Vol. 139: 79–93, 1996 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published August 29

Role of cyclopoid copepods *Oithona* spp. in North Sea plankton communities

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ABSTRACT: Copepod production was investigated in the North Sea, with special emphasis on the trophodynamic role of the cyclopoid copepod *Oithona similis*. During a cruise in May-June 1992, no significant correlation was found between the specific egg production rate (SEP) of *Oithona* spp. and available food. However, *O. similis* SEP was positively correlated to the protozooplankton, in contrast to the co-occurring calanoid *Paracalanus parvus* SEP which was significantly correlated to the chlorophyll *a* concentration. In the shallow Dogger Bank region *Oithona* spp. contributed 50 and 70% of the total copepod biomass and production, respectively. In the northern regions dominated by *Calanus* spp. *Oithona*'s contribution to biomass and production decreased to about 10 and 20%, respectively. These regional differences were confirmed by analysis of seasonal data, in which *Oithona* spp. contributed 40 and 13% of the annual copepod production in Dogger Bank and the northern regions, respectively. Biomass and production of *Oithona* spp. show little temporal and spatial variation as compared to calanoids. When calanoid populations are low or in shallow environments where eggs of the free-spawning calanoid are lost to the benthos, *Oithona* is an important component of the food web.

KEY WORDS: Cyclopoid copepod · *Oithona* spp. Fecundity Production · North Sea

INTRODUCTION

Studies of copepod demography, production and the role of copepods in carbon cycling have until recently, focused on the larger species (mainly calanoid copepods). This bias arises from the widespread use of nets with a mesh size of 200 µm as recommended by UNESCO (1968), which undersample smaller copepod species (i.e. most cyclopoids). For example, the Continuous Plankton Recorder (CPR) data from the North Sea were collected with a 270 µm mesh, so this unique material cannot be used for quantifying populations of the small copepod species, e.g. *Oithona* spp. (Fransz et al. 1991). Recent studies, however, have documented that *Oithona* spp. can contribute significantly to copepod biomass in temperate seas, such as the North Sea and adjacent waters (Hay et al. 1991, Nielsen et al. 1993, Kiørboe & Nielsen 1994). As the potential importance of *Oithona* spp. has become evident, methodological difficulties have arisen. The currently used *in situ* techniques for measurement of calanoid production are not suitable for the small egg-carrying cyclopoid copepods. Thus, small cyclopoids of the genus *Oithona* are often mentioned among the dominating species, but are not included (e.g. Peterson et al. 1991), or are treated as calanoids in estimates of copepod grazing pressure and secondary production (e.g. Peterson et al. 1991, Nielsen et al. 1993, Kiørboe & Nielsen 1994). As a consequence, little information about the actual contribution of *Oithona* spp. to secondary production is available at present (Tremblay & Roff 1983, Roff et al. 1988, McLaren et al. 1989, Fransz & González 1995).

Much less is known about the role of cyclopoids in planktonic communities. It has been suggested that small phytoplankton (<5 to 10 µm), which are inefficiently grazed by the larger calanoid copepods, may support feeding and egg production in *Oithona* spp., resulting in a different spatio-temporal pattern

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of production between calanoid species and *Oithona* spp. (Sabatini & Kiørboe 1994). Several recent studies have stressed their potential role in microbial food webs (González & Smetacek 1994, González et al. 1994).

The Dogger Bank in the southern North Sea is well known for its productive fisheries (Daan et al. 1990). This may be related to the occurrence of fronts with enhanced 'new' production in the region, that leads to a short 'classical' type of food chain (Munk 1993, Nielsen et al. 1993, Munk & Nielsen 1994). Since *Oithona* spp. are found at high concentrations in these areas (Nielsen & Richardson 1989, Nielsen et al. 1993), interest has developed to understand their role in a copepod community that is able to support a large fishery. Potentially, *Oithona* spp. play an important role, since they are quantitatively important food items of fish larvae including cod and haddock (Kane 1984), herring (Cohen & Lough 1983) and anchovy (Kuwara & Suzuki 1984, Mitami 1988, Viñas & Ramírez in press). In particular, *Oithona similis* appears to be a crucial transitional prey for pollock larvae when feeding habits shift from copepod nauplii to larger zooplankton (Nishiyama & Hirano 1985). Euphausids (e.g. Gibbons et al. 1991), chaetognaths (Øresland 1990) and some calanoid copepods (e.g. Ohtsuka et al. 1987, Hopkins & Torres 1989) also are known to feed on cyclopoid copepods, mainly *Oithona* spp.

The aims of this investigation are: (1) to estimate the *in situ* egg production of *Oithona* and its contribution to copepod production; (2) to examine the relationship between fecundity/production and food availability of *Oithona* spp. and calanoids; and (3) analyse the spatio-temporal importance of *Oithona* in comparison with the co-occurring calanoid copepods.

MATERIALS AND METHODS

Study site. This investigation was conducted in the North Sea from May 22 to June 3, 1992 with the research vessel 'Dana' (Danish Fisheries Ministry). Sampling was performed along 3 transects (Fig. 1).

Water column structure. At all stations profiles of temperature, salinity and fluorescence were recorded throughout the water column using a Neil Brown Mark III CTD system and a Q-instrument fluorometer (Hundahl & Holck 1980). The fluorescence was converted to chlorophyll from a linear regression between the fluorescence and several spectrophotometric measurements of chlorophyll (chl *a*) covering all 3 transects (chl $a = 0.015 \times \text{Fluo} - 0.217$, $r^2 = 0.92$, $n = 112$). From the vertical structure of the water column 5 or 6 depths were selected for chemical and biological measurements.

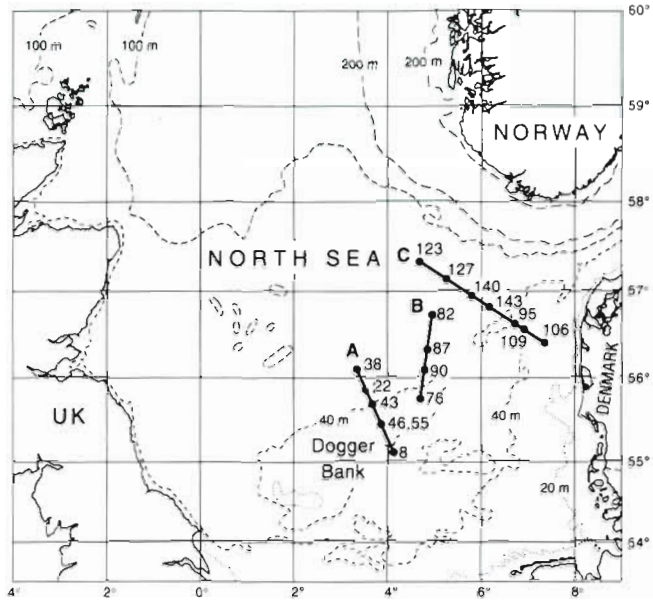

Fig. 1. Map showing the area investigated and the approximate positions of stations

Potential copepod prey. Samples for chl *a* were taken at 3 to 5 depths per station. 1 or 2 l were filtered onto GF/F filters, extracted in 90% acetone and measured spectrophotometrically (Strickland & Parsons 1972). Integrated values of chlorophyll were calculated from the fluorescence profiles and the regression to chl *a*. The relative size distribution of the phytoplankton in the surface and at the subsurface fluorescence maxima along Transect A was measured fluorometrically. Duplicate samples were filtered on to 25 mm GF/F, 3 µm Nuclepore and 11 and 50 µm Nitex filters and extracted in 96% ethanol (Jespersen & Christoffersen 1987).

Samples for enumeration of phyto- and protozooplankton (100 ml) were fixed in 1% acid Lugol's solution and counted after 24 h sedimentation using an inverted microscope. Depending on the abundance of the species in consideration a fraction or the total 50 ml subsample was counted. Biovolume was estimated from measurements of linear dimensions assuming simple geometrical shapes and a conversion factor of 0.11 pg C μm^{-3} for ciliates and naked dinoflagellates and 0.13 pg C μm^{-3} for thecate dinoflagellates (Edler 1979). The depth integrated biomass was estimated from discrete samples by trapezoidal integration.

