Spatial variations in reproductive characteristics of the small copepod *Oithona similis* in the Barents Sea

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ABSTRACT: In the Barents Sea during late summer 2006 and 2007 we investigated spatial variations in the biomass, abundance, reproductive characteristics and production of *Oithona similis* (copepodite stages IV to V and adults), the most abundant small copepod. The species contributed 0.1 to 15.3% of the total mesozooplankton biomass. Adults were the most abundant stage in 2006 while younger copepodites prevailed in 2007. Prosome length of all stages was negatively and significantly correlated with water temperature. The mean ($\pm$SE) relative abundance of ovigerous females and mean ($\pm$SE) clutch size were 31 $\pm$ 1 and 38 $\pm$ 2%; and 22 $\pm$ 0 and 21 $\pm$ 0 eggs per sac in 2006 and 2007, respectively. Egg diameter (D) varied from 45 (in the south) to 70 µm (in the north). Egg production rates (EPR) varied from 0.2 to 1.8 eggs female^{-1} d^{-1} in both periods. Specific egg production rates (SEPR) were 0.005 to 0.029 and 0.008 to 0.04 d^{-1} in 2006 and 2007, respectively. The total secondary production of *O. similis* varied between stations and between years from 12 to 2714 µgC m^{-2} d^{-1}. Copepodites V contributed the main part of the total secondary production (47 $\pm$ 2 in 2006 and 52 $\pm$ 3% in 2007). Multiple regression analysis showed that temperature and salinity explained 50 to 92 and 63 to 93% of the total variations in the log$_{10}$-transformed D, EPR and SEPR in 2006 and 2007, respectively. Although 4 regions were separated on the basis of water temperature and salinity, 3 populations of *O. similis* were delineated by cluster analysis based on the species mean reproductive characteristics. This corresponds with our data based on the analysis of morphological parameters of *O. similis* in the Barents Sea (Dvoretsky & Dvoretsky 2009; Mar Ecol Prog Ser 385:165–178).

KEY WORDS: *Oithona similis* · Copepod · Barents Sea · Biomass · Secondary production

INTRODUCTION

The small cyclopoid copepods of the family Oithonidae are thought to be the most abundant planktonic crustaceans in the World Ocean (Paffenhöfer 1993, Gallienne & Robins 2001, Turner 2004). *Oithona* species are present in subtropical, temperate and polar waters (Shuvalov 1980, Uye & Sano 1995, 1998, Atkinson 1998, Hansen et al. 2004). These cosmopolitan species play an important role in marine ecosystems, linking the lowest trophic levels (bacterio, phyto- and microzooplankton) with higher ones including other zooplankters, ichtyoplankton and some pelagic fishes. In Arctic Seas, investigations of the biology of the copepods have focused mainly on large calanoids such as *Calanus* species and *Metridia longa* (e.g. Melle & Skjoldal 1998, Arnkvaern et

al. 2005, Orlova et al. 2005, Hirche & Kosobokova 2007). However, *O. similis* Claus, 1866 can contribute a significant proportion of the total mesozooplankton abundance, especially in cold years (Degtereva 1979). Recently, studies examining demographic characteristics of *O. similis* (biomass and reproductive characteristics) have been carried out in the Irminger Sea, North Atlantic (Castellani et al. 2005, 2007, 2008), in the Scotia Sea and waters around South Georgia in the Southern Ocean (Ward & Hirst 2007, Hirst & Ward 2008). In contrast, there is little data on the spatial biomass and reproductive variations of *O. similis* in Arctic waters. The year-round variation in abundance and stage-specific distribution of *O. similis* has been investigated in the Arctic Kongsfjorden, Svalbard (Lischka & Hagen 2005). There are a few studies where variations in reproductive char-

acteristics have been studied in Arctic and sub-Arctic waters (Nielsen & Andersen 2002, Madsen et al. 2008, Dvoretsky & Dvoretsky 2009b). However, there are no investigations of reproductive parameters in *O. similis* in the Arctic regions in a large spatial range. At the same time, the biochemistry of the species has been studied extensively in Arctic waters (Lischka & Hagen 2007, Lischka et al. 2007, Narcy at al. 2009).

The Barents Sea (see Fig. 1) is one of the most productive areas in the World Ocean (Zenkevitch 1963) and high mesozooplankton biomass is exploited by such commercial fishes as cod *Gadus morhua*, capelin *Mallotus villosus,* haddock *Melanogrammus aeglefinus* and others (Orlova et al. 2005). The Barents Sea is a relatively shallow region characterized by a wide range of environmental conditions. Four main water masses can be defined; the northern part where there is a strong influence of cold Arctic waters (ArW) typically colder than 0°C and with salinities ranging from 34.3 to 34.8 (Schauer et al. 2002), while in the southern part, warm Atlantic waters (AW) with salinities around 35.0 and temperatures of 2°C or higher prevail. Other regions are occupied by transformed Atlantic waters (TAW) that originate from interactions of Arctic water (ArW) and AW masses (Ingvaldsen et al. 2004) and local waters (LW) near the coasts. Spatial variation in salinity is caused by influxes from the Atlantic, the current regime, ice formation and melting, river run-off, and water mixing. Thus, different hydrological conditions in the Barents Sea allow us to examine how *O. similis* biomass, reproductive characteristics and production vary across temperature and salinity gradients. Such knowledge is necessary to better understand the functioning of the marine ecosystem and the role of *O. similis* in zooplankton communities. The objectives of this paper were to describe spatial variations in the main reproductive parameters, abundance and biomass in *O. similis* and to estimate the production of old copepodites and adults in the different regions of the Barents Sea.

MATERIALS AND METHODS

Sampling. Zooplankton samples were collected in the Barents Sea (Fig. 1) during cruises by the Murmansk Marine Biological Institute in August–September 2006 (15/08–01/09) and in August–September 2007 (19/08–03/09). We used a Juday plankton net (mouth diameter 0.37 m;

length 2.0 m; mesh size 168 µm). Zooplankton net tow samples were taken vertically from 100 to 0 m or near the bottom where the depth was <100 m. After completion of each haul, nets were washed and the samples fixed in buffered 4% formaldehyde-seawater solution. Water temperature and salinity were measured at each station for the whole water column using a SBE 19 plus SEACAT CTD profiler.

Processing. The hydrographic data including temperature and salinity (0 to 100 m) were used to separate the areas investigated into different regions. To achieve this we used station cluster analyses (complete linkage method) based on the Euclidean distances between the mean temperature and salinity in the 100 to 0 m layer.

In the laboratory, each sample was divided into subsamples with a splitter (from 1/2 to 1/8) depending on the zooplankton abundance. All organisms were identified to species or higher taxonomic level and counted using a MBS-10 stereomicroscope (32 to 56 magnifications). A 168 µm mesh net is too coarse to sample nauplii and young copepodites (CI to CIII) quantitatively and therefore only abundances of the older stages
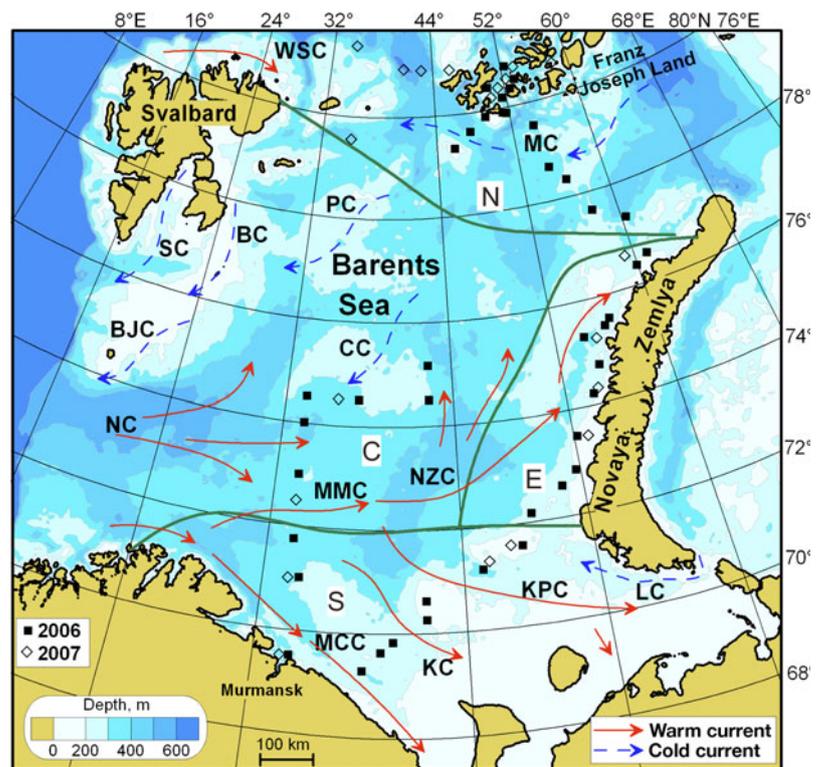

