Regional and temporal variation of *Oithona* spp. biomass, stage structure and productivity in the Irminger Sea, North Atlantic

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Running head: Regional variation of *Oithona* spp. biomass and production

Abstract

Oithona spp. standing stock and production is considered relatively stable in space and time as a result of continuous breeding, low metabolism, reduced predation mortality and the ability of these small cyclopoids to exploit microbial food webs more efficiently than larger copepods. However, through a review of the published literature we show that *Oithona* spp. biomass can vary widely both over the year and with latitude. Thus, the present study set out to investigate the basin scale variability in biomass, stage structure and reproduction of *Oithona* spp. in relation to changes in hydrographic, physico-chemical and biological parameters encountered during three cruises conducted between April and November 2002 in the Irminger Sea, North Atlantic. Here we found that *Oithona* spp. biomass varied significantly with temperature and with dinoflagellates biomass concentration. On the other hand, *O. similis* egg production rates (EPR) increased with both ciliates and dinoflagellates concentrations, rather than with temperature. The inverse relationship we found between *Oithona* spp. naupliar recruitment with *Calanus* spp. and fish larvae abundance suggests that predation pressure may contribute to control the spatial variation in the stage structure and biomass of *Oithona* spp. and that the nauplii of this genus may serve as a food source for other planktonic organisms prior to the spring phytoplankton bloom.

Introduction

The biomass and production of *Oithona* spp. is considered relatively more stable in space and time than that of larger calanoid copepods (Paffenhöfer, 1993; Nielsen and Sabatini, 1996; Pagès *et al*., 1996). Such stability has been mainly attributed to continuous and steady reproduction rates (Nielsen and Sabatini, 1996), low mortality rates (Hirst and Kiørboe, 2002; Eiane and Ohman, 2004), low metabolic rates (Castellani *et al*., 2005a) and the ability of these small cyclopoids to exploit microbial food webs more efficiently than calanoid copepods (Nielsen and Sabatini, 1996). Published data, however, shows that the biomass of cyclopoids can be characterised by large seasonal and spatial fluctuations (Uye and Sano, 1998; Hansen *et al*., 2004). Such contrasting observations raise questions about the factors determining the spatio-temporal variation of *Oithona* spp. biomass and production.

Changes in population abundance depend on the balance between birth rate, mortality rates and the degree of geographical isolation (Townsend *et al*., 2004). Body size, food availability and temperature are all factors which have shown to be important determinants of egg production and growth rates in calanoids (White and Roman, 1992; Castellani and Altunbaş, 2006) but the effect of these variables on the fecundity of cyclopoid copepods is less clear due to paucity of data (Bunker and Hirst, 2004). The year round presence of *Oithona* spp. (Nielsen and Sabatini, 1996; Uye and Sano, 1998; Hansen *et al*., 2004) makes this genus also a potential food source for fish larvae (Kane, 1984), large calanoid copepods (Metz and Schnack-Schiel, 1995) and other planktonic organisms (Hopkins and Torres, 1989). Although, *Oithona* spp. has been reported to have relatively low predation mortality rates (Eiane and Ohman, 2004), field observations (Ussing, 1938) and modeling studies (Carlotti and Slagstad, 1997) have suggested that predation could control the population dynamics of this genus. In addition, spatial changes in copepod abundance and productivity can also arise as a result of frontal systems (Nishikawa *et al*., 1995), advection (Basedow *et al*., 2004) and sampling water masses of different origin (Beaugrand *et al*., 2002).

Investigations on the biology of *Oithona* spp. in the North Atlantic has been temporally and spatially limited (Bainbridge and Corlett, 1968; Gislason, 2003) and determination of changes in the life stages composition and biomass of this genus has been restricted to the use of large ($\geq$ 200 μm) mesh size nets (Gislason, 2003). Thus, the present paper investigates the basin scale variation in population structure, biomass and production of *Oithona* spp. at coastal and oceanic stations in the Irminger Sea. In particular we asked the following questions: How variable is *Oithona* spp. stage composition, biomass and production spatially and seasonally? What are the factors which may determine such variation? Could

Oithona spp. represent a food source for other planktonic organisms prior to the phytoplankton bloom?

Method

Physical and chemical characterization of the study area

The study was carried out during a series of cruises in the Irminger Sea in spring (18th April – 27th May, D262), summer (25th July – 28th August, D264) and winter (6th November – 18th December, D267) 2002 on RRS Discovery (Fig. 1). At each station, temperature, salinity and fluorescence were recorded with a Sea-Bird conductivity-temperature-depth (CTD) and a fluorometer (Wetlabs 117) instrument package mounted on a 24-position (General Oceanics Model SBE 32) rosette equipped with 10 liter Teflon coated Niskin bottles. The continuous CTD data were calibrated by water collected in discrete Niskin bottle samples on the rosette. Samples for inorganic nutrient analyses were drawn directly from Niskin bottles into polystyrene coulter counter vials and stored at 4 °C until analysis, which commenced within 12 h of sampling.

Nitrate and silicate concentrations were determined using a Skalar Sanplus autoanalyser following the methods outlined in Sanders and Jickells (Sanders and Jickells, 2000). Overall, the precision of the data from individual cruises are estimated to be better than ± 0.18 μmol L^{-1} for nitrate and ± 0.15 μmol L^{-1} for silicate (1% of top standard for nitrate, and 0.5% for silicate).

Microplankton composition and chlorophyll-a concentration

Samples of 100 mL for microplankton identification were immediately fixed with Lugol's iodine at a final concentration of 2% (Nielsen and Kiørboe, 1994). Half of the bottle volume was settled (Utermöhl, 1958) and counted with an inverted microscope (Båmstedt *et al*., 2002). Microplankton was sized and counted using a Nikon inverted microscope and taxa identified according to Lessard and Swift (Lessard and Swift, 1986) and Burkill *et al*., (Burkill *et al.*, 1993). Cell volume was converted to carbon according to Strathmann (Strathmann, 1967) for phytoplankton and using a factor of 0.19 pg C μm^{-3} for ciliates (Putt and Stoecker, 1989). Chlorophyll-a (Chl) concentration, microplankton biomass and community structure were determined from samples collected with CTD bottles at different depths (5, 10, 20, 70, 100 and 150 m). Chl concentration was measured fluorometrically with a Turner Design fluorometer (TD700) by filtering between 100 mL and 1L aliquots onto GF/F filters that were extracted for 24 hours in the dark in 90 % acetone.

Copepod biomass and stage composition

Copepod biomass was determined at the stations shown in Fig. 1. The number of stations sampled, however, varied between cruises and therefore, a total of 39, 29 and 7 stations were sampled during spring, summer and winter respectively (Fig. 1). At each station the zooplankton was sampled using a 63 μm bongo net fitted with a back-stop flowmeter (General Oceanics) vertically towed from 120 m depth. The samples were immediately concentrated by sieving through an appropriate filter and fixed in 4% buffered formaldehyde. *Oithona spp.* was enumerated at all stations with a dissecting microscope according to Omori and Ikeda (Omori and Ikeda, 1984). About 50 nauplii (NI-NVI) and 50 copepodites (CI-CVI) were sized and staged, for each sample, according to Gibbons and Ogilvie (Gibbons and Ogilvie, 1933) using a Nikon inverted microscope. A detailed analysis of the spatial distribution of the *Oithona spp.* stages could be carried out only in spring. Although, sizing of the *Oithona spp.* specimens was carried out also for the summer and winter samples, an in depth analysis of the stages could not be undertaken for these two cruises due to lack of time. *Oithona spp.* abundance was converted to biomass by means of the length-weight regression of Sabatini and Kiørboe (Sabatini and Kiørboe, 1994). The nauplii were not speciated and, therefore, the abundance and biomass of the two *Oithona* species found in the study area, *O. similis* and *O. spinirostris*, were considered together as *Oithona* spp.

We also used the plankton data collected during the D262 cruise in spring, by the Marine Productivity "broad scale survey" project (courtesy of S. Hays and M. Heath, Fisheries Research Services, UK) with the ARIES system (Dunn *et al*., 1993) and the OCEAN sampler (Sameoto *et al.,* 2000) at the same stations sampled by the present study. Both samplers were designed to collect a sequential set of discrete plankton net samples delineated by sub-sea pressure intervals during the descent and ascent-legs of an oblique towed deployment. The ARIES used a 200 μm mesh size filtering net and stored a sequence of samples at intervals corresponding to 50 m or 75 m between the sea surface and a maximum of 3000 m depth (i.e. a maximum total of 60 samples per station). The OCEAN sampler was equipped with 7 nets of 95 μm mesh size that were opened and closed in sequence on the ascent-leg of each tow from 400 m to the surface, according to a pressure schedule corresponding to 100 m depth intervals between 400 m and 100 m, and 25 m intervals between 100 m and the surface. Both plankton samplers were fitted with calibrated flow meters, and the volumes filtered per net sample was on the order of 10–15 m^3 for ARIES and 1–2 m^3 for OCEAN sampler.

The ARIES data were used to investigate predation pressure on *Oithona* spp. studying the relationship between an index of naupliar recruitment for *Oithona* spp. (i.e. the nauplii to egg abundance ratio, N/E thereafter) versus the abundance of large (> 200 μm) planktonic organisms, found in the catch, known to be either omnivores or carnivores (Ruppert and Barnes, 1994). Thus, according to this definition the following planktonic organisms were identified, from the ARIES catch, as potential predators on *Oithona* spp.: the stages CI-CV copepodites and CVI females of *Calanus hyperboreus*, *Calanus finmarchicus*, and *Calanus glacialis*, the adult stages of *Pareuchaeta* spp., the adult stages of *Meganyctiphanes norvegica*, the adult stages of the euphausid species *Thysanoessa longicaudata*, *T. inermis*, *T. rascii* and *Euphausia krohnii*, total Chaetognatha, *Sagitta maxima*, *Euchronia hamata*, total jellyfish, *Pleurobrachia* spp., *Beroe* spp. and fish larvae. The OCEAN sampler data were used to investigate the vertical distribution of the nauplii and copepodites of *Oithona* spp.

Eggs per sac, egg production rate, specific egg production rate, the proportion of reproducing females and secondary production

O. similis eggs per sac (ES), egg production rate (EPR), weight-specific egg production rate (SEPR) and relative abundance of reproducing females (RAF) in the population were determined at all the stations sampled (Fig. 1). The eggs sacs of *O. similis* were identified according to Eaton (Eaton, 1971) and from direct observation of the egg sacs produced by the females of this genus during preliminary experiments made in the present study. At each station thirty egg sacs were dissected and the eggs sized and counted using an inverted microscope. Total egg concentration was calculated using both the egg sacs found attached and detached from the female body. Egg carbon content was estimated from egg volume assuming a conversion factor of 0.14 pg C μm^{-3} (Kiørboe *et al.,* 1985). The prosome length of 30 females was also measured in the same way as for the eggs and the length converted to carbon (Sabatini and Kiørboe, 1994). At each station, the EPR (eggs $female^{-1}$ d^{-1}) of the population of *O. similis* were calculated using the egg to female ratio (E/F) estimated from the preserved 63 μm net samples and the egg hatching rate (HR, % d^{-1}) using depth integrated *in situ* temperature (T, ˚C) from the linear equation reported by Nielsen *et al.,* (Nielsen *et al.,* 2002):

$$HR = 4.217 + 1.754\ T \qquad \text{Eq. 1}$$

The EPR of *O. similis* were, therefore, calculated as:

$$EPR = (E/F)*(HR/100) \qquad \text{Eq. 2}$$

O. similis SEPR (d^{-1}) was then calculated multiplying EPR by the ratio of the eggs (Egg C) and the female (Female C) carbon content:

$$SEPR = (EPR)*(Egg\ C/Female\ C) \qquad \text{Eq. 3}$$

Oithona spp. production was then estimated from depth integrated biomass of all the stages and with juvenile specific growth rates equal to SEPR (Berggreen *et al.,* 1988). The proportion of reproducing females (RAF) in each sample was calculated from the ratio of the total number of females and pair of egg sacs, assuming that a female produces two egg sacs and that the egg sacs stay attached to the female body until the eggs hatch.

