mixed and transitional water and a low of about 50 $\mu g\, C \cdot m^{-3} \cdot d^{-1}$ in strongly stratified water. Again, there is a minor peak

at the easternmost station. The first transect is consistent with this pattern, i.e. high rates (2-300 μg C $\cdot$ m^{-3} $\cdot$ d^{-1}) in transitional water (except station 35) and lower rates ($\sim$150 μg C $\cdot$ m^{-3} $\cdot$ d^{-1}) in strongly stratified water.

As for the biomass, gross production can be split into size fractions 30-200 μm and >200 μm. The smaller fraction comprised 67-87% ($\bar{X}$ = 81%) of total production.

Discussion

Copepod egg production

The experimentally measured egg production rates are very low. Egg production rates of *A. tonsa* measured in the laboratory under optimal food conditions may reach about 50 eggs $\cdot$ female^{-1} $\cdot$ d^{-1} (18°C) equivalent to 65% body carbon $\cdot$ d^{-1} (Kiørboe *et al.* 1985b) compared to an average of 1.4% body C $\cdot$ d^{-1} (Table 3) found for the same species during this survey. This is primarily due to the low abundance of phytoplankton algae. From data in Richardson *et al.* (1986b), it is possible to calculate a carbon to chlorophyll$_a$ ratio of 45 μg carbon (μg chl.$_a$)$^{-1}$. The maximum depth integrated concentration of chlorophyll$_a$ during the present survey was about 1.6 μg chl.$_a$ $\cdot$ l^{-1} equivalent to 72 μg C $\cdot$ l^{-1}. From the relationship between food concentration and egg production in *A. tonsa* given by Kiørboe *et al.* (1985b), a maximum egg production rate of 10% body C $\cdot$ d^{-1} is predicted. This is comparable to the maximum rate of 8.3% $\cdot$ d^{-1} found for this species during this survey (Table 3).

The experimentally determined egg production rates are also consistent with the observed egg to female ratios in the water column. The egg to female biomass ratio varied between about 0.02 and 0.14 (μg C $\cdot$ μg C^{-1}) (Fig. 2) equivalent to specific egg production rates between 0.8 and 5.5% body C $\cdot$ d^{-1}. This is similar to the range of egg production rates determined experimentally for the three species considered (Table 3).

The egg production rates of *T. longicornis* and *A. tonsa* showed interpretable relationships to hydrography and concentration of chlorophyll$_a$. This was not so for the other species. There are at least two reasons for the lacking correlations. First, the scarcity of the data for *C. typicus* and *M. lucens* prevent any meaningful relationships to become apparent. Secondly, all copepods are batch spawners. That is, eggs are not spawned continuously, but batches of eggs are shed at time intervals. *Calanus* sp. and *Pseudocalanus* sp. are, however, batch spawners to a much higher degree than e.g. *T. longicornis* and *A. tonsa* (Runge 1984). Thus, for *C. pacificus* Runge (1984) found that spawning frequency varied inversely (hyperbolically) with rate of egg production but that batch size was independent. From the data in Runge (1984) it can be calculated that, at the average egg production rate of *C. finmarchicus* in the present study, the time lapse between spawnings would be more than 5 days. Therefore, in order to see interpretable variations in egg production rate in this study, very high numbers of females should have been incubated at each station or incubations should have been carried out over unacceptable long periods of time.

Judging by the egg laying rates, specific copepod production was markedly increased in the transitional zone between stratified and mixed water, somewhat less in mixed water, and approaching zero with increasing intensity of stratification. The quantitative zooplankton samples and the experimentally measured egg production rates both support this conclusion (cf. Figs 2, 3 and 7).

Zooplankton productivity

The calculation of current production assumes that 1) egg mortality (or sedimentation) is zero, 2) specific egg production rate is a measure of population P/B and 3) the specific egg production rates pooled for the three most common species are representative for all copepod species present. The similarity between the experimentally measured egg laying rates and those inferred from the egg to female ratios warrants the first assumption. The second assumption is supported by the observation that specific egg production rates are similar to weight specific growth rates of nauplii and copepodites in *Acartia clausii* (Sekiguchi *et al.* 1980) and *C. pacificus* (Runge 1984). Additional supporting evidence is provided by Klein Breteler *et al.* (1982) who found that specific growth rates of nauplii and immature copepodites in four species of neritic copepods were similar at food concentrations above 50 μg $C \cdot l^{-1}$. At food concentrations below 50 μg $c \cdot l^{-1}$, however, specific growth rates of late stage, immature copepodites were somewhat less than of nauplii. The phytoplankton concentrations observed in this study were low, and the assumption of similar specific growth rates for all stages may, therefore, tend to overestimate the production of large copepodites. However, since estimated production in the >200 μm fraction contributed only 19% to total production, this presumably only represents a minor error. The data in Table 3 do not support the third assumption. Specific egg production rates of the two largest (but quantitatively less important) species are lower than for the smaller species. Thus, the present estimates are, also in this respect, maximum ones. These estimates do not include production of non-copepod zooplankters. Among these, only gastropods and bivalve larvae are of any quantitative significance.