Fig. 1. Sampling stations in the Barents Sea August–September 2006 (■) and August–September 2007 (◇). Currents are MC: Makarov Current, PC: Persey Current, CC: Central Current, NZC: Novaya Zenlya Current, MMC: Murmansk Current, MCC: Murmansk Coastal Current, KC: Kanin Current, NC: Nordcape Current, KPC: Kolguyev-Pechora Current, LC: Litke Current, BJC: Bjørnøya Current, BC: Barents Current, SC: South Current, WSC: West Svalbard Current. Regions delineated by cluster analysis based on the hydrological characteristics are S: southern, C: central, E: eastern, and N: northern

(prosome length, PL > 400 µm) were considered in the present study. Biomass (*B*, mgC) of *Oithona similis* was calculated using the length–weight regression of Sabatini and Kiørboe (Sabatini & Kiørboe 1994). Biomass of the mesozooplankton was calculated using abundance data and published individual dry masses (Richter 1994), length-mass relationships (Mumm 1991) or nomograms (experimental curves of 3-D forms and shapes of aquatic animals plotted versus their wet biomasses) (Chislenko 1968). Wet or dry biomass was converted to carbon biomass applying conversion factors as follows: 1 wet wt mg = 0.064 mgC and 1 dry wt mg = 0.16 mgC (Vinogradov & Shushkina 1987). A total of 500 to 700 ind. of *O. similis* were taken from subsamples for subsequent analyses. Identification of copepodite stages and sexes of *O. similis* was performed according to Shuvalov (1980). All stages were counted and copepodites' and adults' PLs were measured.

In most cases females with intact egg sacs attached and intact detached egg sacs were present in the plankton samples. The total number of ovigerous females at each station was determined by the sum of attached and detached egg sacs divided by 2. A total of 20 to 100 females carrying egg sacs were taken from each sample. Clutch size (CS) was calculated as the sum of 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 Biman 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} d^{-1}) were determined using the egg-to-female ratio (E/F) and hatching time (HT) according to Edmondson (1971):

$$EPR = (E/F) \cdot \frac{1}{HT} \qquad (1)$$

Egg HT (d) was calculated using the equation of Nielsen et al. (2002):

$$HT = 1504.5 \cdot (T + 7.6998)^{-2.05} \qquad (2)$$

where *T* = water temperature (°C). Specific egg production of *O. similis* (SEPR d^{-1}) was estimated using the egg carbon content (conversion factor is 0.14 pg C µm^{-3}) and female carbon content based on length–weight relationship (Sabatini & Kiørboe 1994):

$$SEPR = EPR \cdot \frac{C_{egg}}{C_{fem}} \qquad (3)$$

The secondary production of females (SP$_F$, µg C m^{-2} d^{-1}) was obtained by multiplying the biomass of females (*B$_F$*) and SEPR:

$$SPF = B_F \cdot EPR_S \qquad (4)$$

The secondary production rates of *O. similis* copepodites IV to V and males (SP$_C$ and SP$_M$, µg C m^{-2} d^{-1}) were calculated as follows:

$$SP_C = B_C \cdot g_C \qquad (5)$$

$$SP_M = B_M \cdot g_M \qquad (6)$$

where *B$_C$* is biomass of the copepodites IV and V, *B$_M$* is males biomass (µgC m^{-2}), *g* is growth rate; *g$_M$* was assumed as equal to SEPR (Sabatini & Kiørboe 1994, Williams & Muxagata 2006) and *g$_C$* is the average specific growth rate over copepodite stages estimated from equations (Hirst & Bunker 2003):

$$Log_{10}(g_C) = -1.528 + (0.0333 \cdot T) - 0.163 \cdot Log_{10}W_C \qquad (7)$$

where *W$_C$* is the mean carbon weight of CIV or CV copepodites (µg ind.$^{-1}$), *T* (°C) is the average water temperature (0 to 100 m) at the station. The total secondary production (SP) of *O. similis* (copepodites IV to V and adults) was calculated as sum of SP$_F$, SP$_M$ and SP$_C$.

The differences among mean total mesozooplankton biomass and mean abundance, *B*, CS, *D*, EPR, SEPR, and SP of *Oithona similis* between 2006 and 2007 were examined using one-way ANOVA. The differences among means were tested with the non-parametric Kruskal-Wallis tests when data were non-homogeneus (Levene's test a = 0.05), even after data transformation.

Simple and multiple linear regression analyses were used to reveal relationships between the physical variables (average temperature and salinity in the upper 100 m layer or 0 to bottom layer) and the log$_{10}$(x + 1)-transformed total abundance, *B*, PL, and reproductive characteristics (the proportion of females with egg sacs, CS, *D*, EPR, SEPR, SP$_F$) of *Oithona similis*.

We used non-metric cluster analysis based on Euclidean distances (complete linkage method) between log$_{10}$-transformed reproductive parameters (egg-carrying female biomass, µgC; CS, egg female^{-1}; mean *D*, µm; EPR, eggs female^{-1} d^{-1}; SEPR, d^{-1}) to compare *Oithona similis* from different regions. The logarithmic transformation was used to stabilize the variances (Zar 1999). To compare the total mesozooplankton biomass and abundance, *B*, PL, the proportion of ovigerous females, CS, *D*, EPR, SEPR, and SP of *O. similis* among the clusters we used multiple comparison procedures (Dunn's method). Data are presented as means ± SE.

RESULTS

Environmental conditions

Salinity and temperature distributions in the surface 100 m during both years across all regions are presented in Fig. 2.

