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ORIGINAL PAPER

Life cycle of *Oithona similis* (Copepoda: Cyclopoida) in Kola Bay (Barents Sea)

V. G. Dvoretsky · A. G. Dvoretsky

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Abstract The annual population dynamics (nauplii, old copepodites CIV–CV and adults) and seasonal variations in reproductive parameters of the cyclopoid copepod *Oithona similis* were investigated on the basis of the data 1999–2006 in Kola Bay, a large subarctic fjord in the Barents Sea. Population density of *O. similis* ranged from 110 to 9,630 ind m^{-3} and averaged 1,020 ± 336 ind m^{-3}. The relative abundance of adults was high during winter (~60%). At the end of winter (mid-March), the population included a large percentage of later-stage copepodites (stage CIV 23% and stage CV 57%). There were two periods of mass spawning, in late June and September. Autumn and summer generations strongly differed in abundance, average prosome length (PL), clutch size (CS), egg diameter (*D*), egg production rates (EPR and SEPR) and female secondary production. Average PL decreased with increasing water temperature, while *D* and CS were strongly correlated with PL but unaffected by temperature. Annual average EPR and SEPR were 0.55 ± 0.18 eggs female^{-1} day^{-1} and 0.0011 ± 0.003 day^{-1}, respectively. Female secondary production averaged 0.8 ± 0.3 μg C m^{-3} day^{-1} (range 0.001–3.58). There were positive relationships between abundance, EPR, SEPR, production and water temperatures. Reproductive parameters appeared to be controlled by hydrological factors and food conditions.

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V. G. Dvoretsky (✉) · A. G. Dvoretsky
Murmansk Marine Biological Institute,
17 str. Vladimirskaya, 183010 Murmansk, Russia
e-mail: vdvoretskiy@mmbi.info

Introduction

The Barents Sea is one of the most productive regions of the World Ocean (Timofeev 2000). Zooplankton play an important role in marine ecosystem structure and function of the Barents Sea, forming a main link between primary producers (phytoplankton) and higher trophic levels (e.g. fishes, sea birds and mammals) (Timofeev 2000). A large amount of data about composition, distribution and dynamics of planktonic animals are already available in the literature for this region (e.g. Kamshilov and Zelikman 1958; Degtereva 1979; Pedersen et al. 1995). In particular, the biology of the copepod *Calanus finmarchicus* and the euphausiids *Thyssanoessa inermis* and *Thyssanoessa raschii* has been investigated more intensively because they are the base food resource for commercial fishes (Timofeev 2000). However, there is little information concerning life cycles and reproductive dynamics of other copepods, especially those with small body sizes.

Recent studies suggest that small copepods may be a more significant component in marine food webs, than that was previously considered (Gallienne and Robins 2001; Turner 2004). *Oithona similis* Claus, 1866 (Cyclopoida) is among the most numerous small planktonic copepods in the Barents Sea. In some seasons, *O. similis* abundance and biomass can exceed that of *C. finmarchicus* (Degtereva 1979). Due to their small size (<1 mm) and their high mean abundance, *O. similis* are thought to have a crucial importance as a food source for other copepods, chaetognaths, fish larvae and even adult planktivorous fishes in cold years in the Barents Sea when *C. finmarchicus* abundance is low (Degtereva 1979). Nevertheless, *O. similis* life history is insufficiently studied in the Barents Sea, although some data on their seasonal population dynamics have been obtained in Eastern Murman coastal waters (Fomin 1978, 1991). The main cause of our restricted knowledge about true population composition, abundance and biomass has been the use of coarse (>200 µm mesh size) nets. Studies on the ecology of *O. similis* in the arctic and sub-arctic regions are rare, although in temperate waters the biology of *Oithona* spp. has been explored well (Kiørboe and Nielsen 1994; Sabatini and Kiørboe 1994; Uye and Sano 1995, 1998; Nielsen and Sabatini 1996; Williams and Muxagata 2006; Porri et al. 2007).

The most thorough investigation of the annual cycle of *O. similis* comes from the arctic Kongsfjorden (northern Svalbard waters) by Lischka and Hagen (2005).

In our study, we have summarized available data about *O. similis* distribution in Kola Bay during 1999–2006. We do not have data about the abundance of *O. similis* during a single period. Data compiled from different years, but with similar climatological conditions, were used in our investigation. The main aim of our paper is to describe "averaged" seasonal cycle and some reproductive characteristics of *O. similis* populations in the sub-arctic zone of the Barents Sea.

Materials and methods

Study area

Kola Bay is typical of the fjords constituting the coastline in the Norwegian and Barents Seas (Fig. 1). The bay is about 51 km long, with its width gradually decreasing from 3.0–3.5 km near its mouth to 1.5–2.5 km in the centre to 1.0–1.5 km at its southern end (Matishov et al. 1997). The fjord's dominant water source is the Atlantic Ocean and the Atlantic inflow entering from the Barents Sea shelf is characterized by high salinity (34.5 psu) and relatively high temperatures (1.5–2°C in April and 7–8°C in August–September). The influx of Atlantic waters keeps most of the fjord from freezing, although in cold winters the southern part is covered with ice (30–40 cm). Water dynamics in the fjord are determined by tidal currents and winds. The water is stratified during the spring–summer period (Fig. 2), so distinct thermocline and halocline are formed in surface layers (Matishov et al. 1997).

The climate is maritime, with maximal and minimal air temperatures recorded in August and February, respectively. Spring temperatures are relatively cold, while autumn temperatures are relatively warm (Matishov et al. 1997). Water temperatures rapidly increase during late spring and early summer (May–July) and slowly decrease during autumn and winter.

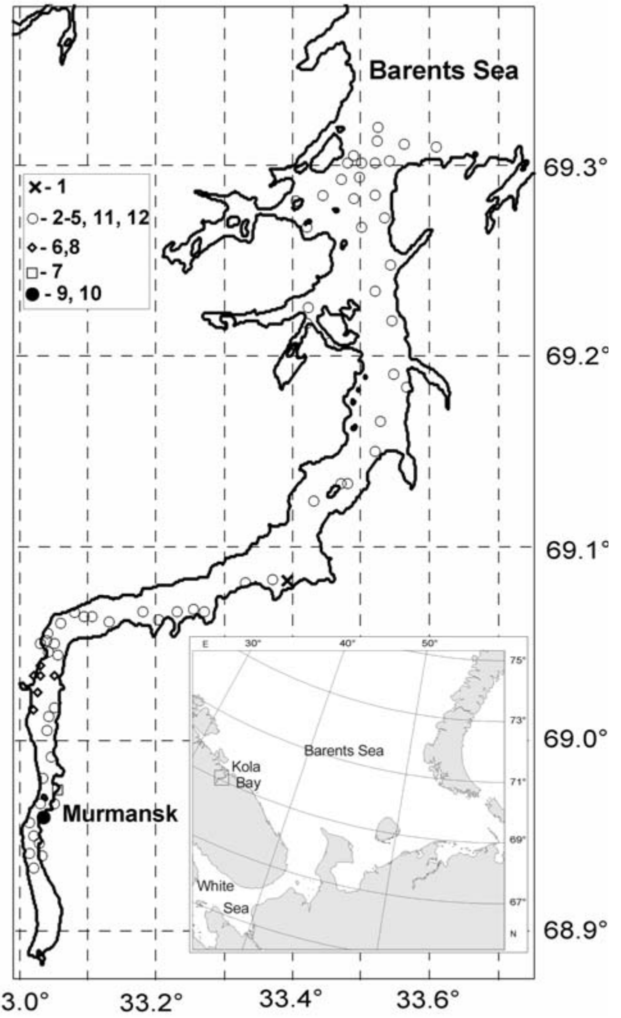

Fig. 1 Location of sampled stations in Kola Bay. Numbers refer to numbers of sampling events as shown in Table 1