Copepod biomass. Copepod biomass was determined at all stations. Sampling was carried out at 2 depth strata: above and below the fluorescence peak, if present, or below the thermocline. Samples were collected by a submersible pump (1200 l min^{-1}) equipped with 30 µm mesh size net that was raised at 10 m min^{-1} through the layer The samples were preserved in 2%

buffered formalin. Zooplankton were later identified and counted. In the case of copepods, at least 400 individuals were classified into eggs, nauplii, copepodites, females and males. Abundance data for copepods were converted to biomass by means of length-weight regressions cited in Kiørboe & Nielsen (1990) and Sabatini & Kiørboe (1994). Egg carbon was assumed to be 0.14 pg C μm^{-3} (Kiørboe et al. 1985, Huntley & Lopez 1992).

Egg production. Calanoid copepod egg production was estimated according to Kiørboe et al. (1985). Females were gently sampled from the thermocline to the surface using a WP-2 net (200 µm) with a large cod end. Immediately after collecting fertilized females were added to 600 ml bottles (1 to 5 female $bottle^{-1}$) with 180 µm screened surface water. Along Transect A additional experiments were conducted with females sampled at the subsurface fluorescence maximum, if present, or below the thermocline. Depending on female abundance, up to 6 replicate bottles were incubated at *in situ* temperature for 24 h. Females from the surface mixed layer and the subsurface fluorescence maximum were incubated at 12 and 7°C, respectively. At the end of incubation, spawned eggs were counted. Samples for *Oithona* spp. egg production (egg:females ratio) were taken at discrete depths throughout the water column using a 30 l water bottle. On deck each sample was concentrated on a submerged filter (45 µm) and then preserved in 2% buffered formalin. At this stage handling was gentle in order to avoid damages or detachment of egg sacs from the females. Adult females and total number of eggs within each sac were counted in subsamples (or total samples when eggs were scarce); normally >400 eggs and all the females present in the same subsample were counted. Cephalothorax lengths of about 10 females were measured for each sample to estimate female carbon biomass from length carbon regression in Sabatini & Kiørboe (1994).

Population specific egg production rates (SEP, d^{-1}) of *Oithona* spp. were calculated from the ratio of eggs to females (E/F), temperature-dependent hatching rates (HR, d^{-1}), and carbon content of the eggs and females:

$$SEP = (E/F)HR(eggC/femaleC) \quad (1)$$

The hatching rate (HR) at the surface temperature was measured on board in incubations at *in situ* temperature. Egg-carrying females (80) collected at Stn 38 were placed individually in 62 ml cell culture screw-cap flasks filled with 45 µm screened surface water and incubated at 12°C. Every 12 h, 10 to 20 females were preserved and the eggs and nauplii counted. The average hatching rate was then estimated from the slope of the regression of hatching % {[no. of nauplii/(no. of eggs + no. of nauplii)] × 100} versus time. The obtained rate was 0.93% h^{-1} or 0.223 d^{-1}, which is about the same as predicted by the temperature-dependent equation,

$$HR\ (d^{-1}) = 0.0604\ e^{0.113T} \quad (2)$$

Hatching rates at any other temperature were thus estimated from Eq. (2) (Sabatini & Kiørboe 1994).

Copepod production. Copepod production was calculated from depth integrated biomass and measured specific egg production rate by assuming equal specific egg production and juvenile growth rate (Berggreen et al. 1988). All the species were included in the calculation to estimate total production. To those species for which no fecundity data were available, the average specific egg production of the other species (excluding *Oithona*) was applied.

Annual copepod production. In order to estimate the contribution of *Oithona* spp. to the standing stock and secondary production of copepods in the North Sea on an annual basis, the results of the present cruise were used in conjunction with literature data covering all seasons (Table 1). Unfortunately no *Oithona* egg:female ratios were available from the months of January and October. Production rates for these months were then calculated from the average of weight-specific egg production in August-September and February-March, respectively.

RESULTS

Water column structure

High solar radiation, clear skies and low wind during the study period increased the stability of the water column, so that even the shallow water over Dogger Bank was thermally stratified. A thermocline at 10 to 20 m depth separated 12°C surface water from 7°C bottom water (Fig. 2). The water column along Transects A and B was almost vertically isohaline and salinities less than 35‰ were only recorded south of the Dogger Bank.

Table 1 Sources of data for the annual pattern of copepod biomass and production shown in Fig. 9

Month	Year	Source
January	1988	Hay et al. (1991)
February/March	1988	Nielsen & Richardson (1989)
May/June	1990	Nielsen et al. (1993)
May/June	1992	This study
August/September	1991	Munk & Nielsen (1994)
October	1987	Hay et al. (1991)
December	1987	Hay et al. (1991)

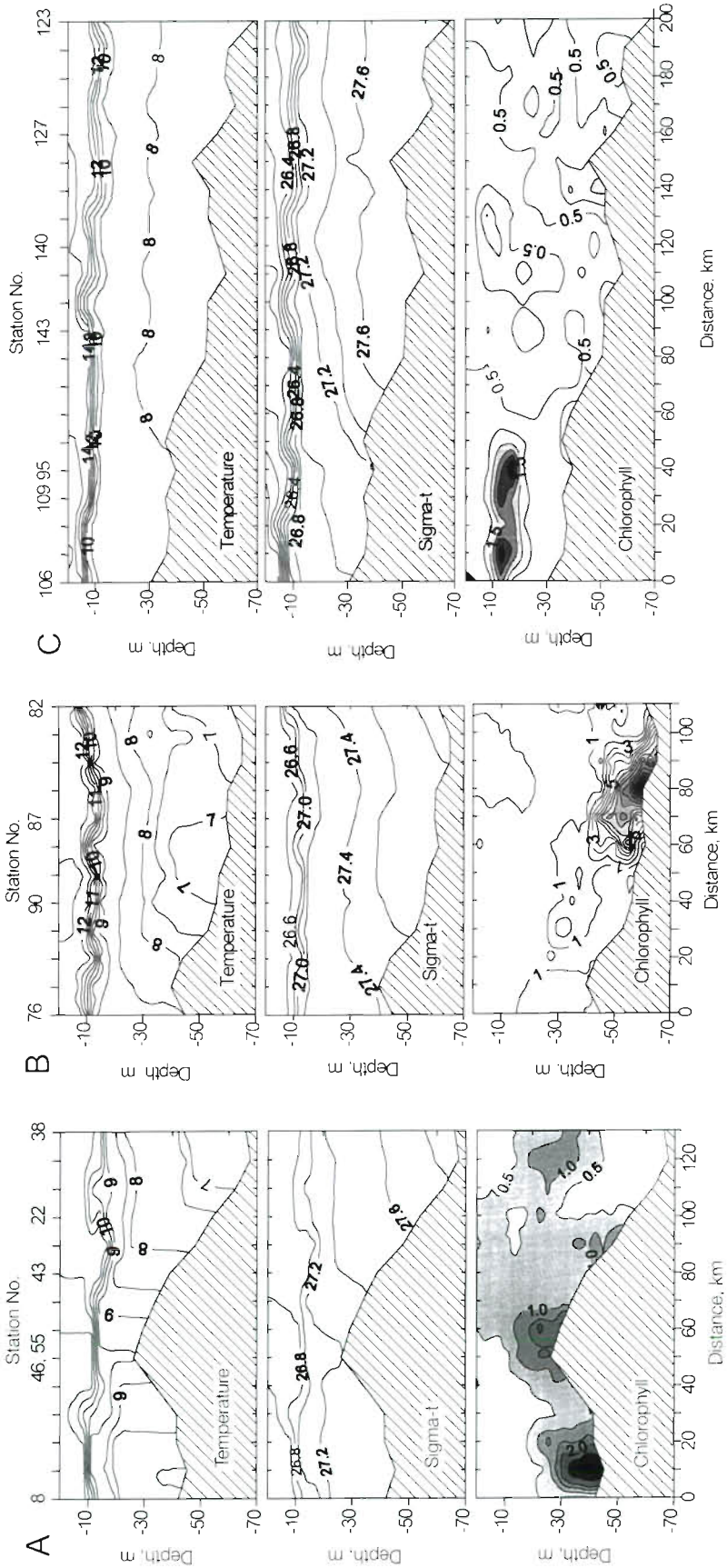

Fig. 2. Vertical distribution of temperature (°C), water density (sigma-t), and chlorophyll *a* µg l^{-1} along Transects A, B and C

Transect C was influenced by the less saline Jutland coastal current which created a front 40 to 60 km from the eastern border of this transect. In general the water column structure was determined by temperature differences, so variation in density (sigma-t) followed the temperature variation. The concentration of chl *a* was low in the surface mixed layer (0.1 to 0.5 µg chl *a* l^{-1}), whereas higher concentrations were recorded in bottom waters (Transects A and B) or at the bottom of the thermocline (Transect C).