Results

Hydrography

The study area is situated within the North Atlantic subpolar gyre and it extends from the south-western part of the Iceland shelf (IS) and the Reykjanes Ridge (RR) to the shelf of Greenland (Fig. 1A). The surface circulation in the Irminger Sea, illustrated in Fig. 1A, is based on analyses by Pollard *et al*., (Pollard *et al*., 2004 and references therein). Oceanographically the Irminger Sea is a diverse region with influences from the subtropical thermocline via the North Atlantic Current (NAC) and from the Arctic via the dense northern overflow. It is dominated by the Irminger Current (IC), a branch of the NAC which enters the Irminger Sea from the south and moves north and west into the Greenland shelf. Most of the IC turns southwards as part of the complex East Greenland Current (EGC) which carries water of Arctic origins along the edge of the Greenland shelf (Fig. 1A).

The results of the physical oceanographic analyses on the three research cruises have already been dealt with in detail in Holliday *et al*., (Holliday *et al*., 2006). In their study, Holliday *et al*., (Holliday *et al*. 2006) have identified six zones in the Irminger Sea on the basis of their salinity, temperature, nutrients and chlorophyll-a (Chl) concentration (Table I). These zones correspond to hydrographic features including major currents [i.e. the IC further subdivided into the Southern Irminger Current (SIC) and the North Irminger Current (NIC), the EGC further subdivided into the East Greenland Current-Polar origin (EGC-P) and the East Greenland Current-Atlantic origin (EGC-A)] and regions of slow circulation [i.e. Central

209 Irminger Sea (CIS) and the Reykjanes Ridge (RR)]. The presence of these zones, in the study
210 area, gave rise to four main marked fronts (Fig1B-D and Holliday *et al.,* 2006): the Polar
211 Front located between the EGC-P and the EGC-A, a front present between the EGC-A and the
212 CIS, one between the CIS and the IC (i.e. NIC and SIC) at about 34° W and another one
213 present between the IC and the RR zones at about 30° W.
214
215 **Physico-chemical characteristics and microplankton biomass composition**
216 The study area was characterized by a gradient in both temperature and salinity
217 summarised in Table I, in relation to the cruises and the zones described by Holliday *et al*.,
218 (Holliday *et al*., 2006). On the Greenland shelf, temperature ranged from 3 °C to 5.9 °C in the
219 EGC-P and from 6.1 °C to 8.9 °C in the EGC-A between spring and summer respectively. In
220 the center of the Irminger Sea (CIS, NIC and SIC) and on the IS values ranged from 6.5 °C to
221 10.6 °C whereas on the RR zone, temperature reached values between 7.7 °C and 11 °C
222 between spring and summer respectively. Salinity followed a similar trend with a minimum of
223 33.95 in the EGC-P and a maximum of 35.18 in the RR in summer. Nutrients were plentiful
224 in spring and winter with concentrations up to 14 μmol L^{-1} for NO_3 and 9 μmol L^{-1} for SiO_3
225 and became depleted only by summer (Table I). In spring Chl concentration was lowest in the
226 CIS (0.5 mg Chl m^{-3}) whereas its concentration increased to 0.8 mg Chl m^{-3} in the frontal zone
227 between the CIS and the NIC/SIC. High Chl up to 1.7 mg Chl m^{-3} was also measured at the
228 frontal areas separating the CIS and the RR. In summer Chl concentration varied from a
229 maximum of 1.3 mg Chl m^{-3} in the EGC-A to a minimum of 0.8 mg Chl m^{-3} in the RR. In
230 winter Chl concentrations were quite low ranging from 0.1 to 0.3 mg Chl m^{-3}.
231 Spatial and temporal changes in microplankton biomass and species composition
232 during the present study have already been presented elsewhere (Irigoien *et al.,* 2003,
233 Castellani *et al.,* 2005b). In spring the Greenland shelf (EGC-P) was characterized by the
234 early development of a mixed flagellate-diatom bloom (*Phaeocystis* sp. > 80 % of the
235 biomass). Such bloom resulted from the strong water column stratification due to the density
236 gradient induced by fresh, ice melt water within the EGC-P zone (Waniek *et al.*, 2005). At
237 this time the rest of the study area was also dominated by flagellates although here
238 concentrations ranging from 5 mg C m^{-3} to 17.7 mg C m^{-3} were much lower than on the
239 Greenland shelf. The stations located on the frontal area between the CIS and the NIC/SIC
240 were characterized by a relatively high biomass of ciliates between 7 mg C m^{-3} and 44 mg C
241 m^{-3} (Fig. 2). Microplankton biomass as high as 65 mg C m^{-3} was also measured at the fronts
242 separating the CIS and the RR, although here the community was more diverse and comprised

mainly diatoms (*Chaetoceros pelagicus*), dinoflagellates (*Dinophysis acuminata*, *Gyrodinium britannicum*) and ciliates (*Strombidium* spp.). In summer total microplankton biomass on the on the Greenland shelf was lower than in spring mainly due to a decrease in the concentration of *Phaeocystis* sp. At this time, however, total microplankton biomass in the NIC, SIC and CIS was higher than in spring due to an increase of diatoms and dinoflagellates concentration (Fig. 2). On the other hand, ciliates biomass in summer was comparable to that measured in spring at most stations with the exception of the Greenland shelf (EGC-P) and the NIC where concentrations where higher in summer.

In winter, the sampling of the mesozooplankton could not be carried out within the EGC-P, EGC-A, and SIC zones due to bad weather conditions. At this time, total microplankton biomass ranging from 3.3 mg C m^{-3} to 8 mg C m^{-3} was much lower than concentrations measured during the previous two cruises (Fig. 2). Flagellates biomass averaging 2.20 mg C m^{-3} dominated the microplankton, followed by dinoflagellates biomass averaging 1.6 mg C m^{-3} and by ciliates biomass averaging 1.4 mg C m^{-3}, whereas the mean biomass of diatoms had dropped considerably (0.19 mg C m^{-3}) compared to spring and summer.

Oithona spp. biomass and stage composition

Oithona similis and *Oithona spinirostris* were the only *Oithona* species found in the study area. Although *O. similis* was always more numerous than *O. spinirostris*, the relative proportion of these two species varied. The contribution of *O. spinirostris* to the total *Oithona* spp. was higher in spring on the IS and the RR where it represented 15 - 20 % of the total copepodite abundance compared to 3 - 10 % on the Greenland shelf and at the off-shore stations. On the other hand, in summer and winter *O. spinirostris* represented only 2 - 5 % irrespective of location.

Fig. 3 summarises the variation of *Oithona* spp. biomass measured during each cruise within the different zones of the Irminger Sea. Throughout the study, the lowest *Oithona* spp. biomass was consistently observed at the shallowest stations located in the inner part of the Greenland shelf (0.08 - 0.7 mg C m^{-3}) within the EGC-P (Fig. 1B and Fig. 3). In spring the highest *Oithona* spp. biomass of about 1 mg C m^{-3} was measured on the RR whereas in summer a maximum of 2 mg C m^{-3} was recorded on the IS (Fig. 3A-B). Overall, the *Oithona* spp. mean biomass (± SE) in spring (0.24 ± 0.027 mg C m^{-3}) was similar to that measured in winter (0.19 ± 0.022 mg C m^{-3}) but significantly lower (ANOVA, $F_{[2,66]} = 45.53$, $p < 0.0001$) than in summer (1.14 ± 0.13 mg C m^{-3}).

Overall, the proportion of *Oithona spp.* nauplii and copepodites was significantly higher than that of the adult females which consistently accounted for between 3 % to 4 % of the total *Oithona* spp. stages abundance throughout the cruises (Fig. 3 and Table II). On the other hand, the relative proportion of adult males and females varied widely both spatially and seasonally. Females were always more numerous than males resulting, on average, in a 1:3 sex ratio.

The proportion of nauplii and copepodites also differed between zones and cruises; in winter and spring the abundance of the nauplii was higher than that of the copepodites, whereas naupliar biomass was comparable or lower. In summer, on the other hand, copepodites became the most important component of the *Oithona* spp. population both in terms of abundance and biomass (Fig. 3B and Table II).

During spring the relative biomass of nauplii in the population was lowest in the inner part of both the EGC-P and IS shelves whereas it increased progressively offshore towards the deeper stations within the CIS, NIC and SIC zones. As a result, in spring, the relative proportion of nauplii in the population of *Oithona* spp. was positively significantly correlated with depth ($df = 35$, $r = 0.56$, $p < 0.0001$) and salinity ($df = 36$, $r = 0.44$, $p = 0.006$) but not with temperature or with microplankton biomass. In summer, the highest relative biomass of nauplii in the *Oithona* spp. population was measured off the Greenland shelf (EGC-A and CIS) whereas the lowest was recorded on the EGC-P and it was inversely correlated with temperature ($df = 28$, $r = - 0.61$, $p < 0.0001$).

The relative distribution of life stages of *Oithona* spp. within each zone during spring is shown in Fig.4. The lowest proportion of the early naupliar stages, NI and NII, was recorded within the EGC-P (14 %) and IS (12 %) whereas higher values were measured within the NIC (19 %), EGC-A (21 %), CIS (33 %) and RR (52 %) zones (Fig. 4A). The proportion of adult stages (CVI), on the other hand, decreased from the EGC-P to the RR (Fig. 4B). The distribution of the NIII-NVI naupliar stages and of the CI-CV copepodites was more variable and did not seem to follow any clear pattern (Fig. 4B).

The ratio between nauplii and total egg concentration (N/E), used here as an index for naupliar survival, suggests that in spring the lowest naupliar recruitment occurred on the EGC-P and IS whereas in summer it was lowest within the NIC, CIS and RR (Fig. 5). Among the planktonic organisms, collected with ARIES by the “broad scale survey”, *Calanus* spp. CV and CVI females ($df = 17$, $r = - 0.73$, $p < 0.001$) and fish larvae ($df = 9$, $r = - 0.73$, $p = 0.017$) were significantly negatively correlated with the *Oithona* spp. N/E during spring. On

the other hand, no significant correlation was found between the N/E and the concentration of potential predators in summer.

Seasonal and spatial trends in *Oithona* spp. stages length

The variation in the size of the stages for the different cruises is summarized in Table III and for different zones in spring in Table IV. The length of the all the stages was overall longer in spring and winter compared to summer (Table III). Spatially, the size of the NI-NIII stages measured in spring was largest in the CIS and smallest in the remaining zones resembling the pattern described for the N/E ratio. Although, the variation in length of the older nauplii (NIV-NVI) and copepodites (CI-CV) was higher, on average, the longest copepods within each stage were found in the EGC, RR and IS (Table IV). The largest females of *O. similis* were commonly found on the EGC-P, IS and RR, whereas the smallest were associated with the CIS, NIC and SIC (Fig. 6). Although, female body weight was overall inversely related to temperature ($df = 53$, $r = -0.66$, $p < 0.001$, Fig. 6), during spring, the females sampled on the IS and RR were larger than those sampled in zones characterized by similar temperatures (Fig. 6).