Sampling

Zooplankton samples were collected in Kola Bay during expeditions and cruises by the Murmansk Marine Biological Institute covering the years 1999–2006 (Table 1, Fig. 1). During cruises 2–5 and 11–12, the entire area including stations in the southern, central and northern parts was investigated. We used a Juday plankton net (mouth diameter: 0.37 m; length: 2.0 m; mesh opening: 168 µm) to determine stage composition of copepodites throughout the study period and OTE PVC bottles (5 l capacity) to estimate the abundance of nauplii during mass reproduction period (June–September) at two to three stations (two replicates at each station). Zooplankton net tow samples were taken from the bottom to the surface or from 100 to 0 m, while bottle samples were taken at 10 m. After the completion of each haul, nets were washed and the samples fixed in buffered 4% formaldehyde-seawater solution.

Fig. 2 Seasonal variations of temperature (**a–c**) and salinity (**d–f**) averaged for 1999–2006 in different water layers in Kola Bay

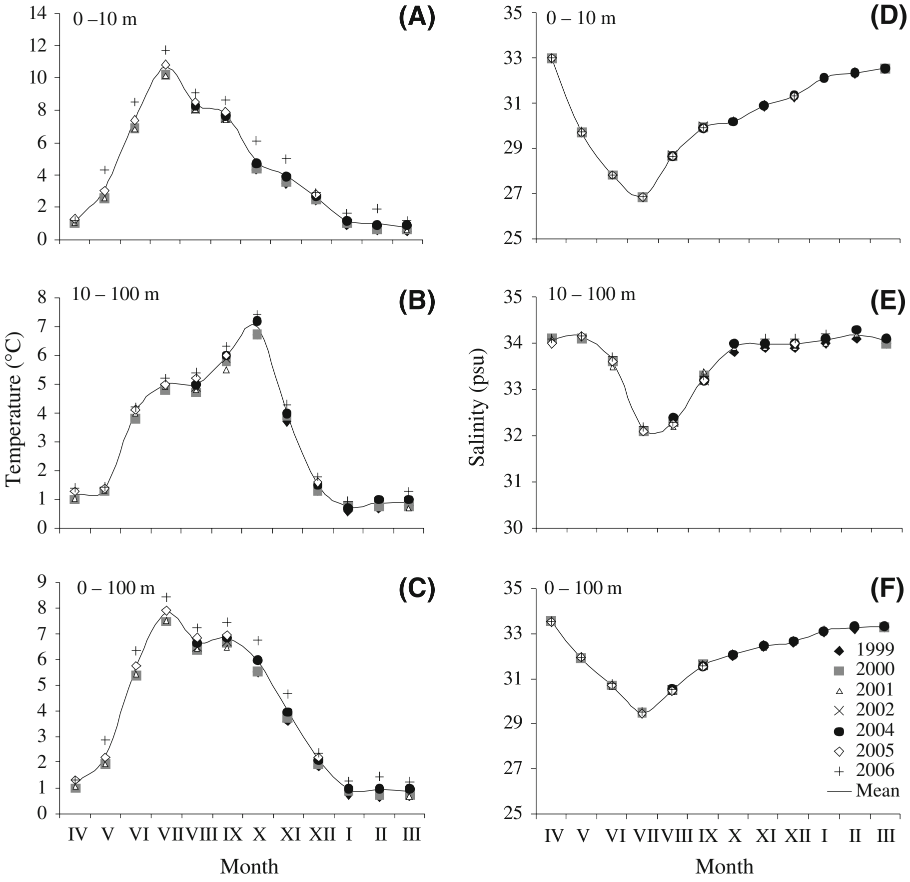

Table 1 Stations, sampling dates and periods of zooplankton collections in Kola Bay

No.	Date/period	Note	Stations	Net/bottle samples
1	21/10/1999–28/7/2000	Fixed coastal station	1	29/5
2	26/9/2000–29/9/2000	Cruise of R/V GSS–440	7	7/0
3	29/5/2001–1/6/2001	Cruise of R/V GSS–440	14	14/0
4	3/12/2001–7/12/2001	Cruise of R/V GSS–440	11	11/0
5	10/9/2002–14/9/2002	Cruise of R/V GSS–440	10	10/2
6	17/6/2004	E/V Belek	3	3/6
7	12/12/2004–23/7/2005	Fixed coastal station	1	37/19
8	12/5/2005	E/V Belek	3	3/6
9	4/8/2005–5/8/2005	Daily station	1	12/6
10	22/12/2005–23/12/2005	Daily station	1	12/0
11	12/9/2005–16/9/2005	Cruise of R/V GSS–440	10	10/0
12	8/7/2006–12/7/2006	Cruise of R/V GSS–440	10	10/0
Total			72	158/47

Numbers refer to numbers of sampling events as shown in Fig. 1

Processing

Each sample was divided into subsamples with a splitter (from 1/2 to 1/8) depending on the zooplankton abundance. A total of 500–700 individuals were taken from subsamples for subsequent analyses. Identification of nauplii, copepodites and sexes of *O. similis* was performed according to Gibbons and Ogilvie (1933) and Shuvalov (1980). All stages were counted and copepodites' and adults' prosome lengths (PL) were measured under a stereomicroscope MBS-10 (32–56 magnifications). A 168-μm mesh net is too coarse to sample nauplii and young copepodites (CI–CIII) quantitatively, and therefore only abundances of the older stages (PL > 400 μm) are considered. In most cases, there were females with intact egg sacs and intact detached egg sacs in plankton samples. The total number of ovigerous females at each station was determined as the sum of the number of females with egg sacs and the number of detached egg sacs divided by 2. A total of 40–50 females carrying egg sacs were taken from each sample. Clutch size (CS) was calculated as the sum of the eggs in both sacs. Average egg diameter (*D*) was obtained by measuring the diameter of each egg from a total of 250 egg sacs under a stereomicroscope (LOMO ES BIMAM R–11–1, 100× magnification). The abundance of eggs was calculated by multiplying the number of ovigerous females by the CS. Egg production rates (EPR, eggs female^{-1} day^{-1}) were determined using the egg-to-female ratio (E/F) and hatching time (HT) according to Edmondson (1971):

$$\mathrm{EPR} = (\mathrm{E/F})(1/\mathrm{HT}).$$

Egg hatching time (HT, days) was calculated using the equation of Nielsen et al. (2002):

$$\mathrm{HT} = 1504.5(\mathrm{T} + 7.6998)^{-2.05},$$

where $T =$ water temperature (°C). Specific egg production of *O. similis* (SEPR per day) was estimated using the egg carbon content (conversion factor is 0.14 pg C μm^{-3}; Kiørboe et al. 1985) and female carbon content based on length–weight relationship (Sabatini and Kiørboe 1994). The secondary production of females (SPF) was obtained by multiplying the biomass of females and SEPR.

Median CS, *D*, EPR, SEPR and SPF in autumn and summer generations of *O. similis* were compared by non-parametric procedures (Kruskal–Wallis tests), because variances for these parameters were heteroscedastic (Levene's test $a = 0.05$) even after attempts at data transformation.