Potential copepod prey

The subsurface phytoplankton population comprised the major part of the depth integrated phytoplankton biomass (Fig. 3). The size fractionated samples, only taken at 2 depths along Transect A, showed that the subsurface phytoplankton community was dominated by somewhat larger cells than the surface community [67 ± 12% and 38 ± 10% were larger than 11 µm (mean ± SE), respectively] (Fig 4). Surface values show that the average cell size was bigger at Dogger Bank (Transect A) than at the 2 other transects where the >11 µm fraction of phytoplankton contributed 19 ± 5 and 23 ± 2% for Transects B and C, respectively. There were no differences in the species composition of the phytoplankton community within the area studied. The phytoplankton was composed of a mixture of small flagellates (2 to 5 µm), diatoms (*Skeletonema costatum*, *Coscinodiscus* spp.) and dinoflagellates (*Dinophysis norvegica*, *D. acuta* and *Ceratium tripos*).

The protozooplankton was dominated by ciliates. The obligate autotroph *Mesodinium rubrum* was the most abundant and comprised 40 ± 14%, n = 20 of the integrated biomass. The heterotrophic/mixotrophic ciliates were dominated by small, 20 to 40 µm, naked oligotrichs (*Lohmaniella* spp., *Strombidium* spp. and *Strobilidium* spp.) and the larger 50 to 70 µm *Cyclotrichium* spp.; tintinnids (*Tintinnopsis* spp. and *Stenosomella* spp.) were of

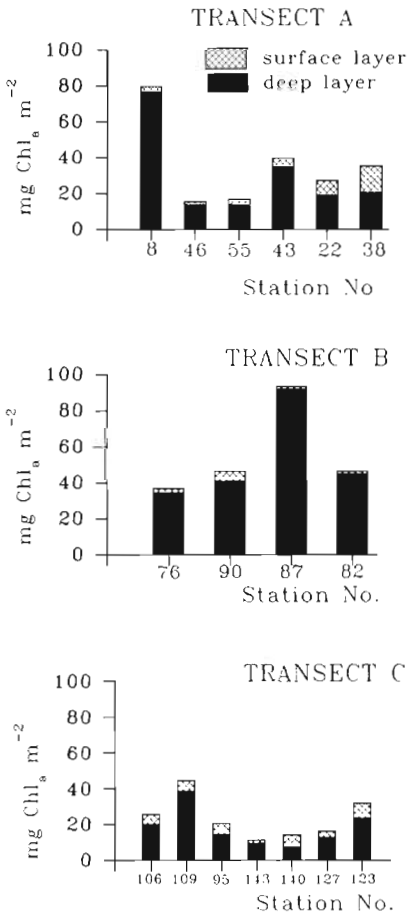

Fig. 3. Depth-integrated phytoplankton biomass above and below the thermocline/depth of maximum fluorescence along the 3 transects

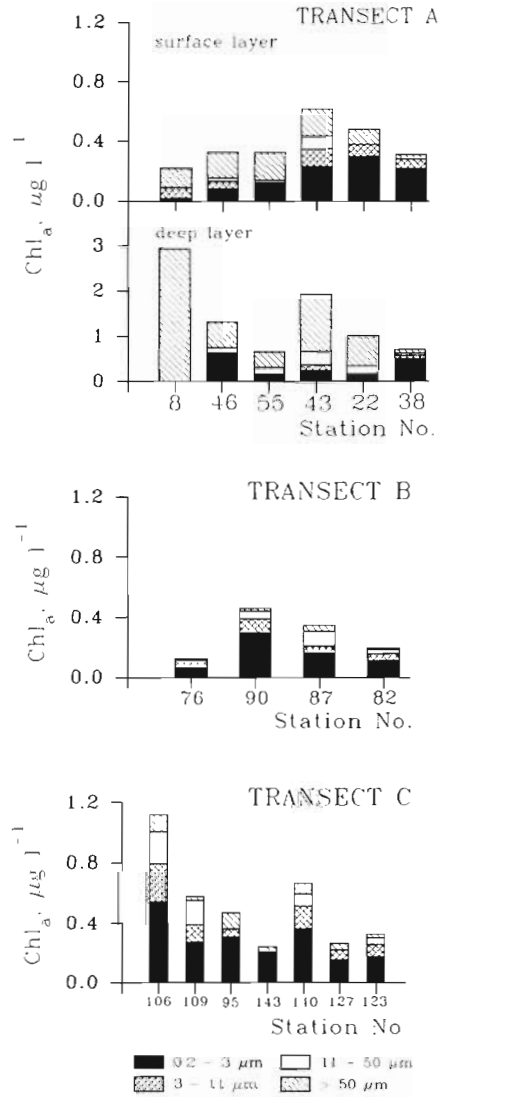

Fig. 4. Size distribution of the surface phytoplankton along the 3 transects. The size distribution below the thermocline is also shown for Transect A

minor importance. The heterotrophic dinoflagellates were dominated by thecate forms (*Protoperidinium pellucidum*, *P. brevipes* and *P. depressum*) contributing 14 ± 12% of the protozooplankton biomass, while naked forms (*Gyrodinium glaucum* and *G. spirale*) only contributed 5 ± 3%. The depth integrated protozooplankton biomass ranged from 100 to 5000 mg C m^{-2} The biomass on Transects A and B was in the range 1000 to 2000 mg C m^{-2}, while the biomass on Transect C was less than 1000 mg C m^{-2} (Fig. 5).

Copepod biomass, composition, fecundity and production

Ten copepod genera or species were identified. Among them, *Oithona* spp., *Paracalanus parvus*, *Temora longicornis*, *Acartia* spp. and *Calanus finmarchicus* dominated the biomass. Their contribution to the depth integrated biomass is shown in Fig 6. *O. similis* made up the major part of the *Oithona* spp. biomass although a few *O. plumifera* and *O. nana* were observed in the samples. Within the area regional differences were observed in the species composition: *Oithona* spp. and *T longicornis* were very abundant on and in the vicinity of Dogger Bank (Transect A) while *Acartia* spp. dominated on the coastal side of the front on Transect C. The deep stations in the northern part of Transects A and B and west of the front on Transect C were dominated by *Calanus* spp., *Metridia lucens* and *Pseudocalanus* sp. (see 'Others' in Fig. 6).

The highest copepod biomass was found at the deep *Calanus* dominated stations towards the central North Sea (along Transects A and B) and on the western side of the front on Transect C. Except on the shallow Bank stations (Stn 46 and 55) where the biomass was homo-

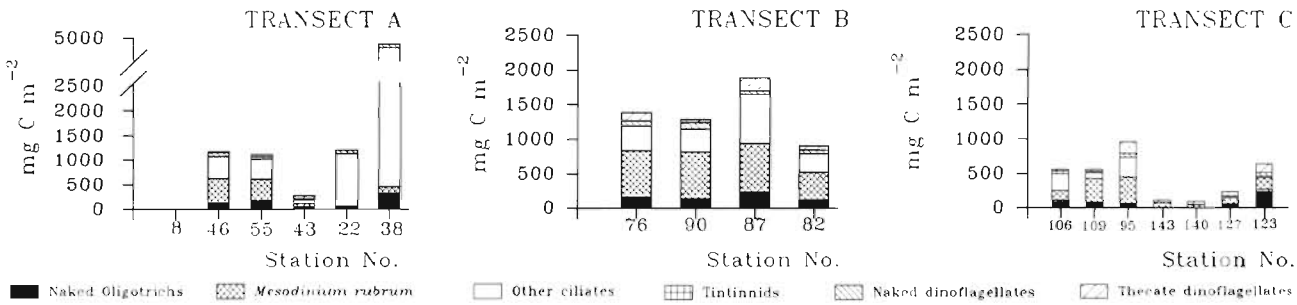

Fig. 5. Depth-integrated protozooplankton biomass calculated from discrete water samples along the 3 transects

geneous throughout the water column, about 80% of the copepod biomass was concentrated below the thermocline (Fig 6). Across the Dogger Bank stations (Transect A) *Oithona* spp. on average accounted for one-third (33%) of the biomass both above and below the thermocline and up to 50% on the bank proper. Along the 2 other transects it was less abundant (about 15% in the surface layer and 10% below the thermocline).