Seasonal and spatial trends in eggs per sac, egg production rate, specific egg production rate and the proportion of reproducing females

Fig. 7 summarises the variation in eggs per sac (ES), egg production rate (EPR), weight-specific egg production rate (SEPR) and the relative abundance of reproducing females (RAF) in the population within different zones and times of the year. Overall, ES varied from a minimum of 5 eggs sac^{-1} to a maximum of 20 eggs sac^{-1}. Mean (± SE) ES was significantly higher (ANOVA, $F_{[2,69]} = 13.6$, $p < 0.0001$) in spring (12 ± 0.31 eggs sac^{-1}, n = 38) compared to summer (10 ± 0.33 eggs sac^{-1}, n = 29) and winter (9 ± 0.30 eggs sac^{-1}, n = 7) EPR varied from a minimum of < 1 egg $female^{-1}$ d^{-1} to a maximum of 6 eggs $female^{-1}$ d^{-1}. Again, mean (± SE) EPR was significantly higher (ANOVA, $F_{[2,66]} = 1.29$, $p = 0.283$) in spring (2.18 ± 0.19 eggs $female^{-1}$ d^{-1}, n = 36) than in summer (1.9 ± 0.12 eggs $female^{-1}$ d^{-1}, n = 29) and winter (1.63 ± 0.06 eggs $female^{-1}$ d^{-1}, n = 7). *O. similis* SEPR varied from 0.017 d^{-1} to 0.13 d^{-1}. Although, SEPR was on average higher in summer (0.059 ± 0.004 d^{-1}, n = 36) than in spring (0.056 ± 0.004 d^{-1}, n = 29) and winter (0.047 ± 0.002 d^{-1}, n = 7) mean rates were not statistically different from each other (ANOVA, $F_{[2,66]} = 0.89$ $p = 0.416$). The RAF values measured at each station varied from 10 % to 100 per cent. Mean (± SE) RAF did not show

any significant temporal variations (ANOVA, $F_{[2,69]} = 0.11$ $p = 0.893$) with mean values of 55.3 ± 3.7 %, 54.5 ± 3.2 % and 51.32 ± 2.3 % in spring, summer and winter respectively.

In spring the highest ES, EPR and SEPR were measured on the RR, IS and NIC whereas the highest RAF was recorded on the EGC-P and the RR (Fig. 7). In summer, on the other hand, the highest ES, EPR, SEPR and RAF were all measured within the EGC-P, EGC-A, NIC and SIC zones (Fig. 7). In winter ES, EPR, SEPR and RAF were only measured within the NIC, SIC, CIS and IS and their respective mean values were similar (Fig. 7).

O. similis biomass, eggs per sac, egg production rate, specific egg production rate and the proportion of reproducing females vs field parameters

The relationship found between *Oithona* spp. biomass and *O. similis* ES, EPR and SEPR with body size and different environmental variables is shown in Table V. Stepwise multiple regression analysis indicated that temperature and ln dinoflagellates explained 40 % of the total variation in the ln biomass of *Oithona* spp. (Table V).

The mean ES and EPR of the *O. similis* female population increased significantly with body weight (Fig. 8). However, Fig. 9 shows that if only the egg sacs found attached to individual copepods are considered, the number of eggs per sac decreases for all the females that were heavier than ca. 0.75 μg C (or longer than ca. 539 μm). Such decrease in ES seemed to be associated chiefly with the females sampled within the shallowest stations on the EGC and IS in spring but not with similarly sized females sampled in summer at the EGC stations at comparable *in situ* temperatures (Fig. 9). The largest egg sacs contained the highest number of eggs ($df = 222$, $r = 0.82$, $p < 0.001$) but not the largest eggs, as we found no difference in egg diameter with either the length of the egg sac or the prosome of the female. The reason for the differences in the lower ES and female weight in Fig. 8 compared to Fig. 9 is that Fig. 8 displays means whereas Fig. 9 shows individual values for female weight and ES. Moreover, in Fig. 9 is a subset of the data since here we show only the eggs measured in the egg sacs that were found attached to females.

ES, EPR, SEPR and RAF were also significantly positively correlated with Chl concentration, microplankton groups and the M:F ratio, whereas no significant correlation was found with either temperature or salinity. Stepwise multiple regression analysis of pooled data indicated that 63 % of the total variability in ES was explained by female body weight followed by M:F ratio and ciliates carbon in the size range of 20 - 40 μm in cell diameter (Table V). On the other hand, 38 % of the total variability in EPR was explained by female body carbon, dinoflagellates carbon and ciliates carbon in the size range of 20 - 40 μm in cell

377 diameter, whereas 36 % of the variability in SEPR was accounted for by dinoflagellates
378 carbon and ciliates carbon in the size range of 20 - 40 μm (Table V).
379
380 **Production**
381 *Oithona* spp. production (P) in the study area varied from 1.61 μg C m^{-3} d^{-1} to 153 μg
382 C m^{-3} d^{-1} (Fig. 10 and Table VI). The seasonal pattern of mean (± SE) *Oithona* spp.
383 production was similar to that of the biomass with the highest mean total production measured
384 in summer (67.02 ± 9.4 μg C m^{-3} d^{-1}), lower production being observed in spring (14.2 ± 2.44
385 μg C m^{-3} d^{-1}) and the lowest in winter (8.8 ± 1.2 μg C m^{-3} d^{-1}). In spring the highest
386 production was measured on the RR whereas there was no clear difference between the other
387 areas. In summer the highest production was measured on the SIC, NIC and RR whereas the
388 lowest on the EGC-P. In winter the highest productions were measured on the RR and CIS
389 and the lowest on the NIC and IS, although, at this time sampling was not undertaken within
390 the other zones. The production of the naupliar stages was comparable to that of the younger
391 copepodite stages both in spring and winter (i.e. 40 % of the total P) and it was always higher
392 than that of the adult female stage (Table VI).
393
394 **Discussion**
395 The present study investigated the regional variation of *Oithona* spp. stage structure,
396 biomass and productivity in the Irminger Sea, North Atlantic. Besides a general paucity of
397 data for this oceanic region on an important genus such as *Oithona* spp., our study was
398 motivated by gaining insights of the factors which may determine the reported temporal and
399 spatial stability in biomass and production of these cyclopoids in some areas (Nielsen and
400 Sabatini, 1996) and high variability in other areas (Uye and Sano, 1998). For this reason the
401 survey was carried out at different times of the year and over basin scale, in regions with very
402 different hydrographic, physico-chemical and biological attributes (Holliday *et al*., 2006).
403
404 **Eggs per sac, egg production rate, specific egg production rate and the proportion of**
405 **reproducing females**
406 In the present study *O. similis* reproduced during all sampling occasions reaching
407 peaks of breeding activity in spring, as indicated by both the production of higher ES, EPR
408 and the proportion of reproducing females (RAF) compared to values measured during the
409 summer and winter cruises (Fig. 7). The highest mean EPR, SEPR and RAF were measured
410 on the Greenland (EGC-P) and Iceland (IS) shelves, the NIC and on the RR where both

411 female body carbon and microplankton biomass were also high (Fig. 7). Most of the
412 variability in *O. similis* ES and EPR was explained by female body weight, followed by
413 ciliates and dinoflagellates biomass (Table V), whereas the effect of temperature was not
414 significant over the range considered. Although, copepod reproductive rates increase with
415 temperature under laboratory saturating feeding conditions (Runge, 1984), field studies have
416 shown that, in nature, copepods EPR can be food limited and that the effect of temperature on
417 fecundity is indirectly mediated by body size (Gislason, 2005; Castellani and Altunbaş, 2006).
418 Nevertheless, using a large compilation of data from the literature (present study, Uye and
419 Sano, 1998; Nielsen and Sabatini, 1996), over a wide temperature range, the effect of
420 temperature on *Oithona* spp. SEPR (i.e. EPR standardized for copepods of different body
421 weight) becomes discernible (Fig. 11).
422 The significant increase in EPR we found with ciliates and dinoflagellates biomass
423 (Table V) suggests that these organisms represent an important food source for the
424 reproductive success of *O. similis*. Such result is consistent with published literature showing
425 that EPR increases with the percentage of ciliates in the diet of this species (Castellani *et al*.,
426 2005b). Moreover, the significant positive relationship shown here between ciliate carbon in
427 the size range of 20 - 40 μm with ES, EPR and SEPR also supports the view that *O. similis*
428 females tend to feed selectively on specific ciliates sizes (Castellani *et al*., 2005b). Although,
429 phytoplankton can make up a considerable fraction of the diet of *Oithona* spp., this copepod
430 genus has been reported to prefer motile to non-motile prey, selecting ciliates preferentially to
431 diatoms of similar shape and size (Atkinson, 1996). Despite finding positive correlations
432 between ES, EPR and SEPR with Chl and diatoms, these variables were eliminated during the
433 stepwise regression procedure. The highest Chl concentrations (i.e. > 3 μg Chl L^{-1}) were
434 measured during a bloom of *Phaeocystis* sp. and, therefore, low EPR even at these high
435 phytoplankton concentrations is not surprising as *O. similis* does not tend to feed on this algal
436 species (Castellani *et al*., 2005b).
437 Increases in ES, EPR, SEPR and RAF occurred at the fronts between the EGC-P and
438 EGC-A, the CIS and the NIC/SIC, the CIS and RR and stratified water in the EGC-P, where
439 Chl, ciliates and dinoflagellates concentrations were particularly high (Fig. 2 and Fig. 7,
440 Holliday *et al*., 2006; Yebra *et al*., 2006). During a concomitant study in the Irminger Sea in
441 summer, Yebra *et al.,* (Yebra *et al.,* 2006) reported that the higher Chl concentrations up to
442 1.6 mg Chl m^{-3} they measured at the front between the NIC and CIS, (compared to the 0.25 -
443 0.5 mg Chl m^{-3} in the CIS) were associated with a five-fold increase in ciliates potential
444 production and a nine-fold increase in ciliate biomass. Thus, results from our study, suggests

445 that the higher phytoplankton concentrations measured at frontal regions were transferred via
446 the microzooplankton up through the food web and resulted in the higher reproductive output
447 of *O. similis* at these sites (Fig. 7).

448 The low EPR, SEPR and RAF measured within the CIS, where microplankton
449 concentration was lower than in the other zones, also suggest that *O. similis* in the CIS region
450 might have been food limited. This argument is supported by results showing that in the
451 Irminger Sea, the energetic cost of reproduction exceeded the energy ingested by *O. similis*
452 females (Castellani *et al.*, 2005b). Nielsen and Sabatini (Nielsen and Sabatini, 1996) have
453 argued that the lack of correlation they found between *O. similis* SEPR with Chl and
454 microplankton in the North Sea was due to the fact that *Oithona* spp. was not food limited.
455 The higher total microplankton and ciliates concentrations measured by Nielsen and Sabatini
456 (Nielsen and Sabatini, 1996) in the North Sea compared to those recorded, in the present
457 study, would support the argument put forward by these authors. Nevertheless, it cannot be
458 excluded that additional food preys, which were not considered here such as copepod nauplii
459 (Nakamura and Turner, 1997) and faecal pellets (Gonzalez and Smetacek, 1994) might also
460 have made an important contribution to the diet and reproduction of *O. similis*.