Linear regression analyses were used to reveal relationships between the physical variables (average temperature and salinity in upper 100 m layer or 0 in bottom layer) and the $\log(x + 1)$-transformed abundance of each stage, PL and reproductive characteristics (proportion of females with egg sacs, CS, *D*, EPR, SEPR, SPF). In order to describe annual population dynamics of *O. similis*, we used average data for each month.

Results

Hydrology

The annual minimum temperature was usually registered in February or March (<+0.8°C). By July, the temperature of the surface layer rises up to 10.5°C. The salinity regime of Kola Bay is determined by interactions between a weak river run-off (only in a little area in the southern part) and the Barents Sea water masses. There are strong temporal and spatial salinity variations in the upper 10 m layer of water. Winter and spring salinity values ranged between 20 and 34 psu. In summer, salinity typically decreased to around 15 psu (in southern part), but increased again during autumn (up to 25–34 psu). Typical annual cycles in mean water temperature and salinity in Kola Bay, as recorded with our SBE 19plus SEACAT profiler, are presented in Fig. 2. Literature information (Terziev et al. 1990; Matishov et al. 1997) and unpublished cruise reports (temperature in upper 10 m and 10–100 m layer) were also used during those occasions in 2000, 2001 and 2004 when our in situ sensors were not registering hydrological parameters.

Phytoplankton dynamics

According to published data, during the winter season (from November 2004 to March 2005) in the surface layer of the southern bend of Kola Bay, the values of chlorophyll *a* concentration varied from 0.01 to 0.04 mg m^{-3} (0.02 ± 0.01 mg m^{-3}). During the spring season (April–June 2005), the chlorophyll *a* concentration gradually increased from 0.06 to 0.78 mg m^{-3} (0.27 ± 0.22 mg m^{-3}) (Trofimova 2007). Within summer (July–August 2005) the concentrations of chlorophyll *a* were considerably higher than spring values (0.14–4.07 mg m^{-3}) (Trofimova 2007). During autumn (September–October 2005), the concentrations of chlorophyll *a* considerably dropped to 0.06–0.09 mg m^{-3} (0.07 ± 0.02 mg m^{-3}). The chlorophyll *a* concentration reduction continued into winter (0.01 mg m^{-3}) (Trofimova 2007) (Fig. 3).

Seasonal variations of stage composition, abundance and PL in *O. similis*

During our "mean" year, population density of *O. similis* ranged between 110 and 9,630 ind m^{-3} (or between 110

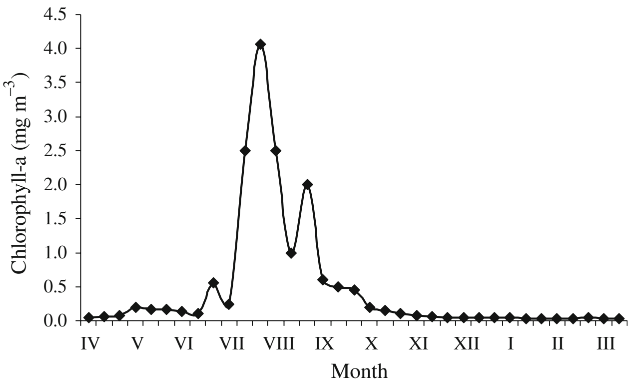

Fig. 3 Seasonal dynamics of chlorophyll *a* mean concentration (mg m^{-3}) in the surface layer in Kola Bay based on the results 2004–2005 (after Trofimova 2007)

and 560 ind m^{-3} with nauplii excluded) and averaged 1,020 ± 336 (or 208 ± 19) ind m^{-3}.

In the beginning of winter (November–December), the population was dominated by adults (about 52%), late-stage copepodites accounted for 48% and nauplii were absent (Fig. 4). By March, the relative abundance of adults decreased to 32%, the percentage of late-stage copepodites increased to 68% (Fig. 4b, c) and young copepodite stages were rare. At the end of winter (the middle of March), the population was made up of 23% stage-CIV copepodites, 57% stage-CV copepodites, 18% adult females and 2% adult males (Fig. 4). By the end of March, the number of adult males increased slightly due to growth and development of copepodids CV. Thus, it is possible to speak of sex differentiation beginning during the March period. Mean total abundance of *O. similis* varied from 109 to 256 ind m^{-3}.

During April–May, adult male and female relative abundances increased (from 2% to 20% and from 18% to 71%, respectively) due to moulting of the copepodites from the previous year. Abundances of CV-stage copepodites decreased by 9%, and CIV were not found in plankton in mid-May, obviously, due to their development to CV stages (Fig. 4b, c). At the beginning of June, we saw mass reproduction of *O. similis*. Total abundance of nauplii sharply increased to where they accounted for 97% of *O. similis* population (Fig. 4a). By mid-to-late June, nauplii still dominated in the plankton (95%), however, all copepodite stages were found (Fig. 4). Total abundance of *O. similis* during this period was 120–2,670 ind m^{-3} (Fig. 4).

The beginning of the summer period (end of June–end of July) was characterized by a high proportion of nauplii. Nauplii abundances gradually fell from 96% to 87% (Fig. 4a), while relative abundance of old copepodids increased (from 0% to 4% CV and from 0% to 2% CIV, respectively) (Fig. 4b, c). Maximum population densities (including nauplii) for the "mean" year were recorded during this period (4,700–9,600 ind m^{-3}). In the second half of summer season (the end of July–the end of August), nauplii relative abundance decreased from 87% to 49% of the population (Fig. 4a). However, proportions of old copepodites and adults increased by 25% and 26%, respectively (Fig. 4b, c, d). There were some young copepodites present during this period. The species total abundance varied between 410 and 1,300 ind m^{-3}.

Mass spawning of the new generation of females was observed in September. All stages of *O. similis* were recorded in the samples. Subsequently, nauplii made up 70–73% of the *O. similis* population (Fig. 4a), adults accounted for 18–20% (Fig. 4d) and old copepodids accounted for 7–12% (Fig. 4b, c), respectively. By the beginning of October, the abundance of nauplii was 7%, old copepodids CIV–CV reached 36% and adults dominated the population (57%). The total population density had decreased from 1,300 to 300 ind m^{-3} over this month (Fig. 4). In the end of autumn, the population was made up of 60% adult males and females, and 40% old copepodites. There were no nauplii in the plankton. In winter, the total abundance varied from 300 to 400 ind m^{-3}.