The hydrogrological conditions varied strongly across the area studied. In 2006, temperature in the
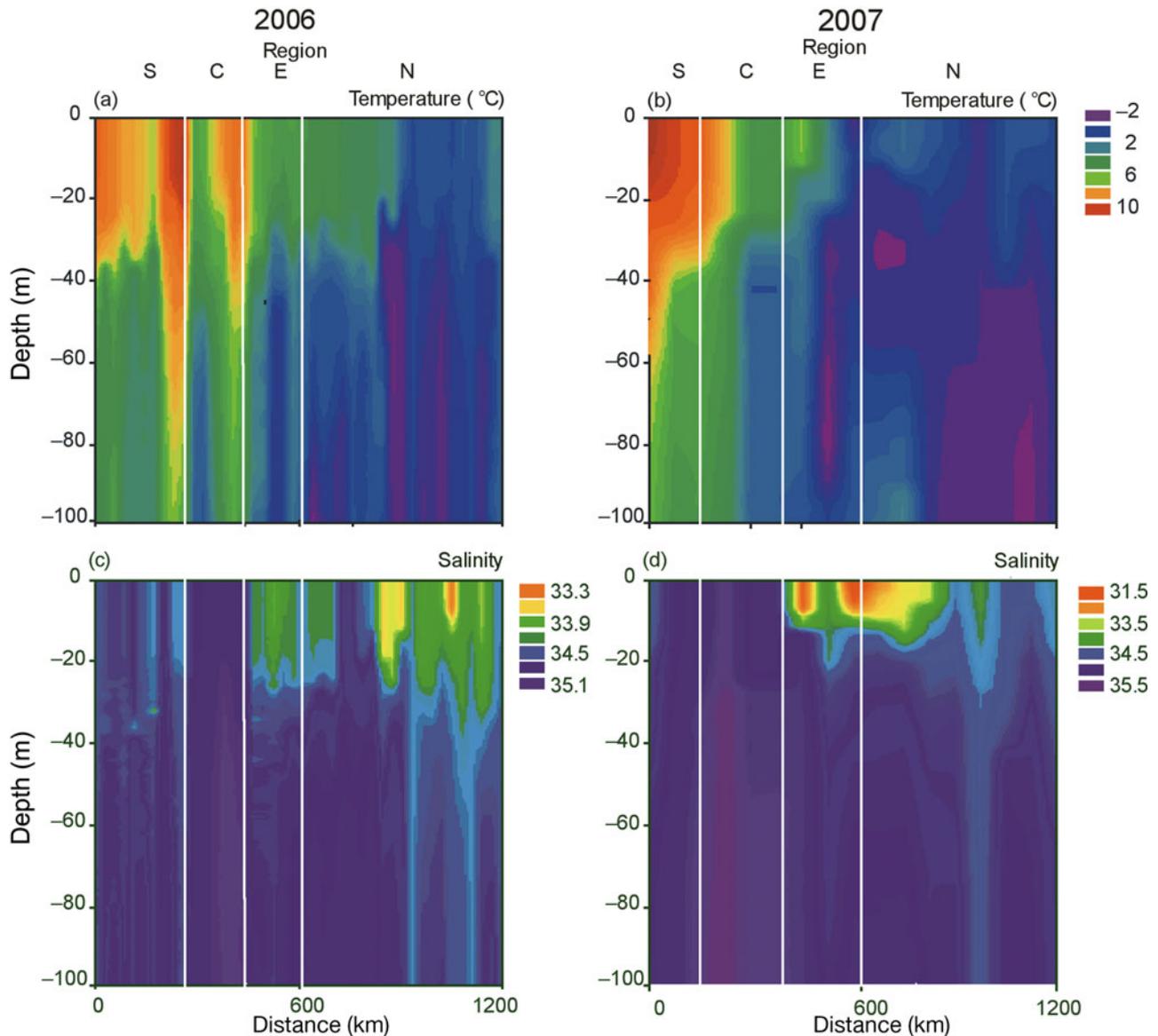
Fig. 2. Vertical profiles of (a,c) temperature and (b,d) salinity in the upper 100 m layer of the Barents Sea in August–September 2006 and August–September 2007 within regions delineated by cluster analysis based on the hydrological characteristics (see Fig. 1). Regions are S: southern, C: central, E: eastern, N: northern

region varied from –1.68 to 10.5°C, averaging 2.46 ± 0.05°C and there was a clear decreasing gradient from the south to the north. Salinity was 33.27 to 35.14 (34.60 ± 0.01). In 2007, temperature varied between –1.57 and 10.70 (average 1.67 ± 0.08°C) and salinity was 31.32 to 35.12 (34.36 ± 0.02).

Cluster analysis revealed 4 regions in the Barents Sea (see Fig. 1): (1) a southern region (S) along the mainland coast, with shallow waters (100 to 200 m) and high salinity (> 34.3) and temperature (> 6.5°C), strongly affected by warm AW; (2) a central region (C) with deep waters (200 to 300 m), high salinity (34.8 to 35.0) and intermediate surface temperature (4.3 to 7.8°C), charac-

terized by the mixing of AW and Barents Sea waters; (3) an eastern region (E) along the Novaya Zemlya archipelago coast with shallow waters (100 to 200 m), high salinity (34.2 to 34.7) and intermediate surface temperature (2.0 to 4.7°C), characterized by the mixing of transformed AW and coastal waters and (4) a northern region (N) with high salinity (33.9 to 34.7) and low temperature (–0.5 to 2°C), influenced by cold ArW. In 2006, mean temperature in the northern region was significantly higher compared with 2007 (Kruskal-Wallis test, $H = 4.21$, p < 0.05). There were no statistical differences between the periods studied in the 3 other regions (ANOVA or Kruskal-Wallis test, p > 0.40).

Oithona similis biomass, abundance and length

In 2006, the total mesozooplankton biomass varied between stations from 109 to 12180 mgC m^{-2}. Spatial variation was characterized by low mean values in the east and maxima in the north. *Oithona similis* contributed 0.1 to 9.5 % of the mesozooplankton biomass. The maximum average (4.3 ± 1.3 %) was registered in the central region while the minimum average (1.3 ± 0.4 %) was in the east (Table 1). Abundance of *O. similis* varied between 450 and 138800 ind. m^{-2}, minimum values were in the southern region and maxima were again in the north (Table 1). Adults were the most numerous stages accounting for 62 to 82 % (73 ± 5 %) of the *O. similis* population (CIV to CVI stages) (Fig. 3). The lowest relative abundance was noted in *O. similis* CIV copepodites (6 ± 2 %). Overall, females dominated over males. Mean sex ratio was 4:1, varying from 3:1 (in the south) to 5:1 (in the center).

In 2007, the total mesozooplankton ranged between 37 and 2873 mgC m^{-2}. *Oithona similis* mean biomass was 1.2 higher than in 2006. *O. similis* reached their maximum (15.3 % of the total mesozooplankton biomass) in the eastern region delineated by the cluster analysis, while the lowest value (0.1 %) was recorded in the north. *O. similis* abundance varied between stations, ranging from 810 to 112000 ind m^{-2} with the minimum number in the center and maximum in the east. Older copepodites (CIV to CV) of the species dominated among stages studied consisting of 50 to 74 % in their abundance (Fig. 3).
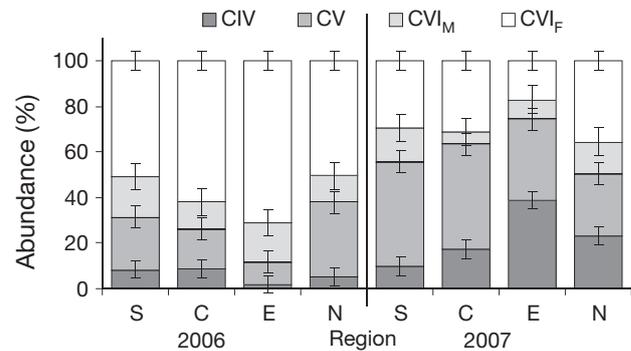

Fig. 3. *Oithona similis*. Relative mean abundance of stages (CIV and CV: copepodites IV and V, CVI$_M$: males, CVI$_F$: females) in the Barents Sea in August–September 2006 and in August–September 2007 within regions delineated by cluster analysis based on the hydrological characteristics. Regions are S: southern, C: central, E: eastern, N: northern

The proportion of females was significantly lower in 2007 compared to 2006 (ANOVA, $F = 25.53$, p < 0.001) while the relative abundances of males was similar in both periods (Kruskal-Wallis test, $H = 1.45$, p = 0.904). Sex ratio varied between regions from 2:1 (southern region) to 6:1 (central region), averaging 3:1.

In 2006, PL of all stages was overall shorter in 2006 compared with PL in 2007. Minimum and maximum mean sizes were recorded in the southern and northern regions, respectively (Table 2). In 2006 and in 2007, PL in all stages of *Oithona similis* were negatively and significantly correlated with water temperature or a combination of temperature and salinity, and positively with salinity (Table 3). There were no correlations between abundance and *B* of *O. similis* with temperature and salinity in 2007, while in 2006 they were correlated significantly with temperature and a combination of temperature and salinity (Table 3).

There were no significant differences in total mesozooplankton biomass between years, which was also true for *Oithona similis* abundance and *B* in the southern and central regions (Table 1). However, in 2006 population densities of this species were significantly lower in the eastern region and higher in the northern region (Kruskal-Wallis test, $H = 2.77$, p < 0.05). Clear inter-annual differences in PL were apparent for the copepodite stages in all regions except CIV in the central region, males in the eastern and northern zones and females in the south (Table 2).