Differences between the measured egg production rates of calanoid copepods and *Oithona* spp. were found. Maximum weight-specific egg production rates of *Oithona* spp. (Table 2) were lower and relatively constant within the area considered. Specific fecundity of calanoids (Table 3) was highly variable and a distinct spatial pattern was evident (Fig. 7). Across Dogger Bank (Transect A) the average egg production rate of the small calanoids and *Calanus* spp. was relatively low. Much higher specific egg production rates were found for the calanoid copepods along the 2 other transects. The egg production rate of small calanoids increased with distance from the Bank on Transect B and at the coastal side of Transect C. There were no measurements of *Calanus* spp. egg production on Transect B (no females were available in surface waters since their biomass was concentrated in the deeper layer; Fig. 6). Their highest fecundity rates were measured in the stratified and deeper northern waters where, in contrast, very low egg production rates were measured for small calanoids.

The most complete series of data for examining the vertical distribution of copepod egg production was gathered for *Oithona* spp. (Fig. 8). Rates actually realized by *Oithona* were near constant or decreased with depth. However, if standardized to surface temperature rates (tempera-

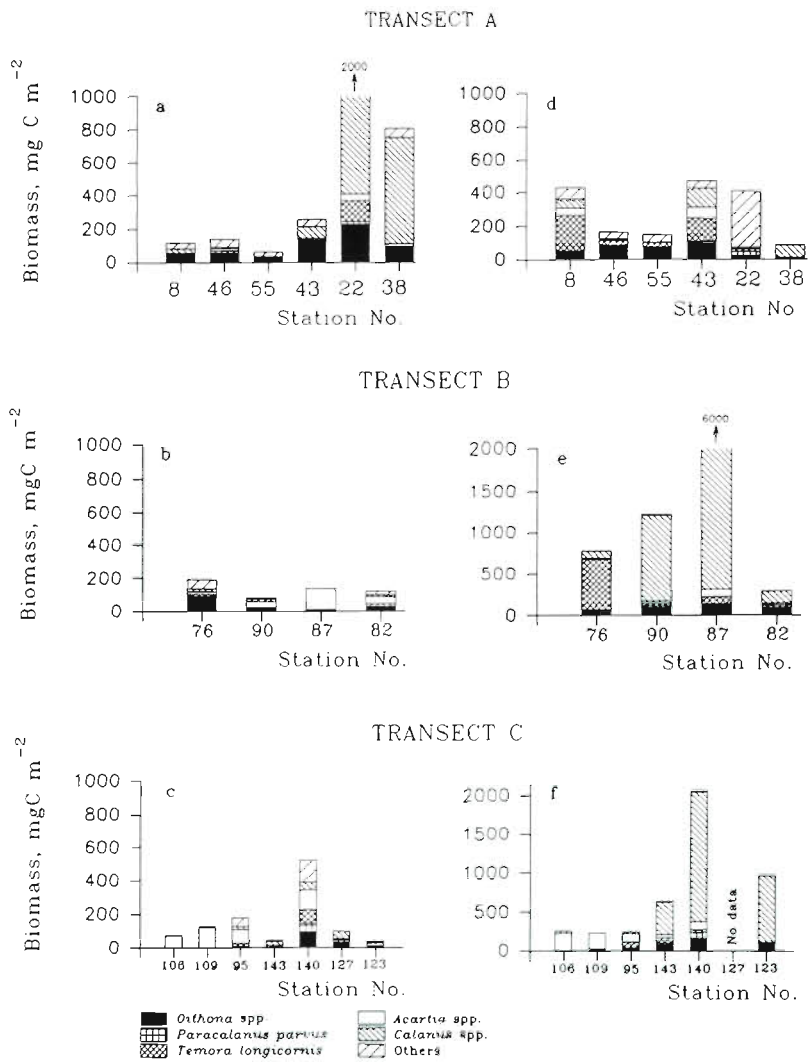

Fig. 6. Depth-integrated copepod biomass (a, b, c) above and (d, e, f) below the pycnocline, obtained from pump samples along the 3 transects

Table 2. Specific egg production rates (SEP) of *Oithona* spp. Estimated from egg:female ratios and hatching times along the 3 transects. Rates converted to 12°C (Q_{10} = 3) are also shown

Transect A	Stn:	46	46	55	55	43	43	43	22	22	22	38	38	38	38
Depth, m		5	22	5	22	5	26	33	14	26	45	6	20	34	60
Temperature, °C		12	9.6	12	9.5	12	8.2	8.2	12	7.7	7.7	12	8.5	7.6	6.7
No. of eggs		450	961	501	884	406	715	691	432	435	438	862	481.7	862	523
No. of females		36	95	36	47	27	88	76	28	62	55	86	29	86	27
Average no. eggs sac^{-1}		11.3	12.5	10.4	11.6	11.9	12.1	12.1	12.0	10.9	11.5	11.5	12.7	11.5	12.8
SD		1.5	1.8	1.7	1.6	1.5	1.9	1.5	1.4	2.2	1.8	1.8	1.5	1.8	1.8
Female length, µm		539	501	537	543	528	504	503	539	516	493	572	533	563	526
Hatching time d^{-1}		4.3	5.6	4.3	5.7	4.3	6.6	6.6	4.3	6.9	6.9	4.3	6.3	7	7.8
Eggs $female^{-1}$ d^{-1}		2.93	1.81	3.26	3.32	3.52	1.24	1.39	3.61	1.01	1.15	2.34	2.62	1.11	2.49
SEP, d^{-1}		0.053	0.038	0.05	0.052	0.067	0.026	0.029	0.065	0.02	0.025	0.041	0.048	0.02	0.048
SEP, 12°C, d^{-1}		0.053	0.05	0.05	0.068	0.067	0.039	0.044	0.065	0.032	0.04	0.041	0.071	0.033	0.085

Transect B	Stn:	76	76	76	90	90	90	90	87	87	82	82	82	82
Depth, m		5	20	38	10	32	40	51	20	55	5	16	32	55
Temperature, °C		12	8.6	8.5	12	7.8	7.6	7.5	9.0	7.0	12.0	8.6	7.8	6.7
No. of eggs		489	470	257	370	1550	425	315	488	391	404	208	730	512
No. of females		22	35	19	50	70	53	16	58	33	54	40	53	25
Average no. eggs sac^{-1}		11	12	11	10	11	12	11	11	13	11	13	13	13
SD		1	1	2	2	2	2	2	2	4	2	2	2	2
Female length, µm		536	511	510	551	492	505	500	531	532	551	498	516	510
Hatching time d^{-1}		4.3	6.3	6.3	4.3	6.9	7	7.1	6	7.5	4.3	6.3	6.9	7.8
Eggs $female^{-1}$ d^{-1}		5.21	2.14	2.14	1.73	3.23	1.14	2.78	1.41	1.55	1.75	0.83	2.01	2.64
SEP, d^{-1}		0.095	0.043	0.043	0.03	0.071	0.024	0.059	0.024	0.023	0.03	0.018	0.04	0.054
SEP, 12°C, d^{-1}		0.095	0.063	0.064	0.03	0.113	0.038	0.097	0.034	0.039	0.03	0.026	0.063	0.096

Transect C	Stn:	106	106	106	109	109	109	95	95	95	143	143	143	143	140	140	140	127
Depth, m		5	15	24	5	15	25	6	16	36	6	23	35	45	6	25	45	40
Temperature, °C		12.0		8.0	12	8.0	8.0	12.0	8.0	8.0	12.0	8.5	7.5	7.5	12.0	8.0	7.2	7.0
No. of eggs		73		91	193	88.7	412	209	243	181	476	900	256	567	173	455	844	628
No. of females		7	1	4	8	5	23	24	41	23	29	47	25	35	23	55	61	34
Average no. eggs sac^{-1}		12.2	0	15.2	12.9	12.7	15.2	12.3	14.3	15.1	11.9	12.5	11.1	12.9	11	11.7	12.8	13.7
SD		0.4		2.2	2.2	0.5	1.1	3	2.8	1	1.3	1.7	2.1	1.9	1.1	1.9	2.2	2
Female length, µm		562		557	562	504	506	585	576	539	553	528	523	498	547	512	502	528
Hatching time d^{-1}		4.3		6.7	4.3	6.7	6.7	4.3	6.7	6.7	4.3	6.3	7.1	7.1	4.3	6.7	7.3	7.5
Eggs $female^{-1}$ d^{-1}		2.44	0	3.39	5.65	2.65	2.67	2.04	0.88	1.17	3.85	3.02	1.44	2.28	1.76	1.23	1.89	2.46
SEP, d^{-1}		0.04	0	0.057	0.093	0.055	0.055	0.032	0.014	0.021	0.066	0.057	0.028	0.049	0.031	0.025	0.04	0.046
SEP, 12°C, d^{-1}		0.04	0	0.088	0.093	0.086	0.086	0.032	0.022	0.033	0.066	0.084	0.046	0.08	0.031	0.039	0.067	0.08