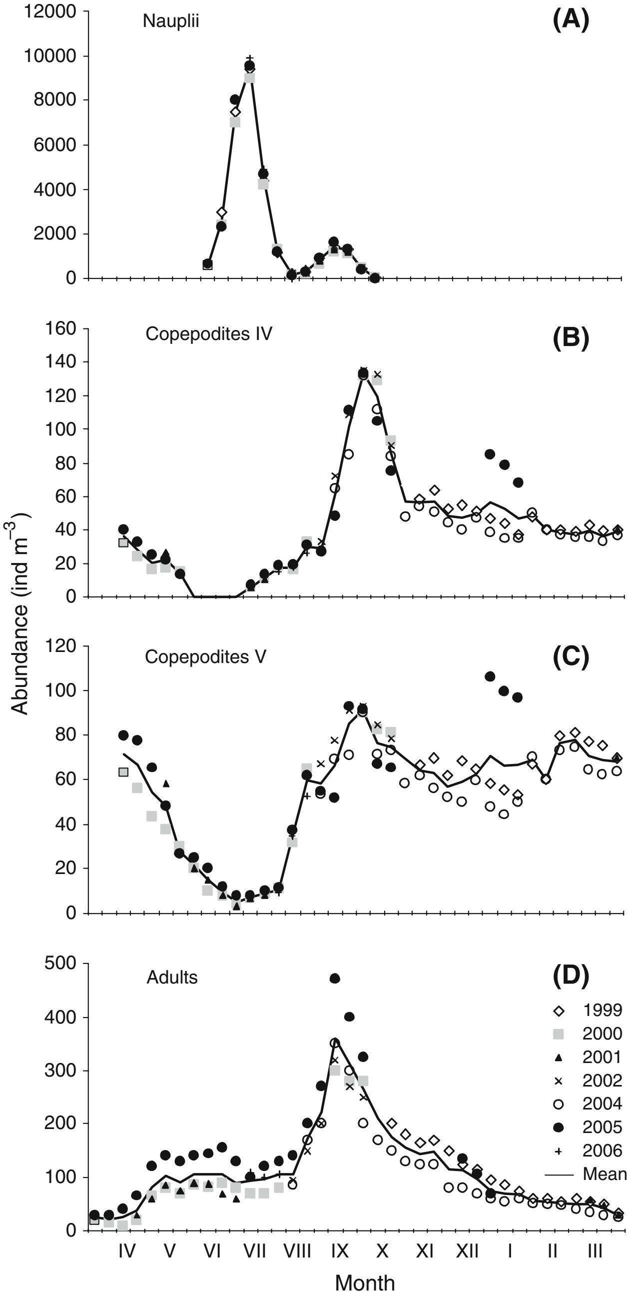

Fig. 4 Seasonal dynamics in absolute abundances of *Oithona similis* stages: **a** Nauplii abundance estimated from bottle samples. **b–d** Late copepodites and adults abundances estimated from net samples. The symbols correspond to the data points for different years. The line indicated mean value for all years studied

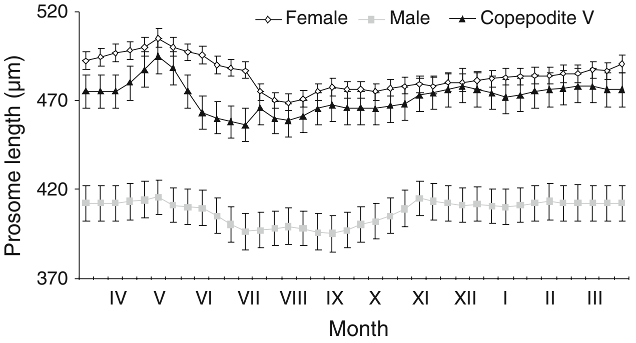

Fig. 5 Seasonal variations in mean prosome length (µm) of *Oithona similis* copepodites V, males and females

Variations in PL in *O. similis* were observed over the year. In Fig. 5, seasonal variations in body size are presented for adults and stage-CV copepodites (the only stages that were present in the whole year). The average sizes (PL) for all groups were largest in May: 505 µm in females, 415 µm in males and 493 µm in CV copepodites. Average PL of females decreased somewhat, reaching minimal values by August (469 µm) then again increased to 480 µm by December. Males were smallest in September (395 µm), their average PL increased to 415 µm by November and remained at that size during the winter period. Similar yearly patterns of PL variability were observed in CV-stage copepodites, with minimum PL observed in July (456 µm) and the second maximum in October (473 µm).

Seasonal variations of reproductive characteristics in *O. similis*

Oithona similis apparently reproduced year-round in Kola Bay, as females with egg sacs were found in all seasons (single females carrying eggs found during winter season were not included in Fig. 6). Number of females carrying egg sacs in May was 1–2% the total female number. Two peaks in the abundance of ovigerous females were found, one in the beginning of July (39%) and one in the beginning of September (28%) (Fig. 6). The average percentage of the females with egg sacs was 12 ± 2% during the reproductive period (May–November).

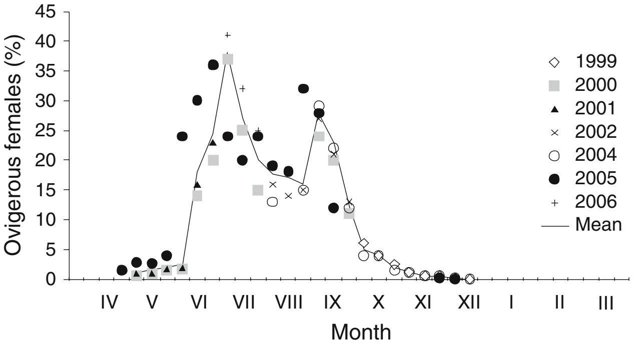

Fig. 6 Seasonal variations in relative abundance of *Oithona similis* ovigerous females. The symbols correspond to the data points for different years. The line indicated mean value for all years studied

The mean CS of *O. similis* varied from 20 to 26 eggs per female. Peaks in CS were observed in June, September and November, with the largest values found in the beginning of June (Fig. 7a). CS in the autumn generation noted in the summer period (22 ± 1) was lower, than CS in the summer generation noted in autumn (24 ± 1).

The mean egg diameter (*D*) of *O. similis* differed across seasons. Maximum egg diameter was registered in May (65–70 µm), while minimum egg sizes (51–44 µm) were noted in July–August (Fig. 7b). In late autumn and early winter, *D* varied between 48 and 52 µm. Mean egg diameter was 52 ± 2 µm over the period when female with egg sacs occurred in the plankton.

Oithona similis EPR and SEPR were lowest in May and from October to December (no more than 0.04 eggs female^{-1} day^{-1} and 0.0006 day^{-1}) (Fig. 8a, b). Maximum values reached 2.2 and 1.2 eggs female^{-1} d^{-1} (0.046 and 0.023 day^{-1}) in July (autumn generation) and in September (summer generation), respectively (Fig. 8a, b). Average EPR and SEPR were 0.6 (±0.2) eggs female^{-1} day^{-1} and 0.0011 (±0.003) day^{-1}, respectively.

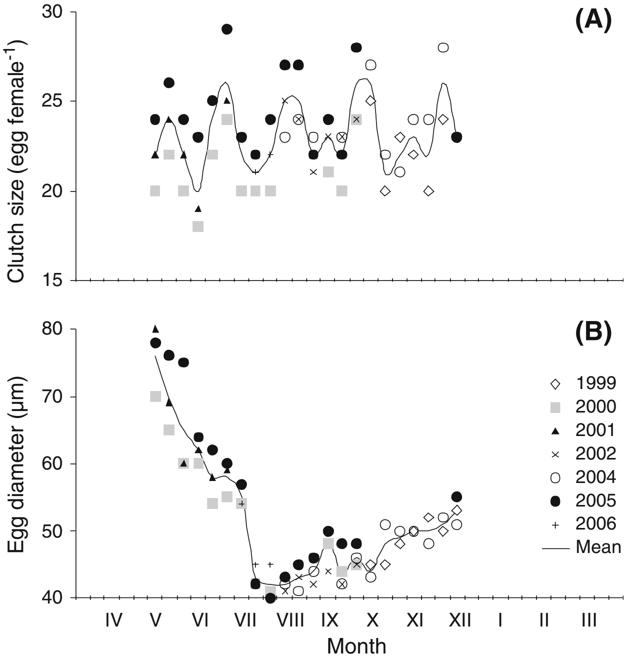

Fig. 7 Seasonal variations in mean clutch size (**a**) and mean egg diameter (**b**) in *Oithona similis*. The symbols correspond to the data points for different years. The line indicated mean value for all years studied