Table 1. Mean (±SE) total mesozooplankton integrated biomass and *Oithona similis* abundance and biomass in August–September 2006 and August–September 2007 within regions delineated by cluster analysis based on the hydrological characteristics and results of ANOVA or Kruskal-Wallis tests. Regions are S: southern, C: central, E: eastern, N: northern

Region	2006	2007	ANOVA test		Kruskal-Wallis test	
			F	p	H	p
Total biomass (mgC m^{-2})						
All	1808±374	936±170	–	–	0.82	0.37
S	889±436	602±136	–	–	1.28	0.26
C	567±96	304±266	–	–	1.00	0.32
E	994±245	305±53	–	–	1.70	0.19
N	3516±841	1448±240	–	–	2.77	0.10
Oithona **biomass (mgC m^{-2})**						
All	16.2±2.4	18.4±3.8	–	–	0.18	0.67
S	6.5±2.0	28.3±10.8	–	–	2.42	0.12
C	20.1±5.0	6.6±6.1	1.97	0.21	–	–
E	9.1±2.2	28.4±10.6	7.52	<0.05	–	–
N	26.3±5.1	12.7±3.7	–	–	4.92	<0.05
Oithona **abundance (ind. m^{-2})**						
All	27171±4094	32201±6913	–	–	0.12	0.73
S	12534±3710	50305±19410	–	–	2.42	0.12
C	22800±5525	11730±10920	1.84	0.22	–	–
E	21303±6725	52625±20266	8.20	<0.05	–	–
N	42980±8547	20883±6123	–	–	4.92	<0.05

Table 2. *Oithona similis*. Mean (±SE) prosome length (µm) of adults and cope-podites IV to V within regions delineated by cluster analysis based on the hydro-logical characteristics in August–September 2006 and August–September 2007, and results of ANOVA or Kruskal-Wallis tests. Regions are S: southern, C: central, E: eastern, N: northern

Region	2006	2007	ANOVA test		Kruskal-Wallis test	
			F	p	H	p
Copepodite IV						
All	433±2	438±2	–	–	8.09	<0.05
S	426±2	428±3	5.06	<0.05	–	–
C	430±2	432±7	2.68	0.15	–	–
E	432±4	438±5	32.96	<0.001	–	–
N	439±4	443±4	22.25	<0.001	–	–
Copepodite V						
All	461±2	487±2	–	–	24.86	<0.001
S	448±1	478±3	2068.33	<0.001	–	–
C	451±3	478±7	–	–	4.10	<0.05
E	454±3	479±5	–	–	8.32	<0.05
N	479±8	495±4	35.91	<0.001	–	–
Male						
All	429±1	437±2	–	–	3.08	0.08
S	400±1	400±2	–	–	0.05	0.83
C	421±1	423±7	–	–	0.03	0.87
E	427±2	431±5	16.32	<0.05	–	–
N	453±5	457±4	5.28	<0.05	–	–
Female						
All	508±1	517±2	5.79	<0.05	–	–
S	495±4	508±3	–	–	8.00	<0.05
C	499±24	508±6	3.59	0.11	–	–
E	506±34	509±54	0.11	0.75	–	–
N	522±54	525±44	0.96	0.34	–	–

Variations in reproductive characteristics and production of *Oithona similis*

Female *Oithona similis* carrying egg sacs were present in both years. In 2006, the relative abundance of ovigerous fe-males varied between stations from a minimum of 23 (northern region) to a maximum of 41 (eastern region) averag-ing 31 ± 1%. In 2007, the proportion of reproducing females (ranging from 22 in the south to 52 in the center, mean 38 ± 2%) was significantly higher com-pared with 2006 (Kruskal-Wallis test, $H = 12.36$, $p < 0.001$) (Fig. 4a). There were no differences in relative abun-dance of ovigerous females between the 4 regions (ANOVA or Kruskal-Wallis test, $p > 0.08$) in both years. CS varied between stations from 14 to 28 and from 14 to 32 egg per sacs in 2006 and 2007, respectively. Mean CS was 22 ± 0 and 21 ± 0 egg per sacs in 2006 and 2007, re-spectively. This parameter significantly differed between years in the northern (ANOVA, $F = 6.06$, $p < 0.05$) and in the southern regions (Kruskal-Wallis test, $H = 8.02$, $p < 0.05$) (Fig. 4b). In 2006 and 2007, D varied from 45 to 70 and from 51 to 70 µm, respectively. Mean D was sig-

Table 3. Regression analysis relating the dependent $\log_{10}$-transformed population variables in *Oithona similis* (B: total biomass, N: to-tal abundance and PL_{CIV}, PL_{CV}: prosome length of copepodite IV and V; $PL_{CVI,M}$, $PL_{CVI,F}$: prosome length of male and female) to independent parameters: temperature (T, °C) and salinity (S)

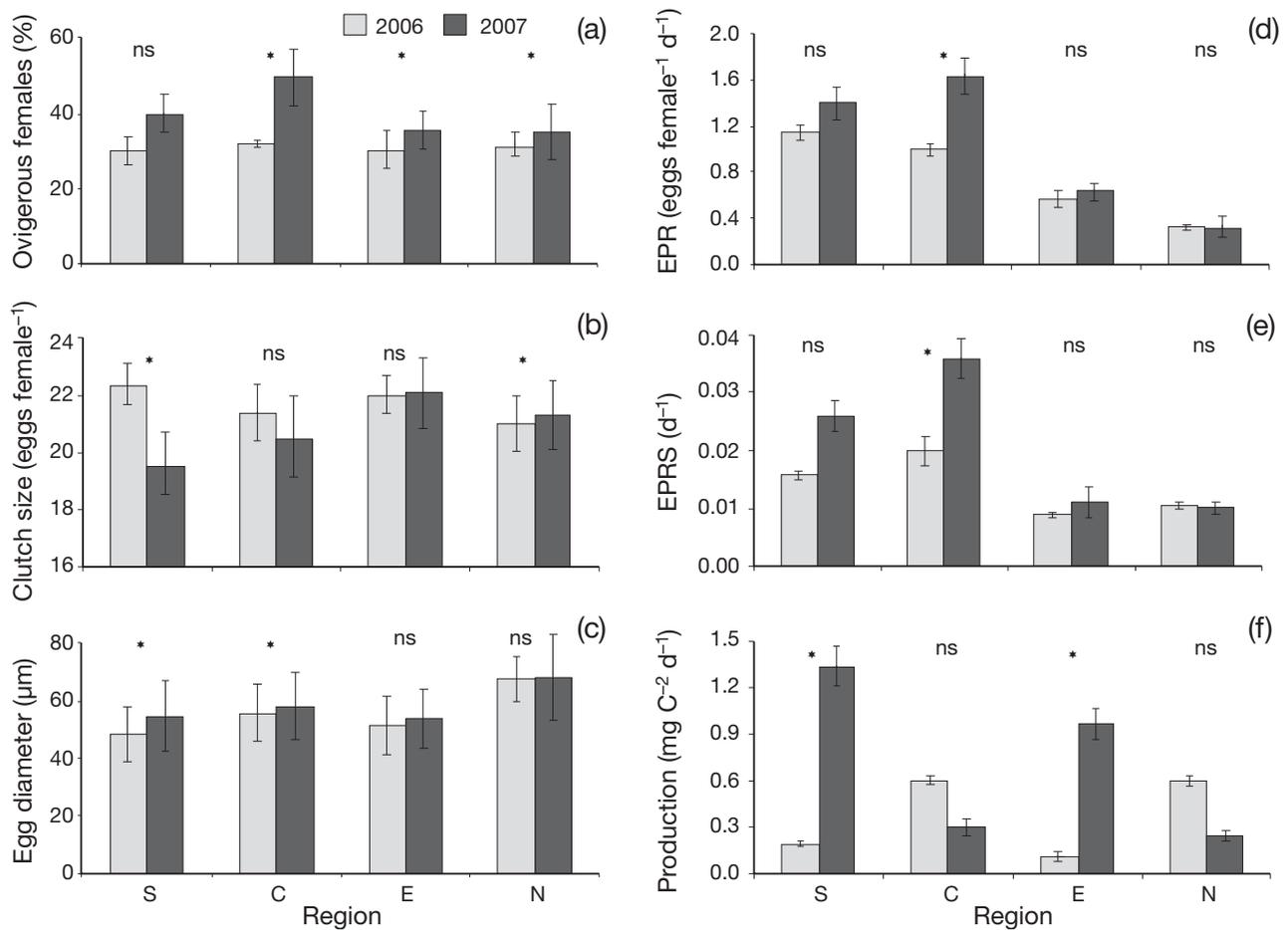| Variable (y)	$\log_{10}(y) = aT + b$				Simple linear regression $\log_{10}(y) = aS + b$				Multiple linear regression $\log_{10}(y) = aT + bS + c$				
	a	b	R^2	p	a	b	R^2	p	a	b	c	R^2	p
2006													
B	−0.0490	1.2450	0.1297	<0.05	0.0864	−1.9074	0.0037	0.702	−0.0889	0.6666	−21.5871	0.2639	<0.05
N	−0.0459	1.4333	0.1012	<0.05	0.1450	−3.7261	0.0093	0.544	−0.0896	0.7297	−23.5596	0.2441	<0.05
PL_{CIV}	−0.0016	2.6429	0.7644	<0.001	−0.0091	2.9511	0.2344	<0.05	−0.0017	0.0019	2.5769	0.7708	<0.001
PL_{CV}	−0.0036	2.6779	0.6901	<0.001	−0.0263	3.5726	0.3306	<0.001	−0.0034	−0.0042	2.8212	0.6952	<0.001
$PL_{CVI,M}$	−0.0064	2.6562	0.8017	<0.001	−0.0369	3.9041	0.2432	<0.05	−0.0069	0.0082	2.3765	0.8090	<0.001
$PL_{CVI,F}$	−0.0032	2.7185	0.7131	<0.001	−0.0168	3.2851	0.1754	<0.05	−0.0037	0.0072	2.4727	0.7326	<0.001
2007													
B	0.0055	1.0816	0.0018	0.860	0.0778	−1.5639	0.0064	0.737	−0.0042	0.1004	−2.3246	0.0069	0.943
N	0.0061	1.2866	0.0019	0.856	0.0901	−1.7760	0.0072	0.722	−0.0053	0.1188	−2.7431	0.0079	0.935
PL_{CIV}	−0.0017	2.6465	0.9050	<0.001	−0.0092	2.9575	0.4908	<0.05	−0.0016	−0.0004	2.6599	0.9054	<0.001
PL_{CV}	−0.0018	2.6931	0.4422	<0.05	−0.0124	3.1112	0.3605	<0.05	−0.0013	−0.0052	2.8690	0.4726	<0.05
$PL_{CVI,M}$	−0.0063	2.6579	0.9258	<0.001	−0.0341	3.8053	0.4815	<0.05	0.0001	−0.0063	2.6574	0.9258	<0.001
$PL_{CVI,F}$	−0.0017	2.7187	0.4422	<0.05	−0.0117	3.1127	0.3604	<0.05	−0.0049	−0.0012	2.8845	0.4725	<0.05