Table 3. Measured copepod egg production (in terms of egg female^{-1} d^{-1} ± SD and weight-specific rate, d^{-1}) within the surface layer and at the maximum fluorescence depth (or below thermocline). Females were incubated in water from the sampling depth and at *in situ* temperature (12 and 7°C, respectively). –: no measurements. Number of experiments in parentheses

Transect A	Stn: 8	46	55	43	22	38
Surface						
Calanus finmarchicus	2.4 0.005 (1)	–	–	0.0 (1)	26.9 ± 25.8 0.059 (5)	0.3 ± 0.8 0.001 (6)
Centropages typicus	19.7 0.043 (1)	–	48.1 ± 42 0.106 (4)	–	–	–
Centropages hamatus	–	–	23.5 0.094 (1)	–	–	–
Paracalanus parvus	6.1 ± 2.9 0.043 (2)	2.7 0.019 (1)	7.0 ± 2.5 0.049 (4)	–	4.4 ± 0.6 0.031 (4)	5.4 ± 3.8 0.038 (7)
Temora longicornis	16.5 ± 3.1 0.050 (2)	–	24.0 0.072 (1)	17.7 ± 5.2 0.053 (2)	– –	– –
Acartia spp.	2.3 ± 4.1 0.030 (6)	–	–	–	–	–
Fluorescence maximum						
Calanus finmarchicus	–	–	–	0.0 (2)	14.4 ± 9.5 0.032 (6)	14.7 ± 29.9 0.032 (9)
Centropages typicus	–	0.0 (1)	–	–	–	–
Centropages hamatus	–	–	17.1 0.068 (1)	–	–	–
Paracalanus parvus	–	–	3.9 ± 2.5 0.027 (5)	–	0.5 0.004 (1)	0.9 ± 0.4 0.006 (4)
Temora longicornis	16.5 ± 2.5 0.050 (4)	15.9 ± 6.2 0.048 (3)	15.0 ± 1.3 0.045 (5)	15.7 ± 8.9 0.047 (9)	–	–

Transect B	Stn: 76	90	87	82
Calanus finmarchicus	–	–	–	–
Centropages typicus	–	105 ± 39.6 0.231 (2)	33.5 ± 14.5 0.074 (6)	–
Centropages hamatus	–	–	38.0 0.152 (1)	–
Paracalanus parvus	6.9 ± 4.1 0.048 (7)	15.0 ± 3.6 0.075 (6)	21.6 ± 5.3 0.150 (7)	13.6 ± 2.8 0.095 (7)
Temora longicornis	7.4 ± 7.3 0.022 (3)	–	–	–

Transect C	Stn: 106	109	95	143	127	140
Calanus finmarchicus	–	–	–	28.0 0.062 (1)	55 0.121 (1)	22.5 ± 3.5 0.050 (2)
Centropages typicus	–	–	77.0 0.169 (1)	–	–	–
Centropages hamatus	–	–	26.2 ± 3.5 0.105 (2)	–	–	–
Paracalanus parvus	–	26.7 0.188 (1)	33.4 ± 4.7 0.234 (3)	1.5 ± 2.1 0.011 (2)	2.9 ± 1.3 0.020 (4)	0.4 ± 0.5 0.003 (4)
Temora longicornis	–	–	17.1 ± 10.4 0.051 (2)	16.4 ± 13.7 0.049 (8)	26.0 0.078 (1)	2.0 0.020 (1)
Acartia spp.	14.4 ± 11.1 0.187 (7)	11.0 0.143 (1)	21.3 ± 5.2 0.276 (5)	1.5 0.020 (1)	–	–

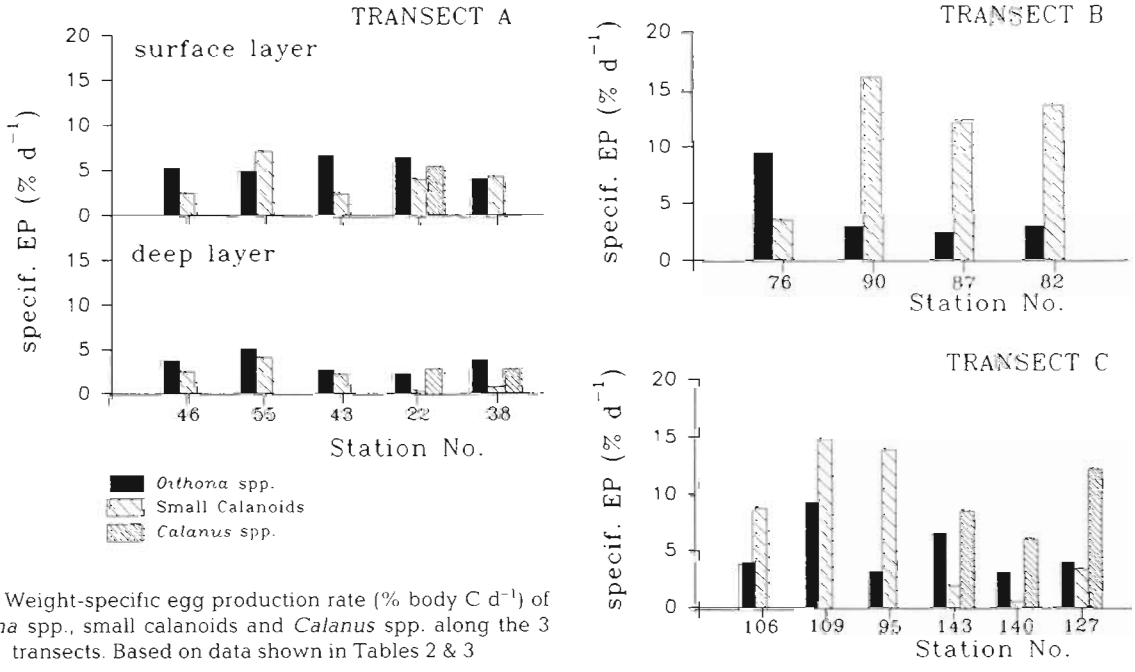

Fig. 7. Weight-specific egg production rate (% body C d^{-1}) of *Oithona* spp., small calanoids and *Calanus* spp. along the 3 transects. Based on data shown in Tables 2 & 3