461 Fertilisation depends on the encounter rate between mature males and females and,
462 therefore, if the number of males becomes deficient the proportion of females fertilized and
463 producing eggs in the population will decline (Kiørboe, 2006). Thus, the significant
464 relationship we found between the sex ratio with the RAF and the ES suggests that the
465 proportion of males in the population might also have affected *O. similis* reproductive rates
466 and warrants further investigation.

467 The present study has also shown that, although, the mean ES of the *O. similis*
468 population increased with female body carbon (Fig. 8), the egg sacs attached to individual >
469 0.75 μg C from the EGC, in spring, were smaller than those produced by females of similar
470 weight exposed to lower temperatures but to a higher ciliates concentrations in summer (Fig.
471 9). This observation suggests that either low food concentration/quality or copepod age were
472 the most likely causes for the smaller ES measured in spring within the EGC zone. Smaller
473 ES might have been produced, in fact, by older long-lived females (i.e. with lower
474 reproductive potential) transported on the Greenland shelf from Arctic regions by the cold
475 southward flowing EGC-P current. Cyclopoids, however, are characterized by ontogenetic
476 vertical distribution with the nauplii closer to the surface and the larger copepodites
477 positioned further down in the water column possibly to minimise predation risk (Titelman
478 and Fiksen, 2004). Since microzooplankton concentration, in the present study area, decreased

479 with depth (Wilson, D., University of Liverpool, UK, personal communication), the smaller
480 ES might have also resulted from larger copepods occupying a position in the water column
481 below optimal feeding conditions for maximum reproductive output. It cannot also be
482 excluded that females carrying bigger egg sacs may have been preyed upon by visual
483 predators more easily than those with smaller ones. Further investigations are required to
484 verify whether the presence of *O. similis* females bearing smaller egg sacs is the result of
485 senescence, food shortage or selective predation.
486
487 **Spatial and seasonal variations in *Oithona* biomass and production**
488 Previous studies in the Irminger Sea have either focused on larger zooplankton groups
489 (Bainbridge and Corlett, 1968) or used 200 μm mesh size nets (Gislason, 2003) which will
490 have underestimated both the younger stages and the total biomass of smaller but abundant
491 copepod species such as *Oithona* spp. In this respect, the depth integrated *Oithona* spp.
492 biomass of 0.028 mg C m^{-3} in early April and of 0.38 mg C m^{-3} in June estimated [assuming a
493 0.45 carbon to dry weight ratio] by Gislason (Gislason, 2003) in the Irminger Sea using a 200
494 μm mesh size net, are lower than the mean biomass of 0.22 mg C m^{-3} and of ca. 1 mg C m^{-3}
495 we measured for the same area and time of the year using a 63 μm mesh size net. At the time
496 of our survey, *Oithona* spp. abundance in the Irminger Sea decreased with depth (Fig. 12 and
497 Gislason, 2003). Thus, it is possible that the lower *Oithona* spp. biomass estimates reported
498 by Gislason (Gislason, 2003) were due to the sampling methodology adopted by this author
499 who integrated biomass over the whole water column down to a depth of 2500 metres.
500 Our results also show that the spatial and seasonal variation in *Oithona* spp. biomass
501 in the Irminger Sea was related to both the hydrographic and the biological characteristics of
502 the zones described by Holliday *et al*., (Holliday *et al*., 2006). The lowest *Oithona* spp.
503 biomass measured at the innermost stations on the Greenland shelf, the EGC-P, was
504 associated with colder and less saline water of Arctic origin. On the other hand, the increase
505 in biomass observed between the shelf break (EGC-A) and offshore (CIS, NIC, SIC and RR)
506 was associated with progressively warmer and saltier water of Atlantic origin. Hansen *et al*.,
507 (Hansen *et al*., 2004) have recently shown that low salinity was an important factor limiting
508 the distribution and abundance of *O. similis* in the Baltic Sea. Although, in the present study,
509 *Oithona* spp. biomass was overall positively correlated with salinity, such correlation was
510 only significant for the spring data and salinity was rejected by the step-wise multiple
511 regression analysis on pooled data (Table V). Moreover, the lowest salinity of 30.5 measured,
512 on the Greenland shelf, was much higher than the 7 to 16 reported for the Baltic Sea by

513 Hansen *et al*., (Hansen *et al.*, 2004). Therefore, it is reasonable to assume that the salinity
514 concentrations encountered in the Irminger Sea, in the present study, did not significantly
515 affect the observed variation of *Oithona* spp. biomass.

516 The five-fold increase in *Oithona* spp. biomass recorded between the EGC-P and the
517 RR and between spring and summer, in the present study, was statistically significant.
518 Gislason (Gislason, 2003) has shown that in the Irminger Sea in winter and spring, the
519 majority of *Oithona* spp. are found deeper (i.e.100 m to 400 m) in the water column than in
520 summer, suggesting that this genus undergoes annual vertical migration. Therefore, results,
521 from the present study, showing that during spring and summer, 95 % of the *Oithona* spp.
522 were found within the top 60 m of the water column (Fig. 12) is, somehow, at odds with
523 findings by Gislason (Gislason, 2003). It is worth noting, however, that the abundances
524 reported by Gislanson (Gislason, 2003) during April and June are about a tenth of those
525 measured, in the present study, and they will be chiefly represented by larger and older
526 *Oithona* spp. stages (because of the 200 μm mesh size net used by this author) which tend to
527 have a deeper vertical distribution than younger but more abundant stages.

528 The stage structure of the population of *Oithona* spp. in the Irminger Sea varied
529 significantly from spring and winter, when it was largely made up by nauplii, to summer
530 when copepodites predominated. It is reasonable to conclude that the larger 200 μm mesh size
531 net used by previous studies would have missed the bulk of biomass in the surface strata
532 represented by nauplii and younger copepodites in spring. This trend would have also been
533 exacerbated by the fact that in summer the size of the stages is smaller (Table III). Therefore,
534 the increase in *Oithona* spp. biomass we measured in summer was probably primarily the
535 result of population growth rather than vertical migration of cyclopoids from deeper strata.

536 Multiple regression analysis showed that temperature explained the highest proportion
537 of the spatial and temporal variability of *Oithona* spp. biomass followed by dinoflagellate
538 concentration (Table V). *Oithona* spp. biomass ranging from 0.7 mg C m^{-3} at 2.8 °C to 2 mg
539 C m^{-3} at 11°C, in the present study, fits the general trend of increasing biomass with
540 temperature reported in the literature. The lowest *Oithona* spp. biomasses of 0.04 and 0.47 mg
541 C m^{-3} have been reported at ca. 0 °C for the Southern Ocean (Atkinson, 1998 and references
542 therein). Intermediate *Oithona* spp. biomass values between 0.9 - 9 mg C m^{-3} were recorded at
543 temperatures between 7 °C and 12 °C, in the North Sea, by Nielsen and Sabatini (Nielsen and
544 Sabatini, 1996). On the other hand, very high variation in the biomass of *O. davisae* from 2.2
545 mg C m^{-3} at 9 °C to 92 mg C m^{-3} at 28 °C were measured, over the year, by Uye and Sano
546 (Uye and Sano, 1998) in an eutrophic inlet in Fukuyama Harbour. The significant relationship

547 we found between *Oithona* spp. biomass and dinoflagellates also suggests that population
548 growth rates might have been food limited. Interestingly, the increase in *Oithona* spp. biomass
549 with dinoflagellates, in the present study, is in agreement with results obtained by Head and
550 Sameoto (Head and Sameoto, 2005) for the Newfoundland and Scotian shelves using the
551 Continuous Plankton Recorder (CPR) data. Although there was a tendency for *Oithona* spp.
552 biomass to be higher at the fronts, where microplankton production was higher, the pattern
553 was not as evident as that observed for the reproductive parameters. Such result is, however,
554 not surprising as the signal of the link between food web compartments weakens as it
555 propagates up towards higher trophic levels.

556 The present study represents the first attempt to estimate reproduction and
557 productivity of *Oithona* spp. in the North Atlantic. Therefore, a comparison with the literature
558 for this area is not possible. Nevertheless, *Oithona* spp. productions ranging from 0.002 to
559 0.15 mg C m^{-3} d^{-1} found here are lower than estimates between 0.003 and 0.6 mg C m^{-3} d^{-1}
560 estimated for the southern North Sea (M. Sabatini, INIDEP, Argentina, personal
561 communication) and the maximum production rates of 11 mg C m^{-3} d^{-1} reported by Uye and
562 Sano (Uye and Sano, 1998) for *O. davisae* at higher temperature and at food saturating
563 conditions in Fukuyama Harbor. The significant spatial variation in *Oithona* spp. biomass and
564 production we measured in the Irminger Sea contrasts with observations of Nielsen and
565 Sabatini (Nielsen and Sabatini, 1996) who did not observe significant differences between
566 shallow (< 50 m) and deeper (100 - 200 m) stations in the North Sea. Our study, however,
567 was conducted over basin scales at depths varying between about 100 m to 3000 m in coastal
568 and oceanic conditions. On the other hand, the investigation of Nielsen and Sabatini (Nielsen
569 and Sabatini, 1996) took place over a shorter time and within a narrower sampling area
570 characterized by higher microplankton concentration and by relatively more stable
571 environmental conditions. Thus, food limitation and/or higher predation impact, in the present
572 study, compared to the shallower and more productive area, sampled by Nielsen and Sabatini
573 (Nielsen and Sabatini, 1996) in the North Sea, may be among the main reasons for the
574 variability we report in the biomass and productivity of *Oithona* spp.

575 The present study has also shown that naupliar stages contributed a comparable or
576 higher fraction to both the biomass and production of *Oithona* spp. than copepodite stages.
577 This observation contrasts with previous studies (Nielsen and Sabatini, 1996; Uye and Sano,
578 1998) which have assumed the production rate of *Oithona* spp. nauplii to be negligible.
579 Nevertheless, the production rates we report here for *Oithona* spp. nauplii and younger
580 copepodite stages, using adult female SEPR, probably represent a conservative estimate as the

581 growth rates of copepod juveniles *in situ* are considered closer to food saturation rates than
582 the SEPR of adult females (Hirst and Bunker, 2003).
583
584 **Variation in *Oithona* spp. length and stage composition**
585 In the Irminger Sea, the length and the percentage stage composition of *Oithona* spp.
586 varied both spatially and seasonally. Spatial and temporal variation in the percentage stage
587 composition of *Oithona* spp. is surprising as this genus is considered to have relatively stable
588 populations as a result of continuous reproduction (Nielsen and Sabatini, 1996; Pagès *et al*.,
589 1996) and reduced mortality rates (Eiane and Ohman, 2004). Nevertheless, the present study
590 has shown that in spring the nauplii represented up to 80 % of the total abundance whereas in
591 summer the population of *Oithona* spp. was primarily made up of late copepodite stages. The
592 pattern observed suggests that, overall, the seasonal variation in *Oithona* spp. stages
593 composition was probably the result of the natural progression of the life stages initiated by
594 the higher EPR in spring and continued by relatively faster growth rates stimulated by
595 increasing temperatures in summer. On the other hand, spatially, the lowest proportion of NI
596 and NII stages was recorded in spring on the EGC-P and IS compared to the EGC-A, CIS and
597 NIC zones and it coincided with the lowest N/E ratio. Since EPR, RAF and microplankton
598 concentration on the EGC-P, IS and RR were higher or similar to those measured within the
599 EGC-A, CIS and NIC zones, it is unlikely that the lower naupliar recruitment was caused by
600 either low temperature or food limitation. Ussing (Ussing, 1938) speculated that the decrease
601 in the abundance of *O. similis* he measured in the fjord of East Greenland could be due to
602 predation pressure by large *Calanus* spp. Shelf areas in spring are sites of high reproductive
603 activity and recruitment for planktivorous organisms such as fish larvae (Kane, 1984) and
604 *Calanus* spp. (Gislason, 2005). The inverse relationship found between *Calanus spp* and fish
605 larvae abundance and the *Oithona* spp. N/E ratio suggest that predation pressure might have
606 contributed to the lower naupliar recruitment measured on the EGC-P, IS and RR during
607 spring (Fig. 5). The high proportion of NI-NII on the RR, however, also suggest that higher
608 EPR and higher egg hatching rate (i.e. due to higher temperature), in this region, were
609 compensating for naupliar mortality more than in other areas (Fig. 4).
610 The presence of larger stage sizes we describe for spring and winter compared to
611 summer is similar to trends reported in the literature for calanoid copepods (Deevey, 1960).
612 Temperature, food availability (Breteler and Gonzalez, 1988) and selective predation (Warren
613 *et al*., 1986) are considered the most important factors determining changes of copepod stages
614 length *in situ*. In the present investigation, *O. similis* female length was overall correlated with

615 both temperature and microplankton biomass. However, the presence of large females of
616 similar length within the IS, RR and EGC-P, suggests that the copepods sampled in these
617 zones might have all originated from colder water masses of Arctic origin and that, therefore,
618 hydrographic processes might have been important in determining copepod distribution.
619 Surprisingly, the largest NI-NIII naupliar sizes were found in the CIS where phytoplankton
620 and ciliate concentration were lowest compared to other zones. Nevertheless, the striking
621 similarity between the size distribution of the NI-NIII and the N/E ratio within the zones in
622 spring, suggests that predation might have also contributed to determine the pattern in stages
623 length we observed.