Fig. 4. *Oithona similis*. Mean (± SE) reproductive characteristics and production. (a) Ovigerous females, (b) clutch size, (c) egg diameter (µm), (d) egg production rate (EPR, eggs female^{-1} d^{-1}), (e) specific egg production rate (SEPR, d^{-1}) and (f) production (mgC m^{-2} d^{-1}) in different regions of Barents Sea in August–September 2006 and August–September 2007 within regions delineated by cluster analysis based on the hydrological characteristics. Regions are S: southern, C: central, E: eastern, N: northern. *p < 0.05 (ANOVA or Kruskal-Wallis), ns : non significant

nificantly larger (Kruskal-Wallis test, H = 4.76, p < 0.05) in 2007 (62 ± 2 µm) compared with 2006 (57 ± 1 µm). In both periods, there was an increase of D from the south to the north (Fig. 4c).

EPR varied from 0.2 to 1.8 eggs female^{-1} d^{-1} in both years (Fig. 4d). SEPR were 0.005 to 0.029 and 0.008 to 0.04 d^{-1} in 2006 and 2007, respectively (Fig. 4e). There were no significant differences in EPR and SEPR between years for all regions combined (ANOVA, p > 0.43). However, in 2007, EPR and SEPR in the central region were significantly higher than in 2006 (Fig. 4e,d). In 2006, the SP of adults and late copepodites in *Oithona similis* varied between stations from 12 to 2535, averaging 376 ± 76 µgC m^{-2} d^{-1}. In 2007, the range of this parameter was similar to 2006 (24 to 2714 µgC m^{-2} d^{-1}) although the mean SP was approximately 1.6 times higher (615 ± 171 µgC m^{-2} d^{-1}). However, mean rates were not statistically different from

each other except the southern and eastern zones (Fig. 4f). Copepodites CV contributed the main part of the SP (47 ± 2 in 2006 and 52 ± 3% in 2007). The relative proportion of *O. similis* female's SP was 2.4 times higher in 2007 than 2006 (37 ± 1 vs. 16 ± 2%, respectively).

Table 4 summarizes the results of regression analyses relating the dependent reproductive variables on *Oithona similis* to independent parameters (temperature and salinity). The reproductive parameters were strongly correlated with environmental variables (Table 4). Multiple regression analysis showed that temperature and salinity explained between 50 to 92 and 63 to 93% of the total variations in the log$_{10}$-transformed D, EPR and SEPR in 2006 and 2007, respectively (Table 4). The mean EPR and SEPR of the *O. similis* female population increased significantly with temperature while the mean D decreased (Table 4). In

Table 4. Regression analyses relating the dependent reproductive variables in *Oithona similis* (proportion of ovigerous females and log$_{10}$-transformed CS: clutch size, *D*: egg diameter, EPR: egg production rate, SEPR: specific egg production rate, SP: total secondary production) to independent parameters: temperature (*T*, °C) and salinity (*S*)

Variable (*y*)	Log$_{10}$(y) = *aT* + *b*				Simple linear regression Log$_{10}$(y) = *aS* + *b*				Multiple linear regression Log$_{10}$(y) = *aT* + *bS* + *c*				
	a	*b*	R^2	p	*a*	*b*	R^2	p	*a*	*b*	*c*	R^2	p
2006													
Ovigerous female	−0.0019	0.3167	0.0139	0.456	−0.0019	0.3167	0.0139	0.456	0.0105	−0.0025	−0.0435	0.0163	0.726
CS	0.0025	1.3457	0.2306	<0.05	0.0151	0.8349	0.0799	0.070	0.0025	−0.0015	1.3982	0.2311	<0.05
D	−0.0157	1.8159	0.5528	<0.001	−0.0800	4.5181	0.1319	<0.05	−0.0179	0.0367	0.5571	0.5698	<0.001
EPR	0.0304	0.1081	0.9238	<0.001	0.2002	−6.6818	0.3677	<0.001	0.0302	0.0030	0.0055	0.9239	<0.001
SEPR	0.0005	0.0036	0.4708	<0.001	0.0047	−0.1550	0.3221	<0.001	0.0004	0.0019	−0.0604	0.5023	<0.001
SP	−0.0264	2.3586	0.0197	0.375	0.3941	−11.3161	0.0403	0.202	−0.0821	0.9296	−29.4818	0.1565	<0.05
2007													
Ovigerous female	0.0073	0.3577	0.1118	0.150	0.0967	−2.9280	0.3506	<0.05	−0.0042	0.1195	−3.6953	0.3685	<0.05
CS	−0.0036	1.3519	0.2808	0.016	−0.0195	2.0085	0.1423	0.101	−0.0037	0.0006	1.3332	0.2809	0.061
D	−0.0108	1.8229	0.6107	<0.001	−0.0691	4.1557	0.4379	<0.05	−0.0088	−0.0213	2.5466	0.6307	<0.001
EPR	0.0335	0.1280	0.8955	<0.001	0.2205	−7.3191	0.6861	<0.001	0.0257	0.0809	−2.6156	0.9397	<0.001
SEPR	0.0010	0.0043	0.6417	<0.001	0.0068	−0.2245	0.5709	<0.001	0.0006	0.0033	−0.1083	0.7076	<0.001
SP	0.0405	2.3661	0.0631	0.285	0.2841	−7.2369	0.0550	0.320	0.0276	0.1345	−2.1966	0.0690	0.545

2006, there was no significant correlation between the proportions of ovigerous females and hydrological factors (Table 4). In 2007, this parameter was positively scaled with salinity and a combination of temperature and salinity (Table 4). In 2006, total production was positively correlated with a combination of temperature and salinity (Table 4). In 2007, there was no significant relationship between this parameter and hydrological variables (Table 4).