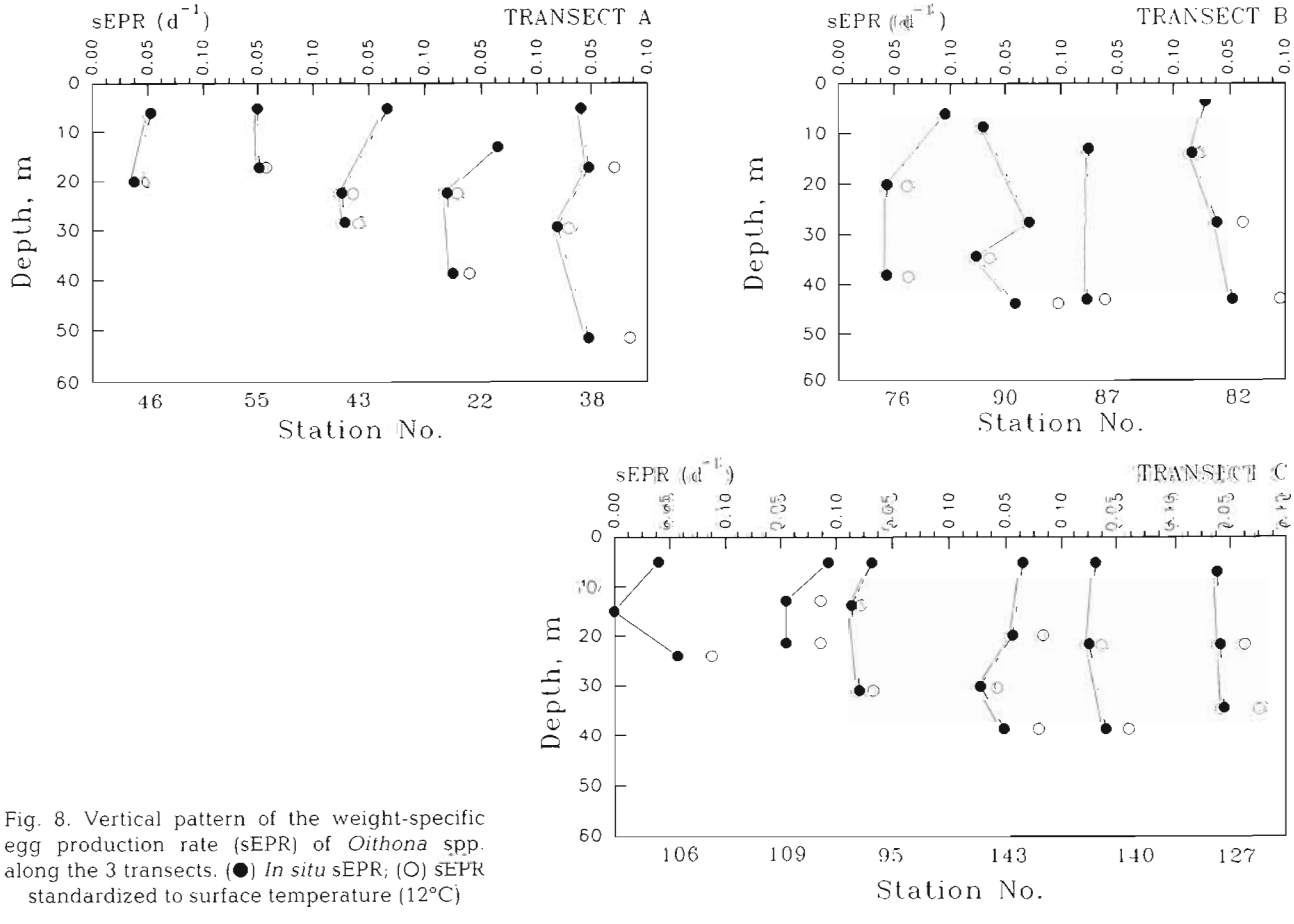

Fig. 8. Vertical pattern of the weight-specific egg production rate (sEPR) of *Oithona* spp. along the 3 transects. (●) *In situ* sEPR; (O) sEPR standardized to surface temperature (12°C)

ture corrected rates by assuming Q_{10} = 3.0; Kiørboe & Sabatini 1995 and references therein) are considered, then *Oithona* spp. egg production was roughly constant throughout the water column or increased with depth. Information for calanoids was restricted to Transect A. The measurements of egg production in surface waters and below the thermocline also show higher temperature corrected fecundity rates in the deeper layer for most of the species (Table 3).

There was no coupling between egg production rate and the observed hydrography or phytoplankton distribution along Transects A and B. However, a response in the egg production rate was observed for *Acartia* spp. and *Paracalanus parvus* on Transect C, associated with the coastal front where their egg production rates increased 5 and 20 times, respectively (Table 3).

The relative contribution of *Oithona* spp. to total copepod production (Fig. 9) varied within the area studied. Across Dogger Bank, *Oithona* spp. on average accounted for 47% of the total copepod production with a peak value of 70%. Along Transects B and C, *Oithona* spp. was less important (18 and 8% respectively). The highest secondary production during this cruise was measured at the deep *Calanus* dominated stations on Transects B and C.

Potential relationships between fecundity and food availability/composition

In order to examine whether there was any differential response in the *Oithona* spp. versus calanoids' fecundity to the food environment a correlation analysis was performed. *Paracalanus parvus* was chosen as representative of calanoids since the most complete set of data was collected for this species. Only surface data were compared because the egg production measurements for *P. parvus* were too few (n = 3) in the deeper layer. Even though *Oithona* fecundity was not significantly correlated to any food item, a positive trend was found in the relation with all the protozooplankton prey while those with both fractionated and total chlorophyll were negative (Table 4). Moreover, the same trends can be observed when the data for the entire water column were pooled. The exactly reverse pattern was found for *P. parvus*, their rates in surface being significantly related to total chlorophyll concentration (r = 0.70). These opposite patterns suggest fairly distinct feeding habits for both species, implying overall a preference of *Oithona* spp. for motile prey.

Annual production of *Oithona* spp. in the North Sea

Broadly, 2 major subregions can be distinguished in the North Sea on the basis of bathymetric and hydrographical characteristics: (1) the southern, relatively shallow area (<50 m) which includes Dogger Bank and surrounding waters; and (2) the northern, deeper area (>100 m) with a strong Atlantic influence. The annual patterns of copepod biomass, fecundity and resulting production within each of the 2 subregions are shown in Fig. 10. Total copepod biomass was highest in the northern subregion, primarily due to the occurrence of *Calanus* spp. and *Pseudocalanus elongatus*. The biomass of *Oithona* spp. was comparable or lower in the

Table 4. Coefficient of correlation (r) and level of significance for *Oithona* spp. and *Paracalanus parvus* weight-specific egg production rate in surface waters (and within the entire water column for *Oithona* spp. only) versus potential food sources. n: number of observations; SEP: specific egg production rate; ns: not significant

SEP	Chlorophyll *a* fraction				Protozooplankton				
	3–11 µm	11–50 µm	3–50 µm	Total	*Mesodinium*	Naked ciliates	Ciliate total	Naked dinos	Thecate dinos
Surface									
Oithona spp.									
r	−0.06	−0.04	−0.01	−0.13	0.32	0.02	0.16	0.052	0.41
n	15	15	15	15	15	35	35	15	
p	ns	ns	ns	ns	ns	ns	ns	0.05	
P. parvus									
r	0.24	0.53	0.49	0.70	−0.07	−0.20	−0.28	−0.48	−0.22
n	12	12	12	12	12	12	12	12	12
p	ns	ns	ns	0.01	ns	ns	ns	ns	ns
Water column									
Oithona spp.									
r	−0.05	−0.06	−0.07	−0.18	0.23	0.01	0.02	0.12	0.14
n	20	20	20	45	44	44	44	44	44
p	ns	ns	ns	ns	ns	ns	ns	ns	ns