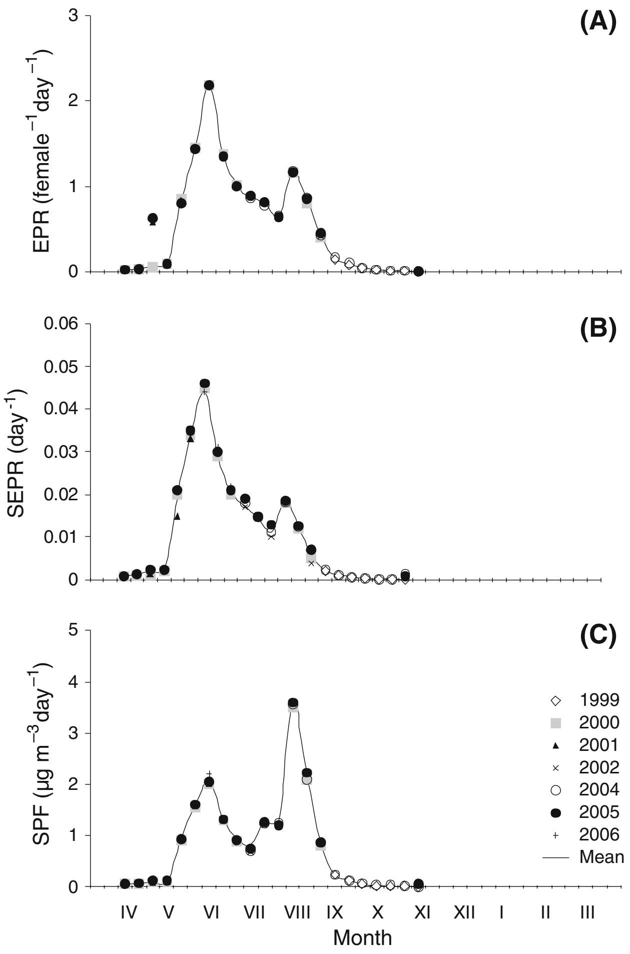

Fig. 8 Variation in the female egg production rate (**a**), specific egg production rate (**b**) and female production (**c**) in *Oithona similis*. The symbols correspond to the data points for different years. The line indicated mean value for all years studied

Secondary production of females ranged between 0.001 and 3.58 (0.8 ± 0.3) µg C m^{-3} day^{-1}. The maxima and minima were found during autumn and winter, respectively (Fig. 8c).

According to Kruskal–Wallis tests, PL, CS, *D*, EPR and SEPR significantly differed in autumn and summer generations of *O. similis* (Table 2).

Analysis of size and reproductive characteristics revealed differences in female PL, CS and *D* of both generations (Fig. 9, Table 3). These parameters were correlated with one another. In the autumn generation females, CS increased with increasing PL. The inverse relationship was found between CS and PL in summer generation females (Fig. 9, Table 3). Egg sizes were positively correlated with PL (Fig. 9, Table 3). There were negative relationships between CS and *D* in both generations (Fig. 9, Table 3).

Relationships between hydrological conditions and population parameters

According to linear regression analyses, oceanographic factors strongly influenced population characteristics of *O. similis*. The mean abundance of all stages (except copepodites CIV and CV) increased with increasing water temperature. PLs of adults and stage-CV copepodites were negatively correlated with water temperature and positively with salinity, the abundances were also negatively correlated to water salinity excepting stage CV (Table 4). In contrast, PLs of nauplii and CIV copepodites were positively scaled with temperature and negatively to salinity. The reproductive characteristics CS and *D* were only poorly related to hydrological parameters. Proportion of females with egg sacs, EPR, SEPR and SPF significantly increased with increasing water temperature and decreasing water salinity (Table 4).

Discussion

Method

Although complete and accurate sampling of cyclopoid copepods requires the use of large water bottles or nets with a mesh size <100 µm (Fransz and Gonzalez 1997), we think that our nets adequately characterized the distribution pattern of late copepodites (CIV–CV) and adults. The 168-µm net and bottles used in our study are appropriate to investigate the abundance of mesozooplankton, i.e. species having a total length of 0.5–3.0 mm (Vinogradov and Shushkina 1987). For this reason, young copepodites (CI–CIII) of *O. similis* with total length <420 µm were excluded from consideration in our studies. Moreover, in some cases coarse nets may be more suitable for *Oithona* sampling than very fines ones. For example, Hansen et al. (2004) found that a 150-µm net better retained all developmental stages of *O. similis*, except nauplii than a 50-µm net. They suggested that the smaller mesh size in conjunction with the towing speed may have created a dynamic pressure wave in front of the net opening that reduced the sampling efficiency. On the other hand, Nielsen and Andersen (2002) found that *O. similis* abundances estimated from the WP-2 net (200 µm) samples were 2.7–10.5 times lower compared with the values estimated from Niskin bottle samples. However, these authors investigate all the stages of *O. similis* while we studied the copepodites IV–VI only. In addition, the net used in our study was too coarse for us to have confidence that detached egg sacs (100–125 µm in width and 300–350 µm in length) would be sampled quantitatively and therefore there would be

Table 2 Differences in the mean prosome length, clutch size and egg diameter in the autumn and summer generations of *Oithona similis*

Parameter	Modified Levene's equal-variance test		Kruskal-Wallis test		
	Test value	*P*	df	H	*P*
PL (μm)	24.915	<0.001	1	10.561	<0.005
CS (egg female^{-1})	30.493	<0.001	1	104.438	<0.001
D (μm)	151.850	<0.001	1	57.774	<0.001
EPR (egg female^{-1} day^{-1})	134.903	<0.001	1	188.402	<0.001
SEPR (day^{-1})	118.894	<0.001	1	105.976	<0.001
SPF (μg m^{-3} day^{-1})	314.310	<0.001	1	747.510	<0.001

CS clutch size, *D* mean egg diameter, *PL* prosome length, *EPR* egg production rate (egg female^{-1} day^{-1}), *SEPR* specific egg production rate (day^{-1}), *SPF* secondary production in female (μg m^{-3} day^{-1})