Analysis of relationships between B_F and their main reproductive characteristics showed that these parameters were correlated with one another except B_F and CS (Fig. 5a,d). In both years, *D* increased with increasing B_F (Fig. 5b,e). The inverse relationship was found between *D* and CS (Fig. 5c,f).

Three clusters were delineated by cluster analysis based on the mean reproductive characteristics of *Oithona similis* in 2006 and in 2007 (Fig. 6). These clusters corresponded with the regions identified on the basis of hydrological conditions. Cluster 1 included stations located to the southern and central regions. Cluster 2 consisted of stations located mainly in the eastern zone although in 2006 3 stations from central region were also included in this cluster, and in 2007 1 station from the southern zone was included. Cluster 3 consisted of stations situated in the northern region. Cluster 1 which included *O. similis* individuals from the southern and central regions corresponded with AW and TAW. Cluster 2 was composed by the eastern population connected with LW and TAW. The northern cluster was composed of stations located in ArW zone.

Significant differences in the total mesozooplankton *B*, PL of CIV to CVI stages and reproductive characteristics (CS, *D*, EPR and SEPR) were revealed in 2006 and in 2007 (Table 5). Multiple pair-wise comparisons of male body sizes and EPR in each cluster showed differences in all cases in 2006. In 2006, there were no differences between clusters in the proportion of ovigerous females. In 2007, similar results were obtained for *Oithona similis* abundance, *B* and secondary production. In most cases, the parameters analyzed were similar in Clusters 1 and 2 (Table 5).

DISCUSSION

The present study was the first attempt to investigate the spatial variations of *Oithona similis* reproductive characteristics in AW over a large scale; although Nielsen et al. (2002) reported variations in *O. similis* female PL, *D* and EPR in some arctic regions. As the Barents Sea is characterized by a wide range of hydrographic conditions, it provides an opportunity to delineate different populations of the species based on analysis of *O. similis* reproductive parameters. Thus, we revealed correlations between the abundance and *B* of *O. similis* and their reproductive variables with water temperature and salinity.
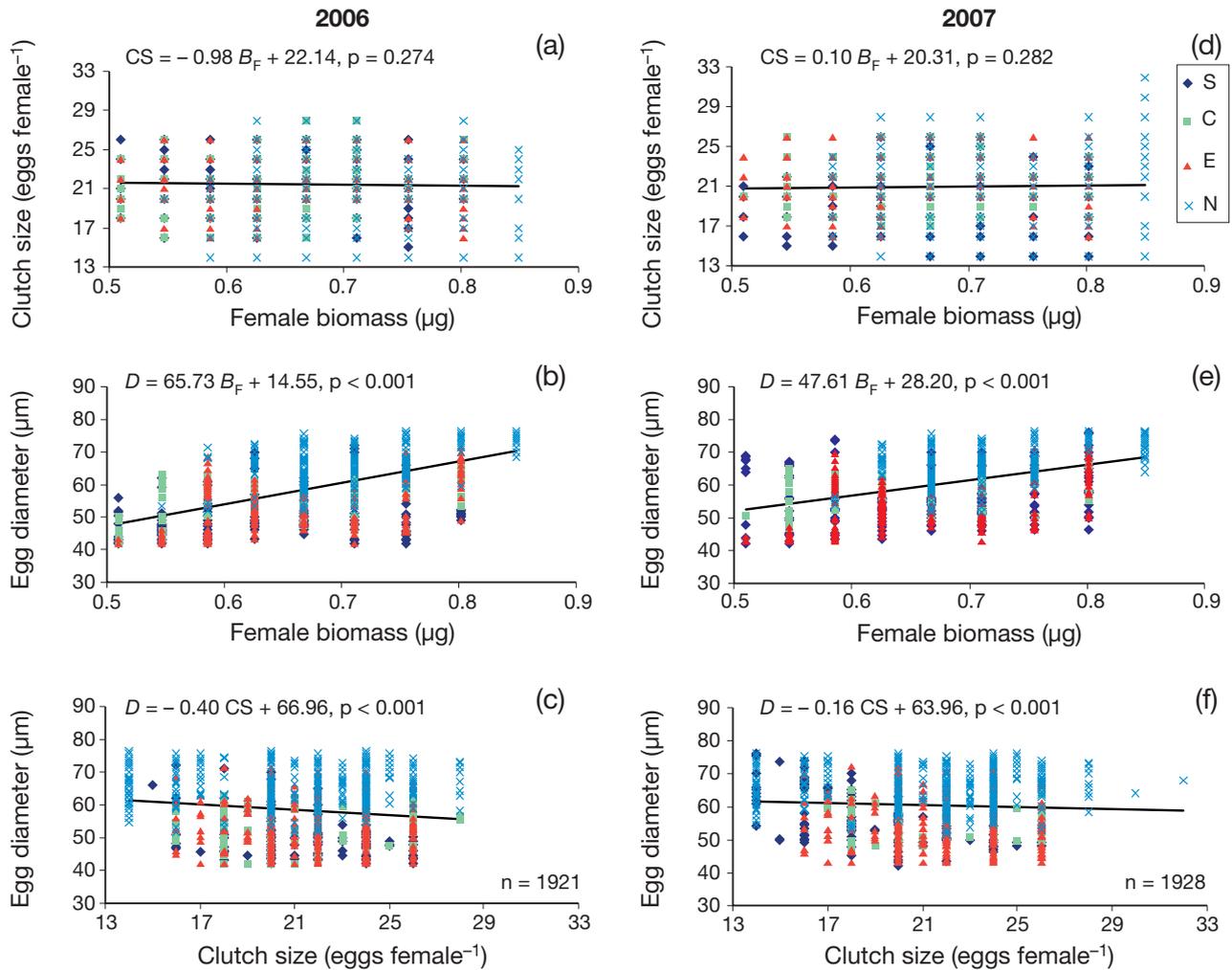
Fig. 5. *Oithona similis*. Relationships between female biomass (B_F, μg), clutch size (CS, eggs female^{-1}) and mean egg diameter (D, μm) of *O. similis* in the Barents Sea in August–September 2006 and August–September 2007 within regions delineated by cluster analysis based on the hydrological characteristics. Regions are S: southern, C: central, E: eastern, N: northern

Environmental factors, biomass and prosome length of *Oithona similis*

A strong influx of warm Atlantic water into the Barents Sea during the last few decades has been well documented (Schauer et al. 2002, Boitsov 2006). Subsequently, water temperature in the periods examined in the present study was higher in comparison with earlier multi-annual values (Matishov et al. 2004). Thus, 2006 and 2007 may be considered as 'warm' years. Such periods are characterized by an increase in total mesozooplankton biomass (Timofeev 2000, Orlova et al. 2005). We also found high total mesozooplankton biomass which exceeded multi-annual summer values by 2 to 3 times (Degtereva 1979, Timofeev 2000, Dalpadado et al. 2003). The higher biomass in 2006 was coincident with a higher mean temperature in 2006 compared to 2007.