624 The spring cruise took place before the start of the phytoplankton bloom. At this time
625 *C. finmarchicus* and *C. hyperboreus* females had already emerged from diapause and they
626 were actively reproducing on the shelves as indicated by the large number of adults, eggs and
627 nauplii found here compared to deeper areas (C. Castellani, personal observation). Although
628 *C. finmarchicus* may begin the spring spawning using its fat reserves, the spring
629 phytoplankton bloom is considered important for continued reproduction of this species
630 (Gislason, 2003). Since phytoplankton, particularly diatoms, were still relatively low in
631 abundance at the time of the spring survey it is possible that microplankton alone was not
632 sufficient to sustain *Calanus* spp. EPR. Based on energy budget considerations, Gislason
633 (Gislason, 2005) concluded that during spring the secondary production of *C. finmarchicus*
634 around Iceland was supported by heterotrophic feeding in addition to phytoplankton.
635 Similarly, using a simulation model Carlotti and Slagstad (Carlotti and Slagstad, 1997) found
636 that in the Greenland Sea *C. hyperboreus* would need to exploit the numerically abundant
637 microzooplankton and *Oithona* spp. to sustain its biomass.

638 Thus, our results stress the role of the early naupliar stages of *Oithona* spp. as a food
639 source for planktonic predators such as *Calanus* spp. and fish larvae particularly prior to the
640 spring phytoplankton bloom. Certainly, temperature and food availability are important
641 parameters determining changes in the natural progression of the life stages of copepods.
642 However, our findings suggest that future experimental and modeling studies should evaluate
643 the importance of predation on the nauplii in shaping the temporal and spatial pattern in
644 abundance, stages composition and biomass not only of *Oithona* spp but also of other small
645 copepod species.

646

647 **Summary and conclusions**

The present investigation has shown that over a wide hydrographically and biologically diverse scale *Oithona* spp. population structure, biomass and production are characterised by both significant spatial and temporal variability. Compared to other oceanic regions, the variation in biomass and life stages structure of *Oithona* spp., in the Irminger Sea appeared to be controlled by temperature, food availability and possibly predation pressure. On the other hand, reproductive rates seemed mainly limited by food resources, female size and sex ratio. Contrary to other copepod genus, in oceanic oligotrophic regions *Oithona* spp. remains active, feeding and reproducing, during the whole year. Thus, during spring *Oithona* spp. nauplii can represent a considerable proportion of the total zooplankton biomass and production and may serve as a food source for larger predators such as *Calanus* spp. and fish larvae particularly prior to the spring phytoplankton bloom.

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Table I: Physical, chemical and biological properties (mean ± sd) of the mixed layer characterising the zones identified by Holliday *et al.,* (2006) and the Iceland shelf (IS) during the spring (D262), summer (D264) and winter (D267) cruises in the Irminger Sea. Number of stations (N), depth of the mixed layer (ML, dbar), mean potential temperature (T, ˚C), salinity, chlorophyll-a (Chl, mg m^{-3}), nitrate (NO_3^-, µmol l^{-1}) and silicate (SiO_3^{2-}, µmol l^{-1}).

Cruise Season	Zone	N	ML	Temperature	Salinity	Chl	NO_3	SiO_3
Spring								
	EGC-P	5	12	3.0 ± 1.4	34.17 ± 0.32	3.2 ± 1.1	7.3 ± 1.4	5.8 ± 0.4
	EGC-A	10	19	6.1 ± 0.1	35.02 ± 0.01	0.9 ± 0.0	13.1 ± 0.1	7.5 ± 0.1
	CIS	3	52	6.9 ± 0.0	35.08 ± 0.00	0.6 ± 0.0	13.6 ± 0.1	8.9 ± 0.8
	NIC	7	91	7.3 ± 0.0	35.13 ± 0.00	0.5 ± 0.0	13.4 ± 0.1	6.8 ± 0.1
	SIC	3	154	6.9 ± 0.0	35.09 ± 0.00	0.4 ± 0.0	13.7 ± 0.1	7.2 ± 0.1
	IS	2	55	6.5 ± 0.1	35.08 ± 0.00	0.9 ± 0.0	–	–
	RR	5	41	7.7 ± 0.0	35.18 ± 0.00	0.8 ± 0.1	11.7 ± 0.5	5.3 ± 0.5
Summer								
	EGC-P	3	0	5.9 ± 0.3	33.95 ± 0.05	0.9 ± 0.2	0.0	0.2 ± 0.0
	EGC-A	10	22	8.9 ± 0.1	34.85 ± 0.04	1.3 ± 0.1	4.0 ± 0.3	1.0 ± 0.2
	CIS	12	21	9.7 ± 0.1	34.91 ± 0.01	0.8 ± 0.0	5.2 ± 0.3	0.8 ± 0.1
	NIC	2	22	10.6 ± 0.0	35.05 ± 0.01	0.8 ± 0.0	3.7 ± 0.4	1.0 ± 0.1
	SIC	5	25	10.0 ± 0.1	34.94 ± 0.01	1.1 ± 0.1	5.9 ± 0.3	1.2 ± 0.1
	IS	1	–	8 ± 0.0	–	–	–	–
	RR	4	14	11.1 ± 0.1	35.15 ± 0.03	0.8 ± 0.1	4.5 ± 0.3	0.8 ± 0.1
Winter								
	EGC-P	0	–	–	–	–	–	–
	EGC-A	6	237	6.1 ± 0.0	34.98 ± 0.00	0.1 ± 0.0	14.6 ± 0.1	7.1 ± 0.1
	CIS	2	54	6.5 ± 0.3	34.73 ± 0.00	0.3 ± 0.0	11.0 ± 0.8	4.9 ± 0.4
	NIC	6	110	7.7 ± 0.0	34.99 ± 0.00	0.2 ± 0.0	10.3 ± 0.1	4.6 ± 0.1
	SIC	6	52	9.1 ± 0.1	34.96 ± 0.01	0.3 ± 0.0	9.6 ± 0.4	4.1 ± 0.2
	IS	0	–	–	–	–	–	–
	RR	4	117	7.9 ± 0.0	35.08 ± 0.00	0.1 ± 0.0	12.7 ± 0.1	6.1 ± 0.1

Table II: Results of ANOVA test between the means (± SE) relative abundance (%) and relative biomass (%) of *Oithona* spp. nauplii (NI-NVI), copepodites (CI-CV) and adult female stages for the spring (D262), summer (D264) and winter (D267) cruises. Significance levels: ***< 1 %, ** < 5 % and * < 10 %.

Variable	Stage	Spring	Summer	Winter	df	F	p	r^2
% Abundance	Nauplii (NI-NVI)	74.9 (1.52)	62.6*** (1.95)	76.9 (1.72)	75	15.4	< 0.0001	29.7
	Copepodites (CI-CV)	21.92 (1.35)	32.23*** (1.61)	19.99 (1.85)	75	14.68	< 0.0001	27.7
	Female	3.23 (0.44)	4.18 (0.44)	3.07 (0.36)	75	1.34	0.268	0.91
% Biomass	Nauplii (NI-NVI)	40.2 (1.75)	23.4*** (2.35)	39.6 (2.20)	66	19.1	< 0.0001	37.4
	Copepodites (CI-CV)	46.46 (1.52)	62.38*** (2.19)	46.23 (3.29)	66	20.60	< 0.0001	37.2
	Female	13.69 (1.47)	14.24 (1.07)	14.12 (1.83)	66	0.04	0.961	0.01

Table III: Mean length (µm) of nauplii (NI-NVI) and copepodite (CI-CVIF) stages measured during the spring (D262), summer (D264) and winter (D267) cruises in the Irminger Sea.

Season		Stages										
		NI-NII	**NIII**	**NIV**	**NV**	**NVI**	**CI**	**CII**	**CIII**	**CIV**	**CV**	**CVIF**
Spring	**Mean**	139.39	161.73	192.15	205.12	240.92	265	323.23	397.44	452.36	493.54	501.83
	SE	1.7	1.57	3.03	2.08	2.26	1.53	2.31	3.56	5.74	6.97	2.33
	n	360	180	180	180	180	180	180	180	180	180	838
Summer	**Mean**	131.56	149.34	174.63	206.67	217.92	238.45	297.17	388	423	482.2	479.33
	SE	2.04	1.73	3.02	4.77	6.92	5.58	5.04	21.3	12.5	26.4	1.32
	n	32	38	27	24	22	26	41	20	22	20	431
Winter	**Mean**	136.5	147.33	182.31	215	271.25	221.6	269.43	372	424.5	450.3	504.7
	SE	2.95	3.55	3.82	7.67	1.25	12	7.7	4.5	10.8	12.1	2.77
	n	20	25	19	26	14	17	24	23	21	14	28

Table IV: Mean length (µm) of nauplii (NI-NVI) and copepodite (CI-CVIF) stages measured during in different zones of the Irminger Sea the during the spring (D262) cruise. The number of measurements (n) and the standard error of the mean (SE) are also shown.