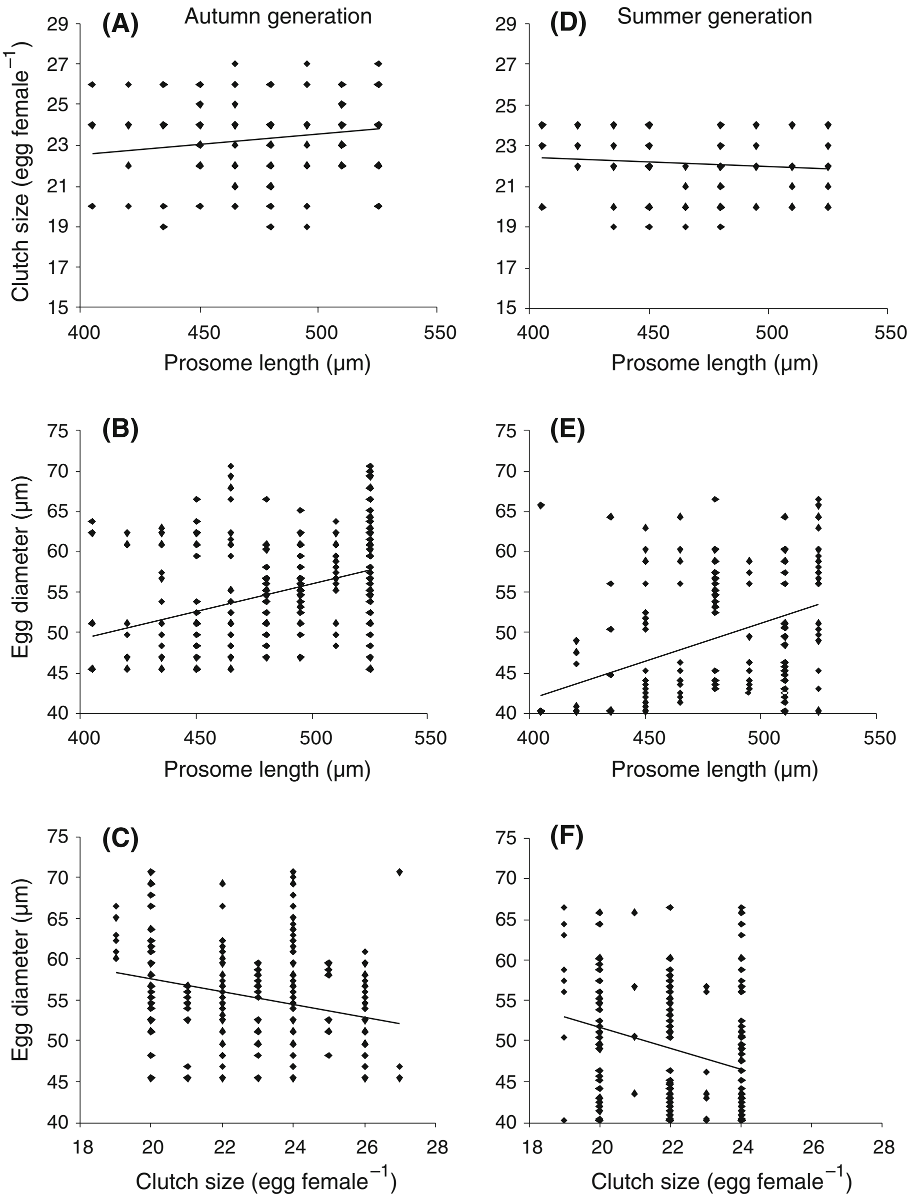

Fig. 9 Length–reproductive relationships in autumn and summer generations of *Oithona similis*. **a**, **d** Relationships between prosome length and clutch size. **b**, **e** Relationships between prosome length and mean egg diameter. **c**, **f** Relationships between clutch size and mean egg diameter. Statistical parameters are presented in Table 3

Table 3 Length–reproductive relationships in autumn and summer generations of *Oithona similis* (see Fig. 9)

Autumn generation			Summer generation		
Equation	*r*	*P*	Equation	*r*	*P*
$CS = 0.0097\ PL + 18.683$	0.141	<0.001	$CS = -\ 0.005\ PL + 24.463$	−0.118	<0.05
$D = 0.0678\ PL + 22.09$	0.354	<0.001	$D = 0.0946\ PL + 3.853$	0.455	<0.001
$D = -\ 0.7906\ CS + 73.443$	−0.283	<0.001	$D = -\ 1.2928\ CS + 77.49$	−0.263	<0.001

CS clutch size (egg female^{-1}), *D* mean egg diameter (μm), *PL* prosome length (μm), *r* correlation coefficient, *P* significance level

Table 4 Linear correlations relating physical properties to abundance, prosome length and reproductive characteristics in *Oithona similis*

Parameters	Temperature		Salinity	
	r	*P*	*r*	*P*
Abundance				
Female	0.490	<0.05	−0.310	0.058
Male	0.748	<0.001	−0.733	<0.001
Copepodite V	−0.369	0.023	0.655	<0.001
Copepodite IV	0.179	0.312	0.024	0.895
Nauplii	0.714	<0.05	−0.725	<0.05
Total/mean	0.702	<0.05	−0.676	<0.05
Prosome length				
Female	−0.409	<0.05	0.128	0.445
Male	−0.865	<0.001	0.664	<0.001
Copepodite V	−0.518	<0.001	0.432	<0.05
Copepodite IV	0.396	<0.05	−0.364	<0.05
Nauplii	0.773	<0.001	−0.806	<0.001
Total/Mean	−0.632	<0.05	−0.474	<0.05
Reproductive characteristics				
Ovigerous females (%)	0.775	<0.001	−0.652	<0.05
Clutch size	−0.048	0.831	0.091	0.686
Mean egg diameter	−0.329	0.134	−0.201	0.369
Egg production rate (egg female^{-1} day^{-1})	0.896	<0.001	−0.685	<0.05
Specific egg production rate (day^{-1}),	0.892	<0.001	−0.750	<0.05
Secondary production in female (μg m^{-3} day^{-1}).	0.690	<0.05	−0.339	0.122

Temperature and salinity are averaged parameters from 0 to 100 m layer or 0 bottom layer. *r* correlation coefficient, *P* significance level

some underestimations in the proportion of ovigerous females, EPR and SEPR. However, we suggest that such underestimations were low because we registered detached egg sacs very rarely in the net samples. Unfortunately, we sampled only the top 10-m layer of water to collect *O. similis* nauplii (although other life stages were collected over the entire water column). We cannot assume that we know the true nauplii depth distribution because the upper layer strongly differed in hydrographical characteristics from the underlying water layers. Nevertheless, we suggest that our data on *O. similis* nauplii represent the general pattern of their distribution because *O. similis* is a true epiplanktonic species preferred to inhabit in the upper water layers (e.g. Shuvalov 1980; Satapoomin et al. 2004; Madsen et al. 2008).

Dynamics of population characteristics in *O. similis*

Oithona similis is one of the most common copepods in the Barents Sea and is found in the coastal zone the whole year-round (Fomin 1991). However, prior to our study, the early life history of *O. similis* in Kola Bay has not been sufficiently investigated. A few studies of *O. similis* life history have been conducted in the Arctic region (Nielsen and Andersen 2002; Thor et al. 2005, 2008). However, only two studies have been conducted to investigate the population dynamics and annual cycle of the species in the Atlantic influenced Svalbard waters, the productive Greenland Sea region (Lischka and Hagen 2005) and in Disco Bay in western Greenland waters (Madsen et al. 2008). We found that there were two peaks of *O. similis* abundance, one in July and one in September, and that the species apparently reproduced mainly from May to November because females carrying egg sacs were largely absent at other times. Our findings are similar to the population dynamics pattern observed by Fomin (1978, 1991) in a coastal zone of the Eastern Murman (southern part of the Barents Sea). The author noted that the number of copepodites and adults was very high during all seasons (mean annual abundance 200–250 ind m^{-3}) and that *O. similis* abundance peaks were reached in June, September, November and late December (1,154, 1,604, 1,344 and 926 ind m^{-3}, respectively).