In the present study, *Oithona similis* copepodite IV to V and adults provided up to 9–15% of the total mesozooplankton biomass in August–September 2006 and August 2007–September 2007. This can be considered as a relatively large contribution in comparison with other Arctic regions. For example, in the Laptev Sea *O. similis* accounted for 2.2 to 4.4% of the total mesozooplankton biomass during late summer (Kosobokova et al. 1998, Lischka et al. 2001). In Canadian Basin waters, the species averaged 1.6% (Hopcroft et al. 2005). In August 2003, *O. similis* maximal biomass (0.6 g dry wt m^{-2}, 4.3%) was in the northern part of the Fram Strait region (Blachowiak-Samolyk et al. 2007). In the Barents Sea, *Calanus finmarchicus* typically predominates in terms of total zooplankton biomass (Timofeev 2000). However, *O. similis* was the most abundant species in cold years due to deceleration of *C. finmarchicus* development (Degtereva 1979). Mean val-
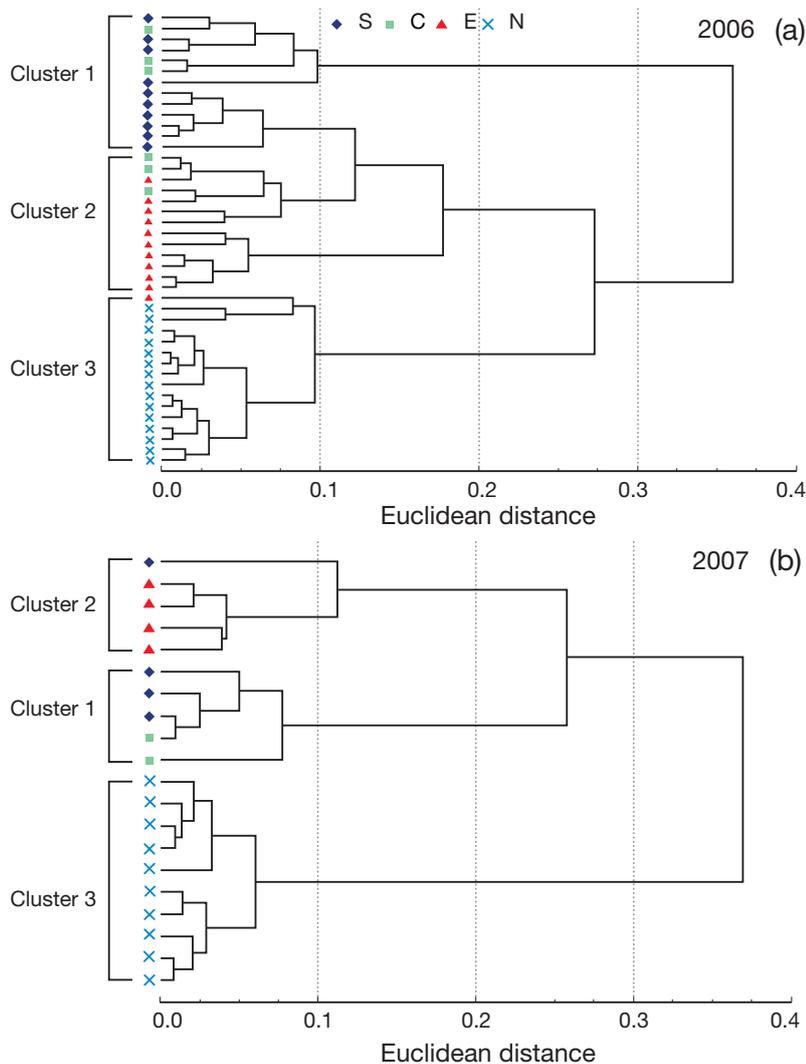
Fig. 6. *Oithona similis*. Dendrograms indicating the result of cluster analysis based on the log$_{10}$-transformed mean reproductive characteristics of *O. similis* (egg-carrying female biomass, µg; clutch size, egg female^{-1}; mean egg diameter, µm; egg production rate, eggs female^{-1} d^{-1}; specific egg production rate, d^{-1}) in the Barents Sea in August–September 2006 and in August–September 2007 within regions delineated with cluster analysis. Regions are S: southern, C: central, E: eastern, N: northern. Symbols show stations located in different parts of the Barents Sea and delineated by cluster analysis based on the hydrological characteristics

agata 2006) and *Oithona* spp. in the Irminger Sea (Castellani et al. 2007). In the latter case, temperature was reported to be more strongly correlated than food resources with biomass.

We found that the average length of *Oithona similis* was larger in the northern regions (Table 2) and that PL was negatively scaled with water temperature (Table 3). An increase in body size with latitude and decreasing temperature has been noted for many marine crustaceans including copepods (Clarke 1983, Timofeev 2000). The mean PL of *O. similis* females found in the present study was higher than in the Greenland Sea, Gulf of Alaska (Nielsen et al. 2002), and the White Sea (Shuvalov 1965, Dvoretskii 2007), but lower than in the North Sea (Nielsen & Sabatini 1996) and comparable with values noted for the Irminger Sea (Castellani et al. 2007). According to Shuvalov (1975), populations of *O. similis* may be classified into different groups (based on female PL), with females from the northern Barents Sea being referred to the Arctic-Okhotsk Sea group and individuals from the southern zones being similar to the Atlantic-White Sea group. Castellani et al. (2007) has also recorded the presence of large and intermediate sized females in the Irminger Sea area. They suggested that the larger copepods might have originated from colder water masses of Arctic origin.

Potential factors responsible for PL in copepods are hydrological conditions and food concentrations (Deevey 1960, Hirst & Bunker 2003). Because *Oithona similis* is omnivorous (Atkinson 1996), phytoplankton biomass seems likely to have a weak affect on PL. Unfortunately, we have no data regarding the distribution of microzooplankton in the Barents Sea although we assume that microplankton concentration may affect PL as this has been found to be the case in the Irminger Sea (Castellani et al. 2007, 2008).

Reproductive characteristics of *Oithona similis*

In the present study, females with egg sacs occurred everywhere reflecting an intensive spawning of *Oithona similis* in the Barents Sea at the end of the

ues of *O. similis* biomass were, however, lower compared with temperate seas; due to only including copepodites IV to VI of *O. similis*. In this respect, the Barents Sea may be regarded as intermediate between temperate and true Arctic regions. Such a result is not unexpected as the Barents Sea is influenced by both cold and warm AW. Spatial trends in *O. similis* biomass were associated strongly with water temperature (Table 3). Similar patterns have been observed for *O. similis* in the southern and eastern Barents Sea (Dvoretsky 2008, Dvoretsky & Dvoretsky 2009a), *O. davisae* in Fukuyama Harbor (the Inland Sea of Japan) (Uye & Sano 1998), *O. nana* in Southampton Water (Williams & Mux-

Table 5. Mean total mesozooplankton biomass and abundance, biomass, prosome lengths (µm), proportion of ovigerous females (%), clutch size (CS, eggs female^{-1}), egg diameter (D, µm), egg production rate (EPR, eggs female^{-1} d^{-1}), specific egg production rate (SEPR, d^{-1}), and total secondary production of copepodites IV to V and adults (SP, mgC m^{-2} d^{-1}) of *Oithona similis* and results of comparisons of these parameters in the Barents Sea in August–September 2006 and August–September 2007 among clusters (Kruskal–Wallis test) delineated by cluster analysis based on the reproductive characteristics of *Oithona similis* (see Fig. 6). Pairs of clusters where the differences were not significant (multiple comparison procedures, Dunn's method, p > 0.05) are presented, CL: cluster

Parameter	CL1	CL2	CL3	H	p	Pairs of Clusters where the differences were not significant (p > 0.05)
2006						
Total biomass (mgC m^{-2})	798	861	3399	17.40	<0.001	CL1–CL2
Oithona biomass (mgC m^{-2})	12	9	25	9.85	<0.05	CL1–CL2
Oithona abundance (ind. m^{-2})	22026	15438	40884	8.48	<0.05	CL1–CL2, CL1–CL3
PL$_{CIV}$ (µm)	427	432	439	33.88	<0.001	CL1–CL2
PL$_{CV}$ (µm)	449	454	478	33.72	<0.001	CL1–CL2
PL$_{CVI,M}$ (µm)	405	426	452	33.58	<0.001	–
PL$_{CVI,F}$ (µm)	496	503	523	31.43	<0.001	CL1–CL2
Ovigerous females (%)	31	31	31	0.72	0.70	All
CS (eggs female^{-1})	22	22	21	14.55	<0.001	CL1–CL2
D (µm)	50	52	67	28.99	<0.001	CL1–CL2
EPR (eggs female^{-1} d^{-1})	1.17	0.63	0.33	35.38	<0.001	–
SEPR (d^{-1})	0.02	0.01	0.01	14.86	<0.001	CL2–CL3
SP (mgC m^{-2} d^{-1})	383	132	569	7.43	<0.05	CL1–CL2, CL1–CL3
2007						
Total biomass (mgC m^{-2})	421	426	1448	9.62	<0.05	CL1–CL2
Oithona biomass (mgC m^{-2})	15	33	13	4.57	0.10	All
Oithona abundance (ind. m^{-2})	27236	59800	20884	4.96	0.08	All
PL$_{CIV}$ (µm)	430	435	443	15.00	<0.001	CL1–CL2
PL$_{CV}$ (µm)	478	479	495	13.19	<0.001	CL1–CL2
PL$_{CVI,M}$ (µm)	410	424	457	14.95	<0.001	CL1–CL2
PL$_{CVI,F}$ (µm)	508	509	525	13.19	<0.001	CL1–CL2
Ovigerous females (%)	47	33	35	10.35	<0.05	CL2–CL3
CS (eggs female^{-1})	20	22	21	7.86	<0.05	CL1–CL3, CL2–CL3
D (µm)	57	53	68	15.55	<0.001	CL1–CL2
EPR (eggs female^{-1} d^{-1})	1.56	0.73	0.31	16.07	<0.001	CL1–CL2, CL2–CL3
SEPR (d^{-1})	0.03	0.01	0.01	12.39	<0.05	CL1–CL2, CL2–CL3
SP (mgC m^{-2} d^{-1})	639	1321	250	4.28	0.12	All