		Stages										
Zone		**NI-NII**	**NIII**	**NIV**	**NV**	**NVI**	**CI**	**CII**	**CIII**	**CIV**	**CV**	**CVI-F**
EGC-P	Mean	134.8	162.2	191.7	206.4	249.03	272.8	331.3	409.8	461.6	480.5	512.4
	SE	2.8	2.45	4.62	2.73	3.83	2.72	4.52	7.38	14.1	13.5	2.44
	n	60	30	30	30	30	30	30	30	30	30	233
EGC-A	Mean	142.8	160.9	202.5	203.75	231.8	261.3	311.1	402.8	463.6	505.8	496.4
	SE	4.49	4.19	8.3	5.4	5.44	3.55	4.45	8.32	15.2	19.2	1.98
	n	60	30	30	30	30	30	30	30	30	30	241
CIS	Mean	150.9	171	168	211.67	240.7	258.8	316.3	384.2	449.9	509.4	498.4
	SE	6.57	5.35	2.55	9.01	7.75	1.52	2.69	4.3	10.7	31.3	3.2
	n	60	30	30	30	30	30	30	30	30	30	67
NIC	Mean	139	156.1	188.8	201.5	236.7	256.8	317.3	382.1	428.1	483.1	473.4
	SE	2.36	2.33	4.4	4.63	3.53	2.34	3.76	4.96	2.48	4.99	10.3
	n	60	30	30	30	30	30	30	30	30	30	162
RR	Mean	133.6	172.5	197.9	200	242	272.1	335.5	405.4	451.3	513.2	526.8
	SE	4.1	8.04	13.6	10.2	9.57	8.54	7.56	10.7	8.95	18.4	3.47
	n	60	30	30	30	30	30	30	30	30	30	57
IS	Mean	132.1	173.4	201.2	212.5	251.1	275.4	340.3	411.7	468.5	517.3	538.8
	SE	3.7	7.8	8.5	10.3	8.6	9.3	10.1	8.8	9.2	15.4	6.90
	n	60	30	30	30	30	30	30	30	30	30	50

Table V: *Oithona* spp. stepwise multiple regression analysis between logarithmically transformed (ln) *Oithona* biomass (biomass, mg m^{-3}), eggs per sac (ES, eggs sac^{-1}), egg production rates (EPR, eggs fem^{-1} d^{-1}), weight-specific egg production rates (SEPR, d^{-1}) and female body carbon (BW, µg C), male to female abundance ratio (M:F), ciliates carbon in 20 - 40 µm cell diameter (cilia 20 – 40 µm, mg C m^{-3}), dinoflagellate carbon (dinos, mg C m^{-3}) and temperature (T, °C). Significance levels: *** < 1 %, ** < 5 % and * <10 %; degrees of freedom (df), F statistic (F). The standard error of the estimated regression coefficients is given in brackets.

Model	df	a	b_1	b_2	b_3	F	r^2
ln biomass = a + b_1 ln dinos + b_2T	53	3.37*** (0.5)	0.32*** (0.10)	0.29*** (0.07)		16.51	39.3
ln ES = a + b_1 ln BW + b_2 ln M:F + b_3 ln cilia (20 -40µm)	41	3.04*** (0.09)	1.18*** (0.19)	0.068*** (0.02)	0.051** (0.01)	21.32	62.74
ln EPR = a + b_1 ln BW + b_2 ln dinos + b_3 ln cilia (20-40µm)	42	0.97*** (0.25)	1.17** (0.54)	0.17*** (0.06)	0.087* (0.04)	7.95	38
ln SEPR = a + b_1 ln dinos + b_2 ln cilia (20-40µm)	43	- 3.09*** (0.065)	0.15*** (0.05)	0.08* (0.04)		10.87	34.7

Table VI: Mean production rate (P, μg C m^{-3} d^{-1}) of different *Oithona* spp. life stages calculated from data collected during the spring (D262), summer (D264) and winter (D267) cruises in the Irminger Sea. *O. similis* mean weight specific egg production (SEPR, d^{-1}). Minimum and maximum values are shown in brackets.

Stage	Spring	Summer	Winter
Nauplii (NI-NVI)	5.9 (0.54 - 32.9)	11.3 (4.7 - 23.3)	3.4 (1.7 – 4.82)
Copepodites (CI -CV)	6.5 (0.86 - 33.3)	39.3 (5.3 - 88.2)	4.1 (2.04 – 6.55)
Female	1.7 (0.09 - 15.9)	8.7 (1.7 - 23.5)	1.3 (0.56 – 2.29)
Total P	14.2 (1.6 – 82.1)	69.4 (13.1 – 153.6)	8.8 (4.9 – 13.6)
SEPR	0.056 (0.017 - 0.078)	0.059 (0.022 - 0.094)	0.047 (0.037 - 0.056)

List of Figures

Fig. 1: The main circulation features of the Irminger Sea. Surface circulation is given by solid lines (NAC is North Atlantic Current, IC is Irminger Current and EGC is East Greenland Current). Mid-depth circulation is given by dot-dashed line (LSW = Labrador Sea Water). Deep circulation is given by dotted lines (ISOW = Iceland–Scotland Overflow Water, DSOW = Denmark Strait Overflow Water). Depth contours are 0 m, 500 m, 1000 m, 2000 m, 3000 m and 4000 m (source Holliday *et al.,* 2006, Fig. 1).

Fig. 1 (continue): Location of the station sampled during D262 a), D264 b) and D267 c) in the Irminger Sea showing the approximate limits of the zones described by Holliday *et al.,* (2006) [East Greenland current Polar (EGC-P), East Greenland current Atlantic (EGC-A), Central Irminger Sea (CIS), North Irminger Current (NIC), Reykjanes Ridge (RR)] and the Iceland shelf (IS). Depth contours are 0 m, 500 m, 1000 m, 2000 m and 3000 meters. The continuous lines and the dotted lines indicate the measured and expected (Holliday *et al.,* 2006 and reference therein) position of the front respectively.

Fig. 2: Mean (± SE) microplankton biomass concentration (mg C m^{-3}) measured within different zones during a) spring (D262), b) summer (D264) and c) winter (D267) cruises in the Irminger Sea. The arrows and dotted lines indicate the position of the front in relation to the zones. Please note the difference in scale.

Fig. 3: *Oithona* spp. Mean (± SE) biomass concentration (mg C m^{-3}) of nauplii, copepodites and adult females measured within different zones during the a) spring (D262), b) summer (D264) and c) winter (D267) cruises in the Irminger Sea. The arrows and dotted lines indicate the position of the fronts in relation to the zones.

Fig. 4: *Oithona* spp. Nauplii and copepodites stages composition measured in different zones of the Irminger Sea during the spring cruise (D262).

Fig. 5:*Oithona* spp. Mean (± SE) nauplii to total egg abundance ratio (N/E) and egg production rates (EPR, eggs $female^{-1}$ d^{-1}) measured within different zones during a) D262, b) D264 and c) D267 cruises in the Irminger Sea. The arrows and dotted lines indicate the position of the front in relation to the zones. The arrows and dotted lines indicate the position of the fronts in relation to the zones.

Fig. 6: *O. similis.* Mean female weight (µg C) vs temperature (°C) within different zones in the Irminger Sea. Regression line fitted to the pooled cruise data excluding observations within the ellipse representing measurements made at the stations in the RR and IS zone during the spring cruise (D262).

Fig. 7: *O. similis.* Mean (± SE) a) eggs per sac (ES, eggs sac^{-1}), b) egg production rate (EPR, eggs fem^{-1} d^{-1}), c) weight-specific egg production rate (SEPR, d^{-1}) and d) the proportion of reproducing females (RAF, %) measured within different zones during the spring (D262), summer (D264) and winter (D267) cruises in the Irminger Sea. The arrows and dotted lines indicate the position of the fronts in relation to the zones.

Fig. 8: *O. similis.* Mean population (i.e. derived from sacs attached and detached to females) eggs per sac (ES, eggs sac^{-1}) measured during the spring (D262), summer (D264) and winter (D267) cruises in the Irminger Sea. Line fitted to data through linear regression.

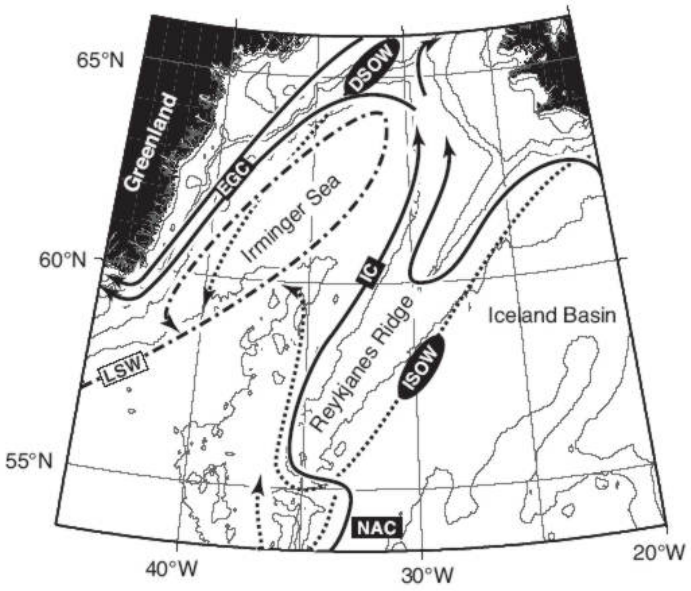
Fig. 9: *O. similis.* Individual eggs per sac (ES, eggs sac^{-1}) derived for b) individuals (i.e. only from sacs attached to females) vs females carbon weight (BW, μg C) measured within different zones of the Irminger Sea. Broken lines indicate the dome shaped trend of ES, the range of increase in ES and the approximate female body size (BW_{ES_Max}) beyond which ES starts to decrease.

Fig. 10: *Oithona* spp. Mean (± SE) production rate (μgC m^{-3} d^{-1}) measured within different zones during the spring (D262), summer (D264) and winter (D267) cruises in the Irminger Sea. The arrows and dotted lines indicate the position of the fronts in relation to the zones.

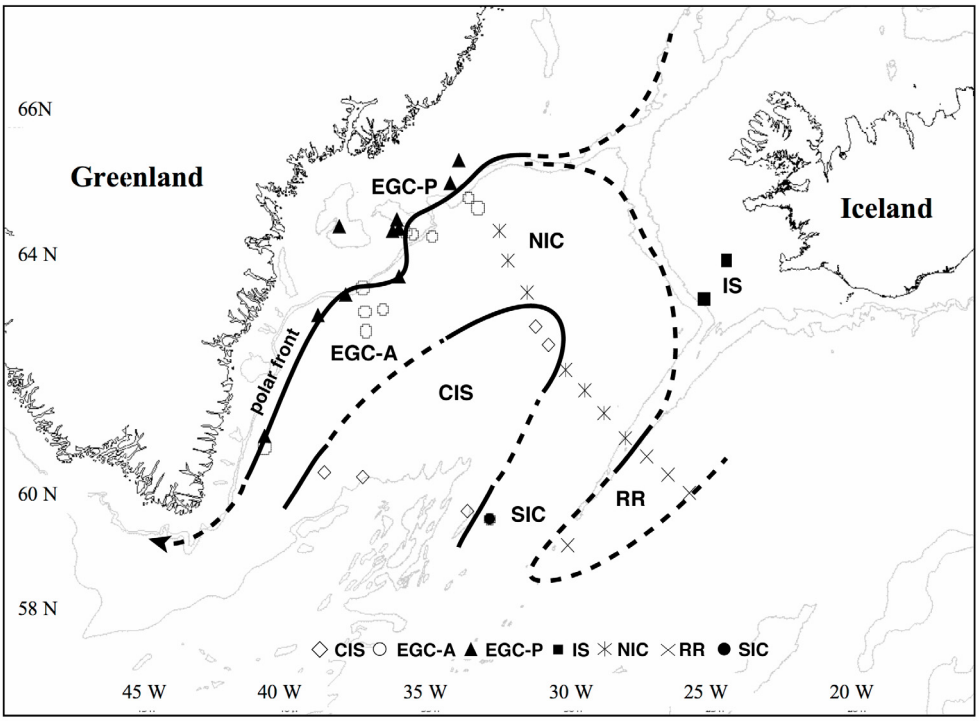
Fig. 11: *Oithona* spp. weight-specific egg production rate (SEPR, d^{-1}) vs temperature T (˚C). Symbols indicate SEPR measured for different species and geographical areas; NS = North Sea (*O. similis*, Nielsen and Sabatini 1996), NA = North Atlantic (*O. similis*, present study), LS = Labrador Sea (*O. similis*, C. Castellani, unpublished data), SJ = Sea of Japan (*O. davisae*, Uye and Sano, 1998).