In an earlier study of the Barents Sea, juvenile stages of *O. similis* were recorded in the second half of summer and in late autumn. Females with egg sacs were found at the end of June (Fomin 1991). In Balsfjorden (northern Norway waters), *Oithona* spp. had two peaks of abundance, in the spring and in autumn, the mean annual abundance varied between 289 (in shallow waters) and 939 ind m^{-3} (in deeper waters) (Barthel 1995). Maximal biomass of *O. similis* (about of 1.4 g dry weight m^{-2}) was registered in the first half of July in the coastal waters of Balsfjorden (Pasternak et al. 2000). A similar pattern of seasonal variation of *Oithona* biomass has been recorded in Lindaspollene, western Norway (Magnesen 1989). Spring–summer and autumn maxima of abundance were connected with mass reproduction of *O. similis* (Fomin 1978; Hopkins 1981) as in our investigation. In Disco Bay, *Oithona* spp. were the most numerically abundant copepod all year round and reached their maximum abundance (~1,500 ind m^{-3}) in late August (Madsen et al. 2008).

It is worth noting that summer *O. similis* abundance apparently varies considerably among years and among coastal sites in the Barents Sea. For example, in July–August 1987, average population density of the species in Yarnyshnaya Bay, a typical fjord of the Barents Sea was only 7,150–15,440 ind m^{-2} (Timofeev 1994), considerably lower in comparison with our finding (385 ind m^{-3} or ca. 42,000 ind m^{-2}). On the other hand, our recent research has shown that in summer of 2004–2006, mean abundance of *O. similis* varied from 42,340 ind m^{-2} or 386 ind m^{-3} to 100,200 ind m^{-2} or 916 ind m^{-3} in the open waters of the southern Barents Sea (Dvoretsky 2008), exceeding the concentrations that we found in Kola Bay.

The population dynamics of females and males suggests the presence of two generations of *O. similis* during the year. One peak of adult abundance occurred in late summer and resulted from development of a new *O. similis* generation which in July was present as nauplii and in August as copepodite stages. The developmental time of the summer generation was therefore ~2 months. On the other hand, maturing of the autumn generation was not complete until late-spring or early-summer of the next year, so the life cycle of the autumn generation was ~9–10 months from the previous September maximum in nauplii numbers to the May–June increases in proportions of adult female and males in the current year. Low abundances of adults in winter plankton indicated that only a small portion of the autumn generation of copepodites were able to finish their development by November–December. Comparing our study to others suggests that *O. similis* life cycles are similar across the Polar regions. The basic differences among populations are related to spawning time and occurrence of abundance peaks, and also to generation development durations. In Kongsfjorden (north-western Svalbard waters), *O. similis* reproduced year round with two main reproductive periods in May–June and in August–September (Lischka and Hagen 2005). However, the maximum abundance was in November (>704,633 ind m^{-2}) and the minimum abundance was found in June (4,483 ind m^{-2}) in contrast to our data. We think that these differences between regions might be explained by colder temperatures in Kongsfjorden in comparison with Kola Bay. In Kola Bay, the life cycle of *O. similis* is quite similar to the White Sea where mass spawning has been found in May–June and July–August (Dvoretskii 2007). Madsen et al. (2008) also reported that all stages of *Oithona* spp. were present year round in Disco Bay and the females constituted 40% of the population in spring and summer.

The mean annual abundance in the White Sea was 2,560 ind m^{-3} (Prygunkova 1974), which greatly exceeds values registered in our study. Developmental times of the first and second generation were 2 and 9–10 month, respectively (Prygunkova 1974). Two reproduction peaks also appear to be present in western Greenland waters (in June and August–September) because of high abundance of adults in these periods (Ussing 1938). However, according to Digby (1954), only one generation was present in Greenland Sea. The author noted that only a small part of the new generations appearing in June was able to develop into adults. In shelf waters of south-western Greenland, the maximum biomass of *O. similis* (65 mg C m^{-2}) was registered in July (Pedersen et al. 2005) which is similar to our data.

In Antarctic seas, *O. similis* also formed two generations during the year (Atkinson 1998), and the same patterns have been observed in Canadian Arctic waters (Hopcroft et al. 2005) and in the northern part of the Bering Sea (Shaginyan 1982). In contrast, only one generation is most likely to occur in the Laptev Sea during all seasons (Lischka et al. 2001).

Hydrological conditions strongly influence population dynamics and generations times. Elevated temperatures can accelerate development of *O. similis* and increase the number of generations in a year, while depressed salinity reduces the species breeding potential in the White Sea

(Shuvalov 1980) and in the Barents Sea (Timofeev 1994). In the Arctic regions, ice cover is usually present during most of the year although intensive melting takes place in May–June. During similar periods of decreasing salinity in the upper water column, declining abundance has been observed in Kongsfjorden (Lischka and Hagen 2005). The authors suggested that decreasing water salinity might reduce the population density because their data showed that in the Baltic Sea, *O. similis* concentrated in the zone of the halocline with high salinity (Hansen et al. 2004). In Kola Bay, the upper water layer (0–10 m) is affected by late spring freshening (in May salinity is about 28–30 psu), but in the other seasons surface water salinity did not drop below 32 psu, and salinity in the deeper water layers varies between 32 and 34 psu during all year round (Matishov et al. 1997 and our observations) (Fig. 2). We therefore think it unlikely that salinity strongly influences the abundance of *O. similis* in Kola Bay.

According to the authors' data and past literature data (Sabatini and Kiørboe 1994; Uye and Sano 1995; Nielsen et al. 2002), water temperature has a pronounced effect on *Oithona* biology (especially, duration of reproduction, HT, EPR and SEPR). If water were warmer, then the number of generations occurring within a year increases. In the Gulf of Maine, there appeared to be at least three and possibly four broods (generations) of *O. similis* in March, May, July and September (at 6.08–9.38°C). A developmental period of 2 months during the early season and about 6 weeks in summer has been found (Fish 1936). *O. similis* reproduced continuously throughout the year with two main abundance peaks forming no more than three generations in the Loch Striven (the Clyde Sea area) (Marshall 1949). According to Kozhevnikov (1975), in the northern Japan Sea the developmental cycle of *O. similis* (from egg to egg) was about 31–37 days (at 15–17°C). In the Japan Sea, *O. similis* populations produced at least 4–5 generations during the year (at temperature range from 6 to 22°C) (Kasyan 2001). In the warm Andaman Sea (Thailand waters), *Oithona* spp. produced five generations in all seasons (at >15°C) (Satapoomin et al. 2004). Positive correlations between water temperature and abundance of *O. similis* confirm the role of this factor in the species dynamics in Kola Bay (Table 4), in the southern Barents Sea (Fomin 1991; Timofeev 1994), in the Arctic waters in the Greenland Sea (Richter 1994), in Iceland waters (Gislason and Astthorsson 2004) and near northern Svalbard (Daase and Eiane 2007).

We found that the average length of *O. similis* varied within season, and that mean body size was larger in summer than autumn; because water temperatures were lower in autumn, there was a negative correlation between PL and temperature. A similar pattern has been noted for *O. similis* in the White Sea (Shuvalov 1965), in the Clyde Sea (Marshall 1949), in the Irminger Sea (Castellani et al. 2007), in the Svalbard waters (Daase and Eiane 2007) and for *O. davisae* in the Japan Sea (Uye and Sano 1995). In addition to water temperature, food conditions are important factors determining copepod sizes (Timofeev 2000). The finding that the presence of largest *O. similis* occurs in Kola Bay during summer can be explained by longer generation time in the autumn brood (10 months). In contrast, summer generation (2 months old) had smaller PL. There is high food availability due to a phytoplankton bloom starting in late April (Matishov et al. 1997) in the Barents Sea, when development of the previous autumn's generation is finished. Significant relationship between *O. similis* abundance and chlorophyll *a* concentrations have been found in Antarctic waters (Ward and Hirst 2007) although some authors showed that protoozoplankton played a more important role in feeding of *O. similis* (Castellani et al. 2005).