As for the specific production rates, production in absolute figures tended to peak in mixed and particularly transitional water and was significantly less in strongly stratified water. The current secondary production does not result in build-up of copepod biomass in the water column. The biomass of copepods during the second transect was significantly less than during the first (cf. Fig. 5). This may be due to sampling in slightly different water masses, but is also consistent with the expectation of a declining zooplankton biomass at this time of the year. Thus, instantaneous production is presumably significantly exceeded by instantaneous mortality.

Zooplankton distribution in relation to hydrography

Richardson *et al.* (1986a) summarized the general hydrography of the Buchan area: During summer temperature stratified water may extend nearly into the Scottish east coast. Over the course of the autumn (September-November), reduced heat input allows mixing of the inshore region followed by a generally

eastward movement of the front separating tidally mixed and temperature stratified water. As argued by Richardson *et al.* (1986b) destratification leads to remineralization of the euphotic zone and an autumn bloom develops with increased primary production and phytoplankton biomass in mixed and particularly frontal water. As shown in this paper, this is followed by an increased egg laying rate of suspension feeding copepods at the front. However, zooplankton abundance and biomass are not necessarily elevated at the front. In one crossing of the front, we found a tendency of elevated abundance and biomass at the front while in the other we found no obvious relationship. However, distribution of zooplankton is a function of both current and former oceanographic conditions and zooplankton population dynamics. It is to a large extent possible to explain the distribution of copepod eggs – with a short prehistory – from the distribution of adult females and current environmental conditions (cf. Figs 1-3). But it becomes increasingly difficult to understand the distribution of succesively older copepod stages from the knowledge available. At the time of the 1. transect, we have only general knowledge of the hydrographic prehistory (cf. above) and we can only explain the distribution of copepod eggs. At the time of the 2. transect, however, we know that the oceanographic conditions, i.e. with peak phytoplankton abundance at the front, had existed during the previous 8 days. Accordingly, both copepod eggs, nauplii and to some extent also copepodites and total copepod biomass peak at the front. Since specific zooplankton productivity is highest at the front, this pattern is predicted to become more pronounced with increasing duration of the period with peak phytoplankton abundance in transitional water. Furthermore, since the production of particles <200 μm make up about 80% of total zooplankton production (even though they constitute only about 30% of total biomass), this pattern is expected to evolve most rapidly for zooplankters of a size potentially releveant for feeding herring larvae.

Herring larval feeding conditions in the Buchan area

During this survey, the patch of herring larvae, that we followed over two weeks, closely tracked the front while drifting towards the south (Munk *et al.* 1986; Richardson *et al.* 1986a). Thus, areas of highest herring larval abundance coincided with the areas of highest specific zooplankton productivity. However, current zooplankton productivity is of no immediate relevance to feeding herring larvae, since they experience the food density rather than the productivity.

Even though food density modifies the swimming activity of herring larvae, i.e. by inducing high swimming activity at low densities (Munk & Kiørboe 1985), this may be considered a non-directional response (a kinesis) and, thus, an inefficient mechanism for the larvae to 'find' patches of high food abundance on scales of nautical miles. It is, therefore, hard to envisage any mechanism related to food concentration *per se* that enables larvae to concentrate in areas of elevated food density. It may be hypothesized, however, that herring larvae, or rather the spawning adults, react (in an evolutionary sense) to longterm average conditions when 'selecting' spawning grounds. And in this respect the front may provide the most luxurious feeding area, even though the conditions at any specific point in time

may be somewhat different. The juxtaposition of young herring larvae and the front is apparently a recurring phenomenon in the Buchan area (Richardson *et al.* 1986a), and it might be understood in this context.

One may finally ask whether the concentration of herring larval food is sufficiently high to allow significant growth and survival of the larvae. In discussing this, we take the biomass of copepods 30-200 μm as a measure of edible larval food. Neither the larvae nor the food organisms are homogeneously distributed in the water column but are concentrated in the upper 30-50 m (unpublished data). Thus, the biomass of food organisms in the depth-integrated zooplankton samples should be increased by approximately 50% to arrive at an estimate of the concentration of food experienced by the larvae (unpublished data). From Fig. 5, the biomass of 30-200 μm copepods in the front ($0<\Delta t<1.5$) averages between 2.0 (1. transect) and 1.3 mg $C \cdot m^{-3}$ (2. transect) and the relevant concentration is, thus, between 2 and 3 mg $C \cdot m^{-3}$. Kiørboe & Munk (in press) related the growth rate of 1-3 wk old larvae to food concentration in the laboratory. At the above food concentrations they found growth rates between 0.05 (Baltic larvae) and 0.24 $mm \cdot d^{-1}$ (larvae of Clyde herring). The growth rate of the present larvae (excluding the oldest/largest group), estimated by Munk *et al.* (1986), was between 0.14 and 0.17 $mm \cdot d^{-1}$. Allowing for 20% shrinkage due to capture and preservation this equals 0.17-0.20 mm live length $\cdot d^{-1}$, and thus fits the laboratory observations. The maximum growth rate of 1-3 wk old herring larvae recorded in the field and in the laboratory under optimal food conditions is about 0.25 $mm \cdot d^{-1}$ (Kiørboe & Munk in press, and references therein). Thus, the food concentration at the Buchan front during the present survey was apparently suboptimal to larval growth in the sense that the growth potential was hardly fully exploited. This underlines the importance of coincidence in time and space of larvae and their food.

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