summer. However, the mean proportions of ovigerous females were lower compared to other studies in the Barents Sea and other regions. This may be due to the coarse net we used. The maximum proportion of *O. similis* females with egg sacs previously reported was 67% in the Southern Ocean (using a 100 µm mesh size net; Ward & Hirst, 2007). This parameter varied from 10 to 100, averaging 54.5 ± 3.2% in the Irminger Sea during summer (using a 95 µm mesh size net; Castellani et al. 2007). On the other hand, our values are comparable with those reported for *O. davisae* (using a 62 µm mesh size net; 30 to 35%, August–September 1987) in the Inland Sea of Japan (Uye & Sano 1995).

There were large variations in CS, we also found that the mean CS in *Oithona similis* differed significantly between years (21 and 22 eggs per sac in 2006 and 2007 respectively). These CS were similar with the summer values recorded in other Arctic and temperate regions including the southern Barents Sea, the White Sea,

the Kara Sea, the Clyde Sea, the North Sea and the Irminger Sea (Marshall 1949, Fomin 1989, Nielsen & Sabatini 1996, Castellani et al. 2007, Dvoretskii 2007, Dvoretsky 2008, Dvoretsky & Dvoretsky 2009b). The results of the regression analyses showed that in 2006 temperature and salinity were correlated with CS whereas in 2007 there was no significant correlation (Table 4). Thus, we can assume that CS is rather stable within the Arctic Seas and, therefore, weakly determined by environmental factors or by female biomass. This assumption is supported by the fact that we found no significant correlation between female biomass of *O. similis* and CS in the Barents Sea (Fig. 5a,d). A similar pattern has been found for the euphausiid *Thysanoessa raschii* in the Barents Sea (Timofeev & Sklyar 2001).

The present investigation showed that *D* decreased from higher to lower latitudes with increasing water temperature. *D* was also positively correlated to salinity (Table 4). This is not surprising, as this phenomenon

has been previously described for many marine crustaceans (Lonsdale & Levinton 1985, Clarke 1987, Lardies & Castilla 2001). Egg size is an important parameter determining amounts of energy given to egg and reproductive investment in future generations (Timofeev 2000). We found that D in the southern, central and eastern zones of this study were similar to data from the White Sea (60 ± 0.2 µm, Dvoretskii 2007), the Irminger Basin (60 ± 8 µm, Castellani et al. 2005), the North Sea (57 µm, Sabatini & Kiørboe 1994) and Kola Bay (52 ± 2 µm, Dvoretsky & Dvoretsky 2009b). At the same time, the values recorded in the northern region of the Barents Sea were comparable with D registered in the Greenland Sea, Smith Sound waters and Gulf of Alaska (58 to 67 µm, Nielsen et al. 2002). In the present study D was scaled with female biomass and CS. An increase of D with female biomass is an expected result due to the fact that large individuals can invest more resources in egg production (Sabatini & Kiørboe 1994). By contrast, D of *Oithona similis* decreased as CS increased (Fig. 5c,f). The same patterns have been previously noted for other marine crustaceans (Wägele 1987, Gorny et al. 1992, Lardies & Castilla 2001). Thus, our data suggest that reproductive characteristics were affected by hydrological conditions and by the size of the female. Another important factor that may have determined female biomass, D and CS is food conditions. Castellani et al. (2007) reported that mean CS increased during periods of low temperature but high protozooplankton concentrations. In the Barents Sea in 2006, we found the largest females and the largest D in the northern region (Table 2, Fig. 4c) although maximum phytoplankton concentrations were recorded in the eastern region in August 2006 (Druzhkova 2008).

We found the highest mean EPR and SEPR in the southern and central regions. Being strongly and positively scaled with temperature and salinity, these parameters decreased towards the north (Fig. 4d,e), (Table 4). Ward & Hirst (2007) also reported that *in situ* EPR significantly and positively related to temperature in the Southern Ocean. A similar pattern has also been recorded in temperate waters; SEPR of *Oithona davisae* females increased linearly with increasing temperature between November 1986 and June 1987 (Uye & Sano, 1995). In contrast, there have been no relationships found between EPR, SEPR and water temperature in the Irminger and the North Seas (Sabatini & Kiørboe 1994, Nielsen & Sabatini 1996, Castellani et al. 2005) but fecundity in *O. similis* was found to be 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 Barents Sea (see Table 3 & 4). Our findings that in Kola Bay

(southern Barents), EPR and SEPR of *O. similis* significantly increased with increasing water temperature and decreasing water salinity support this suggestion (Dvoretsky & Dvoretsky 2009b).

According to our data the depth integrated SP of *Oithona similis* copepodites IV to V and adults averaged 376 to 615 µgC m^{-2} d^{-1}. There are no previous estimations of this species productivity in the Barents Sea and adjacent waters but these summer values were lower in comparison with temperate regions. This was probably due to the use of coarse nets (mesh size 168 µm) to collect *O. similis.* Nielsen & Sabatini (1996), using a submersible pump equipped with 30 µm mesh size net, found that *Oithona* spp. integrated production accounted for 5 to 12 mgC m^{-2} d^{-1}. *Oithona* spp. production (P) estimated from 63 µm mesh size net sampler probes has been found to vary between 13.1 and 153.6 µgC m^{-3} d^{-1} in 0 to 120 m layer during summer in the Irminger Sea area (Castellani et al. 2007). In the Inland Sea of Japan in July–August, *O. davisae* production rate was 2 to 10.9 mgC m^{-3} d^{-1} in 0 to 8 m layer (62 µm mesh size net; Uye & Sano 1998). The production of adults and late-stage copepodites in *O. nana* estimated from the samples collected by plankton nets of 120 µm mesh size (50 m^3 sampled volume) in Southampton Water reached a maximum in July–August (1.5 to 3.0 mgC m^{-3} day^{-1}) (Williams & Muxagata 2006). We suggest that food conditions had a greater effect in determining production than hydrological conditions as we found no significant correlations between total production and water temperature and salinity (Table 4).

Based on our analysis of the reproductive characteristics of *Oithona similis*, we delineated 3 clusters (Fig. 6). These clusters also differed in the total mesozooplankton biomass and PL of *O. similis* (Table 5). Thus, these groups may correspond with different populations of *O. similis*. It is worth noting that there were no significant differences between Cluster 1 and Cluster 2 in some cases (Table 5). This means that these clusters are similar in many resects and, therefore, populations of *O. similis* from the southern, central and eastern regions delineated by this hydrological cluster analysis are also similar. However, the northern population of *O. similis* (Cluster 3, Fig. 6) differed from the other 2 populations. Mesozooplankton distribution in Arctic region is associated with distribution of water masses (e.g. Daase & Eiane 2007). The northern Barents Sea is strongly affected by cold AW and populations of zooplankters in northern parts differ from populations in other parts of the sea. Our finding of 3 populations of *O. similis* is supported by our data concerning morphological parameters of *O. similis* in the Barents Sea (see Dvoretsky & Dvoretsky 2009c). We can, therefore, assume that 3 populations delineated

by 'morphological' and 'reproductive' cluster analyses differ in their environmental response to spatial variation in hydrological factors.

We have demonstrated that the late summer reproductive characteristics, production and biomass of *Oithona similis* varies significantly within the Barents Sea in relation to water masses. *O. similis* made up a relatively high portion (up to 15.3%) of the total mesozooplankton biomass. Hydrological conditions affected the distribution of the species. Another factor responsible for variability in productivity of *O. similis* was presumably food resources.

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