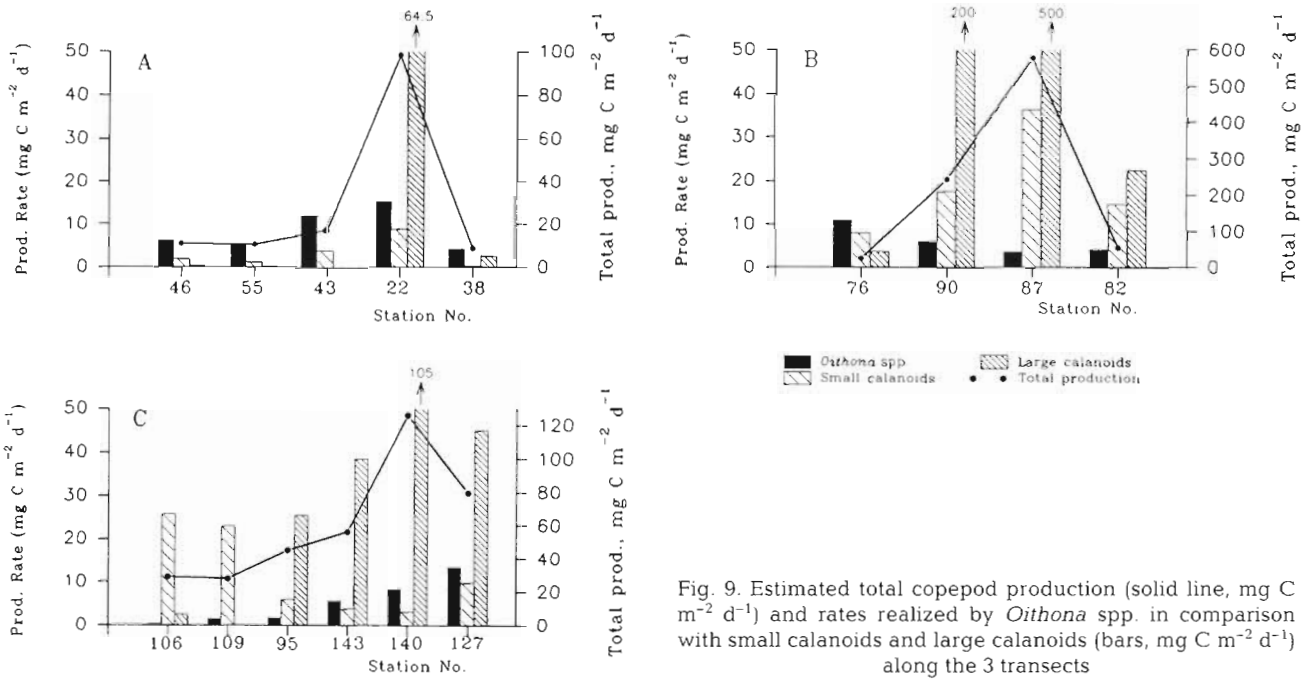

Fig. 9. Estimated total copepod production (solid line, mg C m^{-2} d^{-1}) and rates realized by *Oithona* spp. in comparison with small calanoids and large calanoids (bars, mg C m^{-2} d^{-1}) along the 3 transects

southern than in the northern region. However the relative contribution of *Oithona* to the standing stock of copepods on average was the same in both regions, 25 ± 3% (range 10 to 35%) and 24 ± 3% (range 7 to 39%). In general, the highest weight-specific egg production rates were measured in the southern frontal area. The annual secondary production of the copepod community was estimated to be 5.6 and 14.3 g C m^{-2} for the southern and northern regions, respectively. The annual *Oithona* spp. production was about the same in both regions (2.2 and 1.8 g C m^{-2}) while their relative importance compared to calanoids was quite different, with a contribution to the annual production of 40 and 13%, respectively.

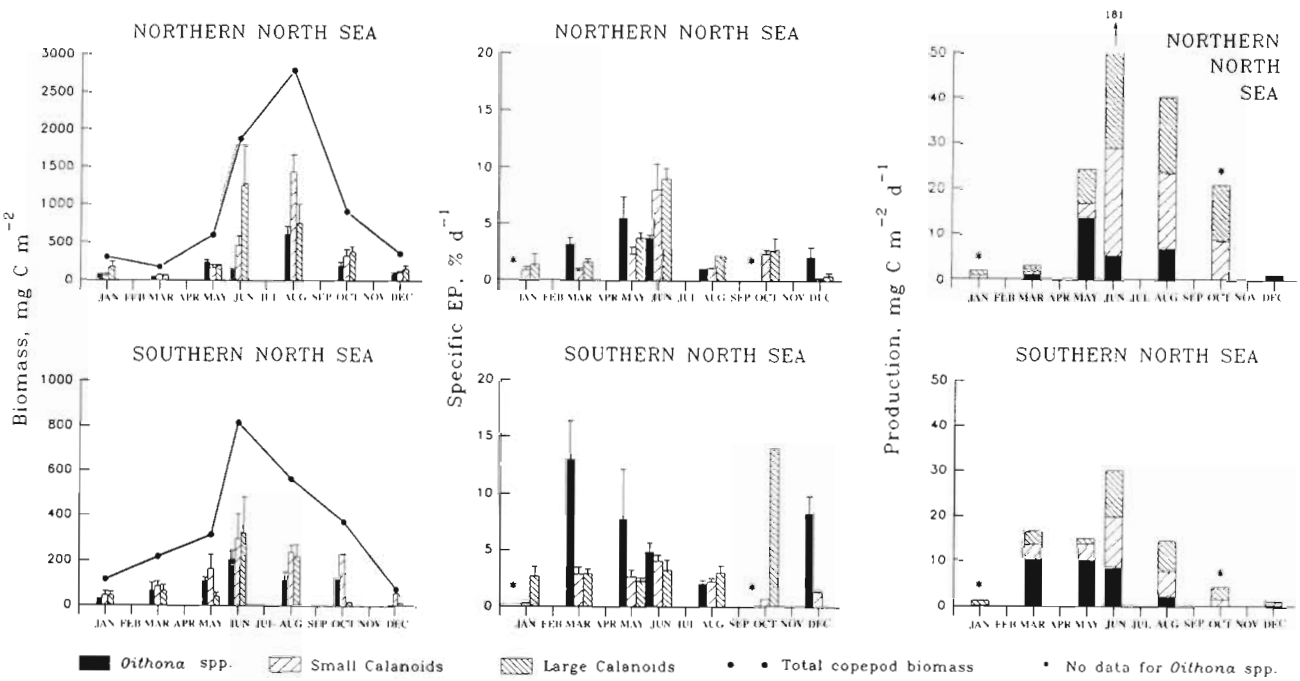

Fig. 10. Seasonal trends in the depth integrated copepod biomass (solid line, mg C m^{-2}), weight-specific egg production (% body C d^{-1}) and secondary production (mg C m^{-2} d^{-1}) in the southern and northern North Sea. Sources of data in Table 1

DISCUSSION

The egg production method used to estimate copepod production in the present investigation has previously been applied to free-spawning copepods, but may also be used for estimating production by the egg-carrying *Oithona* spp. The potential growth of juvenile cyclopoid copepods appears to be constant up to C4 (ca 0.20 d^{-1} at 15°C) whereafter it decreases (Paffenhöfer 1993, Sabatini & Kiørboe 1994). That means that one of the basic assumptions of the egg production approach is not fulfilled (Berggreen et al. 1988). However, we argue that this approach is still valid, since: (1) the maximum weight-specific egg production rate of *O. similis* (0.10 d^{-1} at 15°C) approaches the maximum weight-specific growth rate of older copepodids (0.07 d^{-1}) (Sabatini & Kiørboe 1994); (2) the dominating species in the region studied was *O. similis*; and (3) the biomass of *Oithona* spp., as of copepods in general, is mostly made up of older stages (Krause & Thrams 1983, Mullin 1988, Fransz et al. 1991). The egg:female ratio, which is potentially biased in free-spawning copepods due to egg predation, sinking and advection, is not biased for the egg-carrying *Oithona* (Hay et al. 1991). In our samples, we found that normally 40 to 50% of the egg sacs were still attached to the females during counting and egg sacs of *Oithona* spp. lost during handling and fixation were easily distinguishable from those of the co-occurring, egg-carrying copepods (*Pseudocalanus* sp. and *Microsetella norvegica*).

Our estimates of annual copepod production for the North Sea, though conservative, are within the range reported in the literature from about 5 to 10 g C m^{-2} in the southern to at least 20 g C m^{-2} in the northern area of the North Sea (Fransz et al. 1991). Production of *Oithona* spp. in terms of annual C m^{-2} was also within the range estimated for a few other localities of the North Sea as well as for other temperate areas (Table 5).

Our results show that the weight-specific egg production and daily production rates of *Oithona* spp. did not show as pronounced seasonal and spatial signals as observed for the co-occurring calanoid copepod genera. For example, there was no response to the increased phytoplankton biomass associated with the fronts on Transect C, as observed for *Acartia* spp. and *Paracalanus parvus* (Table 3). It was also apparent that the relative importance of *Oithona* spp. decreased from the shallow Dogger Bank area to the deeper northern stations. The horizontal difference in the relative importance of *Oithona* was also supported by our annual estimates for the 2 subregions of the North Sea. The relative contribution of *Oithona* to total copepod production is primarily determined by the spatio-temporal pattern of productivity of the community as a whole. In other words, the lower the total copepod production, the higher the relative importance of *Oithona*. This is further suggested by the few other estimates reported in Table 5. The same seems to be the case when examining the production of *Oithona* spp. relative to calanoids on a temporal scale. As an example, in the southern Kattegat (Denmark) their relative contribution was 20 to 30% for most of the year, but decreased to <5% when small calanoid species peaked (Fig. 11).