Mean annual PL of *O. similis* females (484 μm) found in our study was higher than in such Arctic areas as the Greenland Sea, Gulf of Alaska and the White Sea (Shuvalov 1965; Nielsen et al. 2002) but lower than in the North Sea (Nielsen and Sabatini 1996). Shuvalov (1975) delineated two different size-morphological forms of *O. similis*. The Atlantic-White Sea group consists of the North Atlantic population with a modal female body size of about 730 μm (PL = 480–490 μm) and a White Sea population with a modal female body size 700 μm (PL of about 460–470 μm). The Arctic–Okhotsk Sea group consists of Arctic populations (the Central Arctic Basin) with a modal body size of 970 μm (PL = 520–530 μm) and an Okhotsk Sea population with a modal body size of 850 μm (PL = 510–520 μm). We think the population of *O. similis* existing in Kola Bay together with populations from the Greenland Sea, Svalbard waters and from others regions affected by warm Atlantic waters are intermediate in female PL between the small boreal form and the large Arctic form.

Variations in *O. similis* reproductive characteristics

In the present study, females with egg sacs were present year round. Similar results have been reported previously for others arctic and temperate coastal water (Kiørboe and Nielsen 1994; Madsen et al. 2008). The maximum proportion of ovigerous females was observed in July and September in Kola Bay. We think that females carrying egg sacs in June and July belonged to the autumn generation of the previous year, while egg-sac carrying females found in September are part of the summer generation of the current year. It is noteworthy that that the proportion of females carrying egg sacs in Kola Bay (0–39%) is rather low fraction compared to other studies. For example, in Yarnyshnaya Bay during the summer of

1987, more than 48% of *O. similis* females carried out egg sacs (a 168 μm net; Timofeev 1994). In the Fukuyama Harbor, more than 60% of *O. davisae* females had egg sacs in November when peak reproduction occurred (a 62-μm mesh net; Uye and Sano 1995). The maximum proportion of *O. similis* females with egg sacs reached 67% in the Southern Ocean (a 100-μm mesh net; Ward and Hirst 2007).

Relatively low rates of reproducing females in Kola Bay may be an artefact produced by losses of egg sacs due to using a coarse mesh net for the sampling. This is supported by occasional findings of females with one or even half of an egg sac. On the other hand, differences in environmental conditions (hydrology and interspecific interactions) might also be responsible for low proportions of reproducing females. This reason is complex, and includes hydrological conditions and inter–specific interactions. For example, low salinity in an estuarine zone might cause losses of egg sacs and high concentrations of specimens might reduce the proportions of ovigerous females in copepods (Timofeev 2000). Kola Bay is a strongly polluted water area, while Yarnyshnaya Bay has practically no anthropogenous influence.

According to our data and other recent investigations in the southern Barents Sea (Dvoretsky 2008), the mean CS in *O. similis* did not vary much (22–24 eggs per sacs). In the Kara Sea, the North Sea, the White Sea, the Irminger Sea and the western Bering Sea, summer CSs (22–24 egg per sacs) were comparable to the values we observed in Kola Bay (Belousova 1977; Fomin 1989; Nielsen and Sabatini 1996; Castellani et al. 2007; Dvoretskii 2007). However, CS obtained in our study was higher in comparison with CS measured during other seasons in other regions. For example, in the Irminger Sea winter CS was 18 ± 0.6 egg per sacs (Castellani et al. 2007), and in the White Sea CS was 8 eggs per sac during autumn (Shuvalov 1980). Our results suggest that CS is rather stable within the Arctic Seas and, therefore, little dependent on environmental factors. Non-significant relationships between physical variables and CS (Table 4) verify this assumption.

Mean egg diameter is an important functional parameter in marine animals. This parameter directly correlates with energy reproductive investment in the future generations (Timofeev 2000). We found that *D* was 52 ± 2 μm in Kola Bay. This value is in a good accordance with data from the southern Barents Sea (55 ± 0.2 μm, Dvoretsky 2008), the White Sea (60 ± 0.2 μm, Dvoretskii 2007), the Irminger Basin (60 ± 0.2 μm, Castellani et al. 2005) and the North Sea (57 μm, Sabatini and Kiørboe 1994). In contrast, in Arctic waters *D* was more variable and high (58–67 μm, Nielsen et al., 2002). Thus, within subarctic and temperate waters, variability of egg size is low and apparently stable. Water temperature and salinity did not influence *D* (Table 4) as was the case with CS.

The lack of effect of hydrological variables on CS and *D* is probably due to how these parameters are related with other aspects of *O. similis* biology. The duration of the lifespan determines CS and *D* in *O. similis*. For example, in the White Sea the large long-lived females of the autumn generation that spawned during May–June were characterized by lower CS and higher *D* (Shuvalov 1980), perhaps because bigger animals (longer PL) are capable of producing bigger eggs. Length-CS, length-*D* and CS-*D* relationships obtained for the different generations (Table 3, Fig. 9) provide support for similar patterns in Kola Bay. Similar data have been obtained in the southern Barents Sea and the White Sea (Timofeev 1994; Dvoretskii 2007; Dvoretsky 2008), although Castellani et al. (2007) concluded that another main factor determining the CS is the food condition and reported that the mean CS increased in periods with low temperature, but high protozooplankton concentrations. As noted above, food availability is highest in summer in Kola Bay. The females of the autumn generation that produce eggs in late June–July might take advantage of good food conditions (chlorophyll *a* varied from 0.78 to 4.07 mg m^{-3}, Fig. 3, Trofimova 2007) to gain high production rates, whereas females producing eggs in September (summer generation) might be more food limited (chlorophyll $a = 0.06–0.09$ mg m^{-3}, Fig. 3, Trofimova 2007).

We found the highest mean EPR and SEPR in July and in September during the periods of *O. similis* mass spawning. Our results are similar to those obtained by Madsen et al. (2008) who reported that SEPR were highest in July (3.5% day^{-1}) and in September (5.9% day^{-1}). In the present study, EPR and SEPR in *O. similis* were strongly scaled with temperature (Table 4). Ward and Hirst (2007) also indicated that in situ EPR (fecundity per female) was significantly and positively related to temperature in the Southern Ocean. SEPR of *O. davisae* females increased linearly with increasing temperature between November 1986 and June 1987, when temperature was less than ca. 22°C in the Japan Sea (Uye and Sano 1995).

In contrast, there were no relationships between EPR, SEPR and water temperature in the Irminger and the North Seas (Sabatini and Kiørboe 1994; Nielsen and Sabatini 1996; Castellani et al. 2005), instead fecundity in *O. similis* was correlated with food conditions and especially protozooplankton concentrations. According to Castellani et al. (2007), the water temperature effect on EPR and SEPR in *O. similis* is indirectly mediated by body size. It seems likely that a similar pattern exists in the Kola Bay because of the strong correlations observed between PL and temperature.

Thus, our study has demonstrated that over the course of a year, two generations of *O. similis* were present in Kola Bay. These broods strongly differed in mean CS, *D*, EPR and SEPR. Population dynamics of the species was characterized by the presence of two abundance peaks (in July and September) corresponding to periods of *O. similis* mass spawning. Temporal differences in reproductive characteristics and production seem to be determined by temperature, food conditions and variations in female body size.

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