Copepod egg production rates are often measured only in surface samples; however, the high frequency of subsurface blooms in the southern North Sea (Riegmann et al. 1990, Nielsen et al. 1993, Munk & Nielsen

Table 5. Annual copepod community production and relative contribution of *Oithona* spp. in selected areas

Area	Total production (g C m^{-2} yr^{-1})	*Oithona* spp. (g C m^{-2} yr^{-1})	%	Method	Source
Emerald Bank	8.5	1.4	13.2	Mass-specific P/B ratios	Tremblay & Roff (1983)
(Scotian Shelf)	15.6	1.0	6.0	Life-history analyses	McLaren et al. (1989)[a]
Kattegat (Denmark)	10.2	1.7	16.6	Egg production approach (egg:female ratios)	Recalculated after Kiørboe & Nielsen (1994)
North Sea					
Southern bight, coast	12–23			Temperature-dependent rates	Fransz & Gieskes (1984)
Southern bight, offshore	5–15				
Central North Sea	10			Temperature-dependent rates	Fransz & Gieskes (1984)
Off Northumberland (UK)	20.2 (10–44)	~3.7	18.3	Temperature-dependent rates (nauplii not considered) Average over 15 yr	Roff et al. (1988)
Northern North Sea	14.3	1.8	13.0	Egg production approach	This study
Southern North Sea	5.6	2.2	40.0	(egg:female ratios)	

[a]Same data set as that used by Tremblay & Roff (1983)

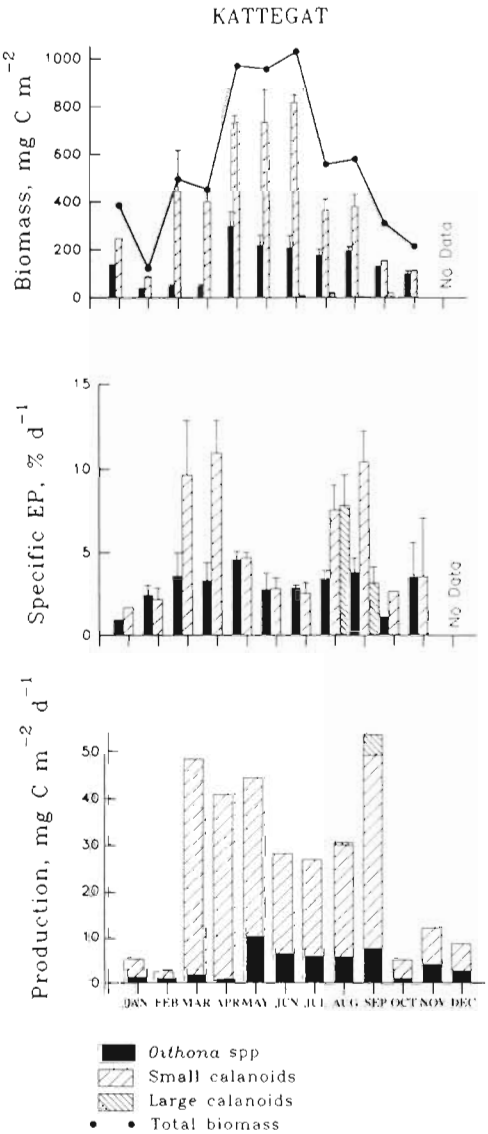

Fig. 11 Seasonal trends in the depth integrated copepod biomass (solid line, mg C m^{-2}), weight-specific egg production (% body C d^{-1}) and secondary production (mg C m^{-2} d^{-1}) in the Kattegat (Denmark). Recalculated from Kiørboe & Nielsen (1994)

1994), combined with food limitation of copepod populations during the summer, led us to estimate copepod production in 2 depth strata: surface mixed layer and subsurface fluorescence maximum. The egg production of *Temora longicornis* and *Calanus* spp. were the same or higher in water from the fluorescence peak, while *Paracalanus parvus* egg production was highest in the surface water. This difference might reflect the ability of the first 2 species to exploit the larger cells located below the pycnocline (Fig 4). The SEP of *Oithona* spp. was about the same throughout the water column (Fig. 8).

The potential food for the copepod community was dominated by diatoms, autotrophic and heterotrophic dinoflagellates and ciliates as observed on other summer cruises to the region (Nielsen et al. 1993). Food conditions were likely suitable for both calanoids and *Oithona* spp. in terms of particle size. Adults of *O. similis* can effectively utilize food particles from 8–10 µm up to 35–40 µm while nauplii can ingest flagellates as small as 2–5 µm (Eaton 1971, Drits & Semenova 1984), overlapping thus the particle size range of calanoids (5–10 to 50–200 µm; Berggreen et al. 1988). Information on *in situ* feeding patterns of cyclopoids is scarce and still quite controversial. Cyclopoid feeding mechanisms appear to be different from and more complex than those of many calanoids (Turner 1986, Paffenhöfer 1993, González & Smetacek 1994). However, we found evidence (opposite trends in the correlation coefficients, r; Table 4) suggesting that *O. similis* preferred motile prey, in contrast to *Paracalanus parvus*, in which specific egg production rate was significant correlated to the chlorophyll concentration (Table 4). *Oithona*'s preference for motile prey is supported by observations by Uchima & Hirano (1986) who found that juvenile *O. davisae* only grew and survived on motile food particles. This also suggests that different behaviours are involved in the feeding of the 2 species. This assumption is supported by laboratory studies on feeding behaviour where it has been shown that *Oithona* do not generate a feeding current; the encounter with food will depend on the signal provided by the food particle (Paffenhöfer 1993). *P. parvus*, on the other hand, is a slow-moving suspension feeder adapted for small prey organisms (Tiselius & Jonsson 1990) and thus it can better take advantage of small non-motile phytoplankton cells.

The importance of *Oithona* spp. compared with calanoid copepods on Dogger Bank proper is actually due to the low biomass of calanoid species rather than to a particularly high biomass/production of *Oithona*. The egg-carrying strategy of *Oithona* may represent a clear advantage in comparison to broadcast spawning species in this particular area. Most of the calanoids release their eggs freely into the water and they often sink to the bottom where they lie until hatching. These eggs may constitute a supply of food for the large biomass of suspension feeding benthos occurring on the Bank (Duineveld et al. 1987), and thus, the recruitment of calanoids will be negatively affected. High mixing rates at the shallow Bank assure a frequent replacement of the water above the benthos that might favour, additionally, the consumption of eggs by suspension feeders. Therefore, the likely inadequate food conditions for calanoid species, which in turn translates into the lower specific fecundity rates realized across Dogger Bank, and potentially their high egg (predation)

mortality, might explain the dominance of *Oithona* spp. in the area.

In summary, it appears that *Oithona* spp. production is less variable in time and space than that of the co-occurring calanoid genera. This may be due to the fact that *Oithona* spp. are specialized to feed on particles which are within the lower part of the food size spectrum for the copepods, likely small protozooplankton, but more important, normally available as related to microbial production. In contrast, most of the calanoid species depend on larger phytoplankton that occur in relatively short blooms or at oceanographic discontinuities. This has the advantage of allowing *Oithona* to maintain stable populations almost continuously.

Though this is overall in accordance with Paffenhöfer's (1993) hypothesis for cyclopoids in general, it may not be related to their presumed metabolic 'slowness', as he argued. It would rather be a matter of life-cycle strategy, as the potential seems to exist, in *Oithona* at least, to reach growth and development rates as high as those of many calanoid species (Kiørboe & Sabatini 1994, Sabatini & Kiørboe 1994).

On account of the above, it can be speculated that *Oithona* is associated to microbial food webs and, therefore, its occurrence and productivity patterns are more stable than those of calanoids. *Oithona* might act as a link between smaller phytoplankton and/or small protozooplankton and larger zooplankton and fish larvae. It follows that their populations may constitute a currently available food item for fish larvae and planktivorous fishes, becoming a key species in areas or seasons where conditions are disadvantageous for calanoid copepods.

Acknowledgements. This work was supported by grants from Danish Natural Science Research Council grant no. 11-0420-1 to T.G.N. and from the Argentinean Science Research Council (Consejo Nacional de Investigaciones Científicas y Técnicas, JUN91/Res. 8) and the Commission of European Communities (B/I1*-913134) to M.S. We thank Dan Conley, Benni Hansen and Thomas Kiørboe for critically reading the manuscript. We are indebted to the captain and crew of RV 'Dana' for help with sampling and we appreciate technical assistance by Jack Melbye and Alice Christoffersen.

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This article was submitted to the editor

Manuscript first received: October 4, 1995
Revised version accepted: April 3, 1996