Fig. 12: Vertical profile of *Oithona* spp. nauplii (NI-NVI) and copepodites (NI-NVI) abundance (Ind. m^{-3}) with depth (m) during the 1) spring (D262) and 2) summer (D264) cruises in the Irminger Sea. Unpublished data collected with OCEAN sampler (courtesy of S. Hay and M. Heath).

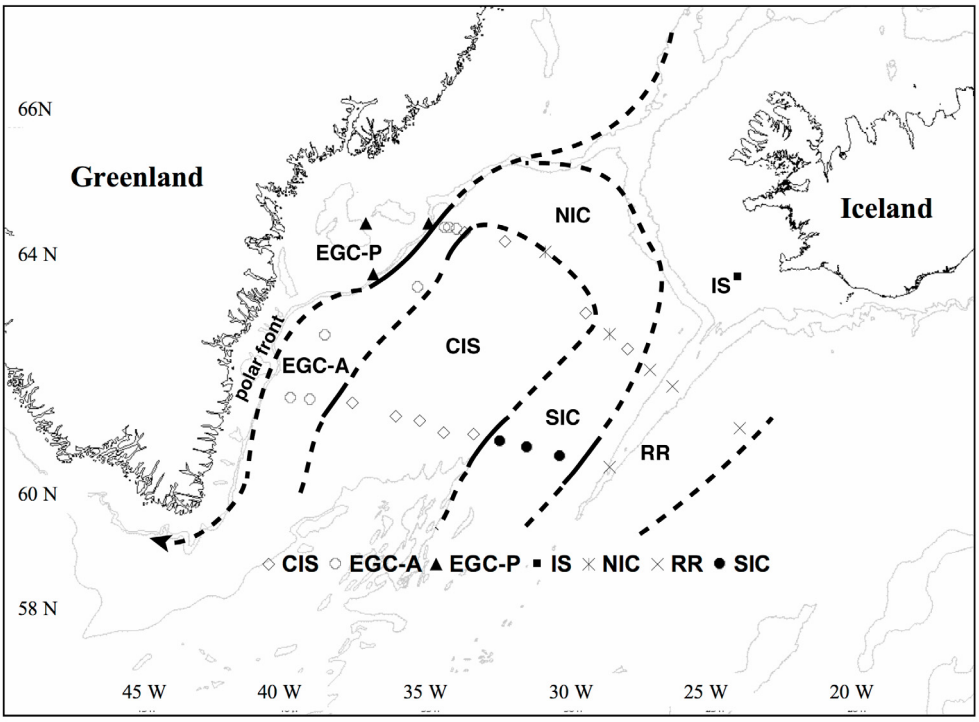
Fig. 1: a)


65°N
60°N
55°N
40°W
30°W
20°W
Greenland
DSOW
EGC
Irminger Sea
IC
Iceland Basin
Reykjanes Ridge
ISOW
LSW
NAC

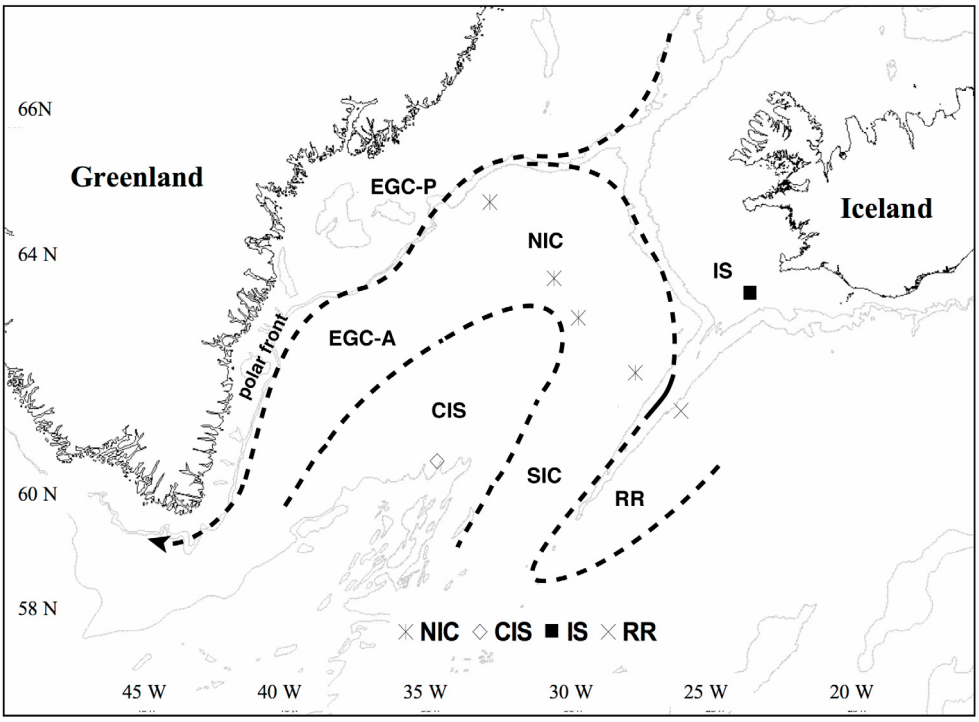
b)


66N
64 N
60 N
58 N
45 W
40 W
35 W
30 W
25 W
20 W
Greenland
Iceland
EGC-P
NIC
IS
EGC-A
CIS
polar front
SIC
RR
◇ CIS ○ EGC-A ▲ EGC-P ■ IS ✳ NIC × RR ● SIC

c)


66N
64 N
60 N
58 N
45 W
40 W
35 W
30 W
25 W
20 W
Greenland
Iceland
EGC-P
NIC
IS
CIS
EGC-A
polar front
SIC
RR
CIS EGC-A EGC-P IS NIC RR SIC

d)


66N
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60 N
58 N
Greenland
Iceland
EGC-P
NIC
IS
EGC-A
polar front
CIS
SIC
RR
NIC CIS IS RR
45 W
40 W
35 W
30 W
25 W
20 W

Fig. 2:

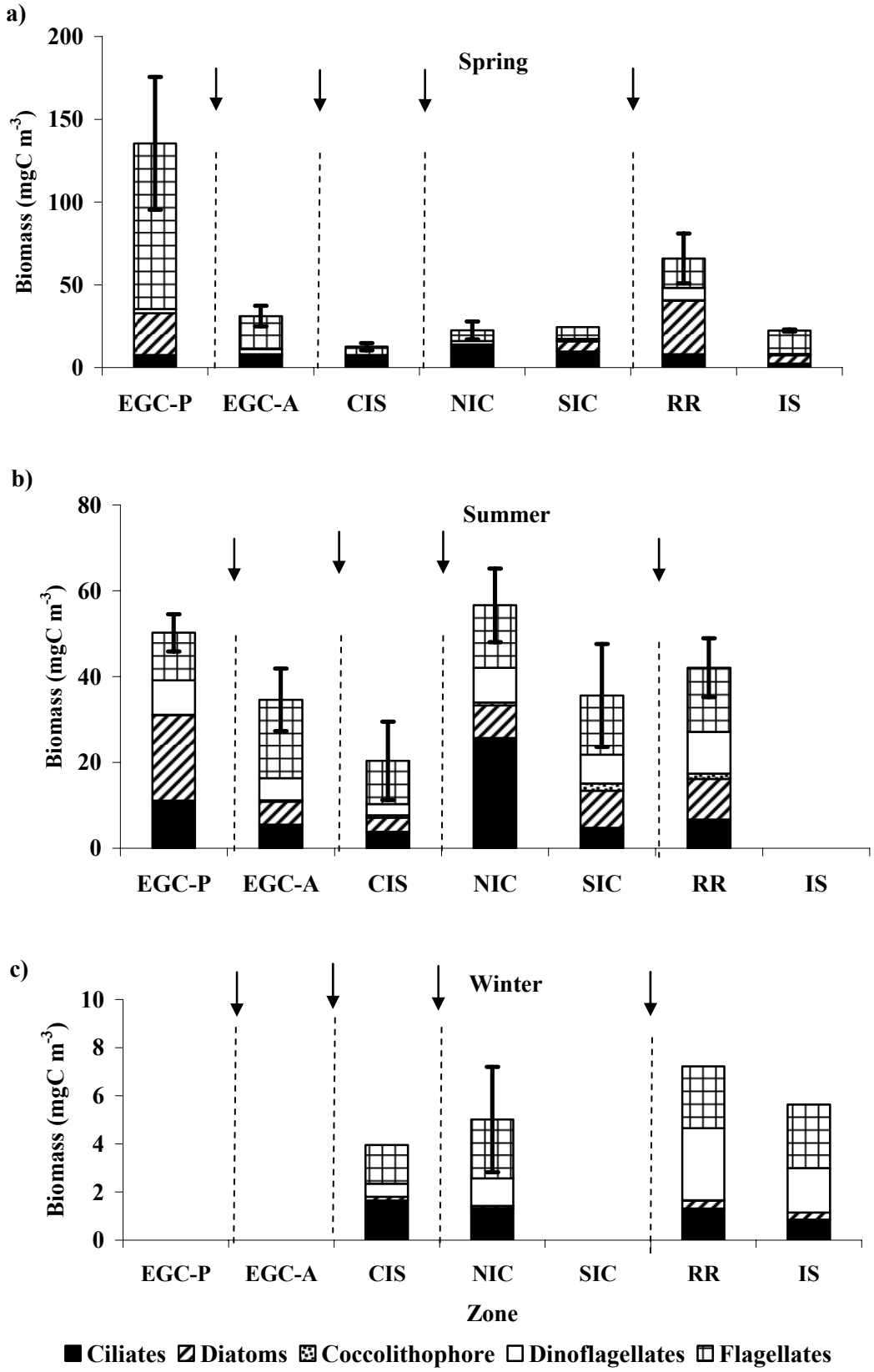

a)
Spring
Biomass (mgC m-3)
200
150
100
50
0
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS
b)
Summer
Biomass (mgC m-3)
80
60
40
20
0
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS
c)
Winter
Biomass (mgC m-3)
10
8
6
4
2
0
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS
Zone
Ciliates
Diatoms
Coccolithophore
Dinoflagellates
Flagellates

Fig. 3:

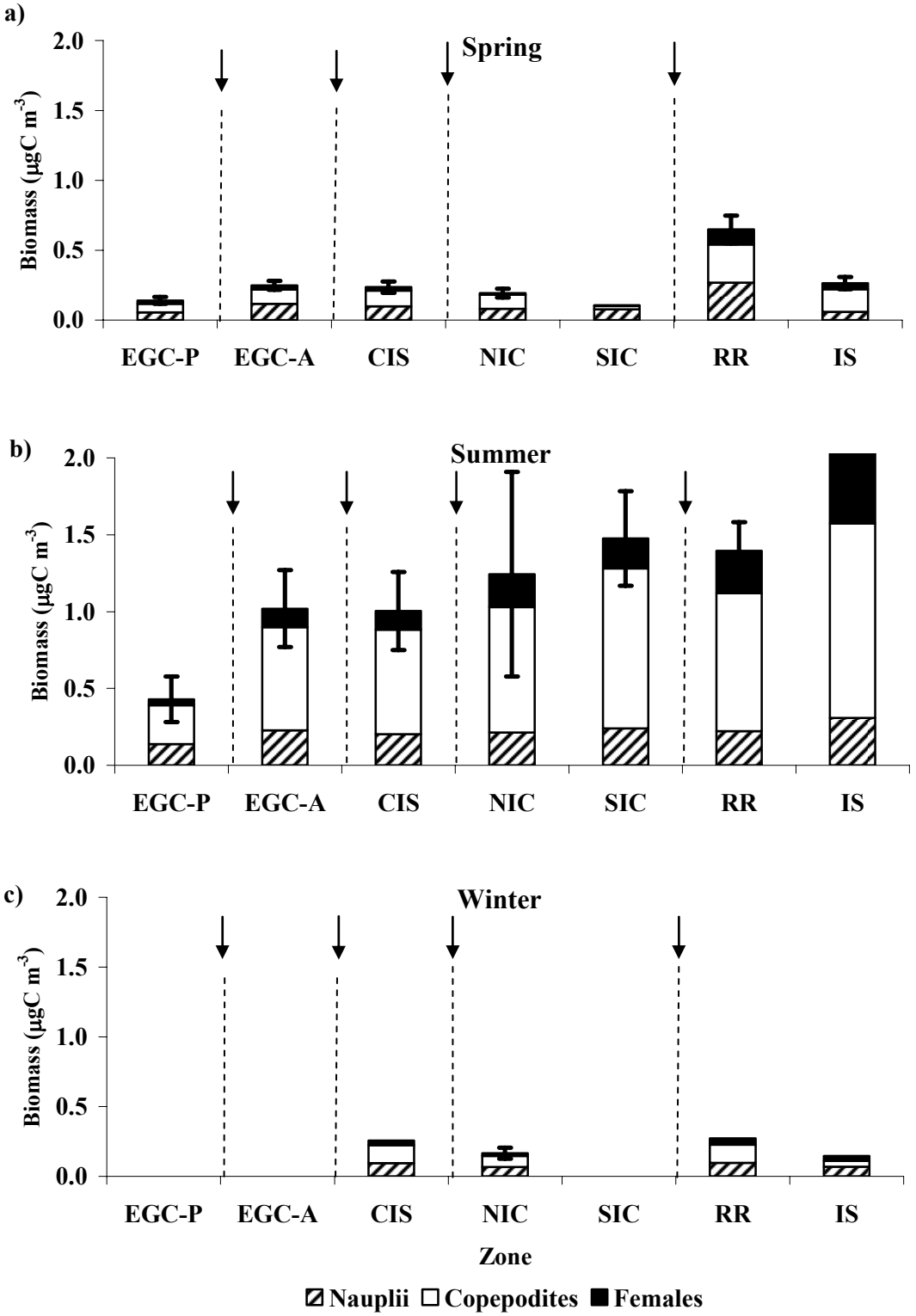

a)
Spring
Biomass (µgC m-3)
2.0
1.5
1.0
0.5
0.0
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS
b)
Summer
Biomass (µgC m-3)
2.0
1.5
1.0
0.5
0.0
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS
c)
Winter
Biomass (µgC m-3)
2.0
1.5
1.0
0.5
0.0
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS
Zone
Nauplii
Copepodites
Females

Fig. 4:

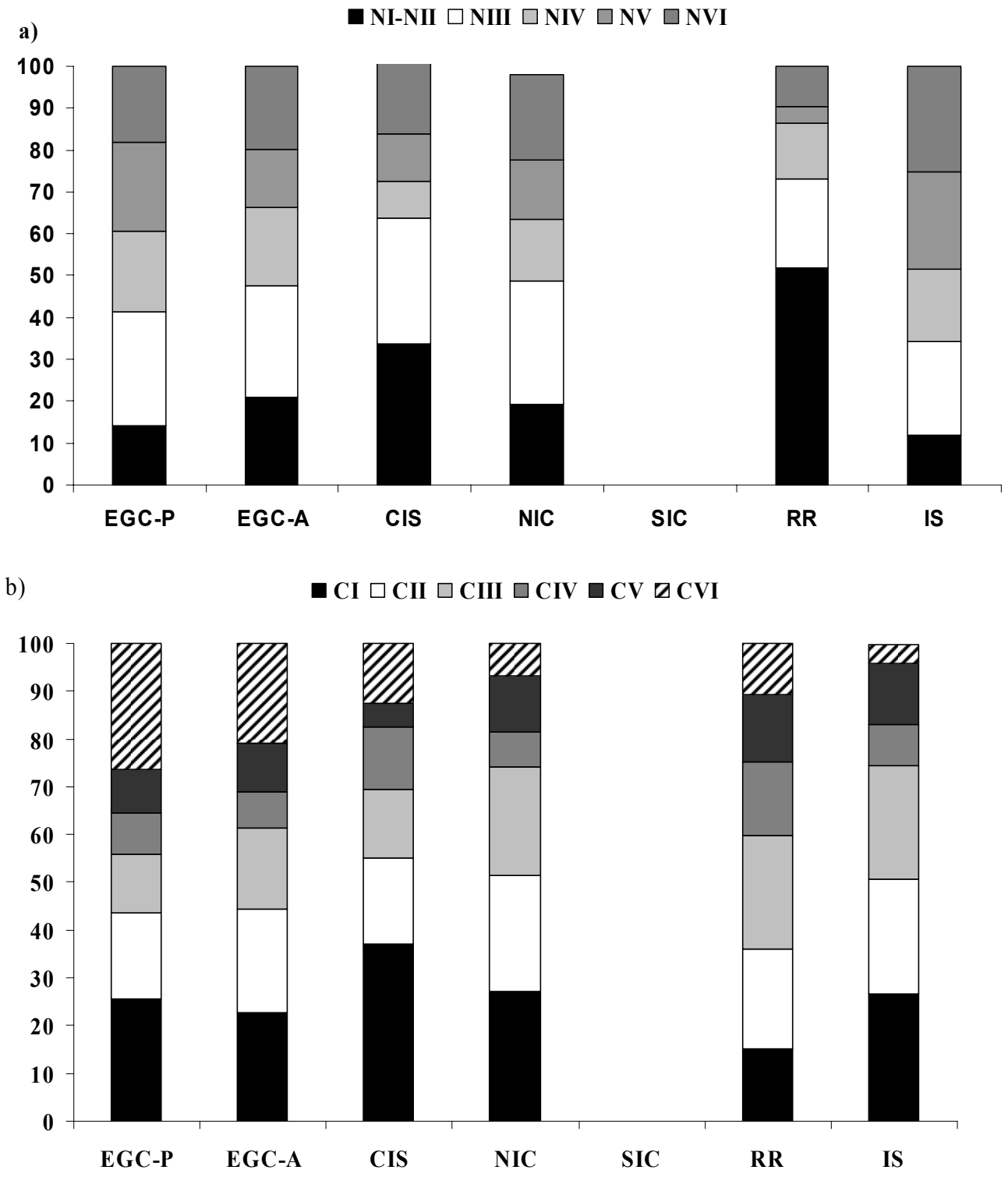

a)
NI-NII
NIII
NIV
NV
NVI
100
90
80
70
60
50
40
30
20
10
0
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS
b)
CI
CII
CIII
CIV
CV
CVI
100
90
80
70
60
50
40
30
20
10
0
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS

Fig. 5:

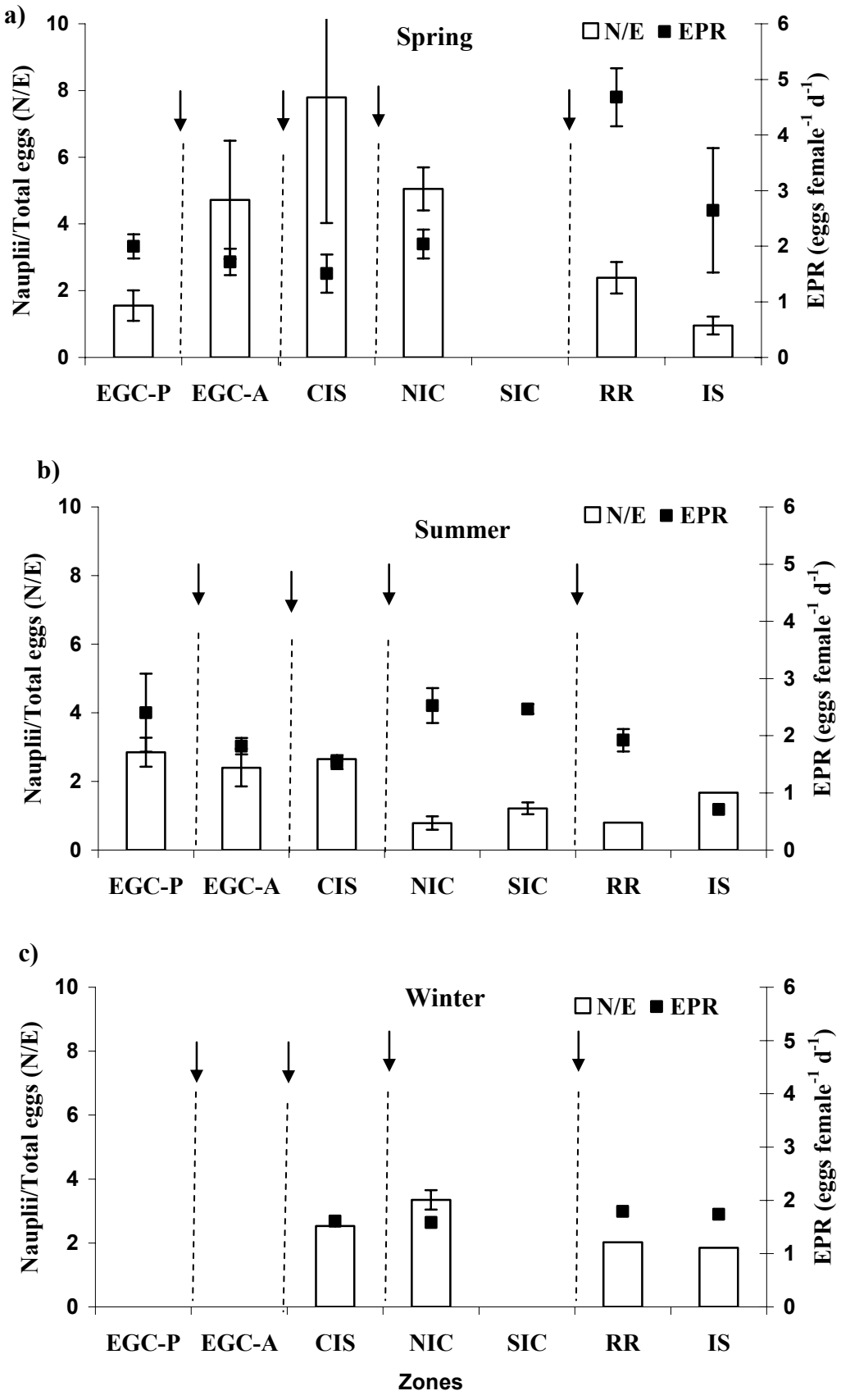

a)
Spring
N/E
EPR
Nauplii/Total eggs (N/E)
EPR (eggs female-1 d-1)
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS
b)
Summer
N/E
EPR
Nauplii/Total eggs (N/E)
EPR (eggs female-1 d-1)
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS
c)
Winter
N/E
EPR
Nauplii/Total eggs (N/E)
EPR (eggs female-1 d-1)
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS
Zones

Fig. 6:

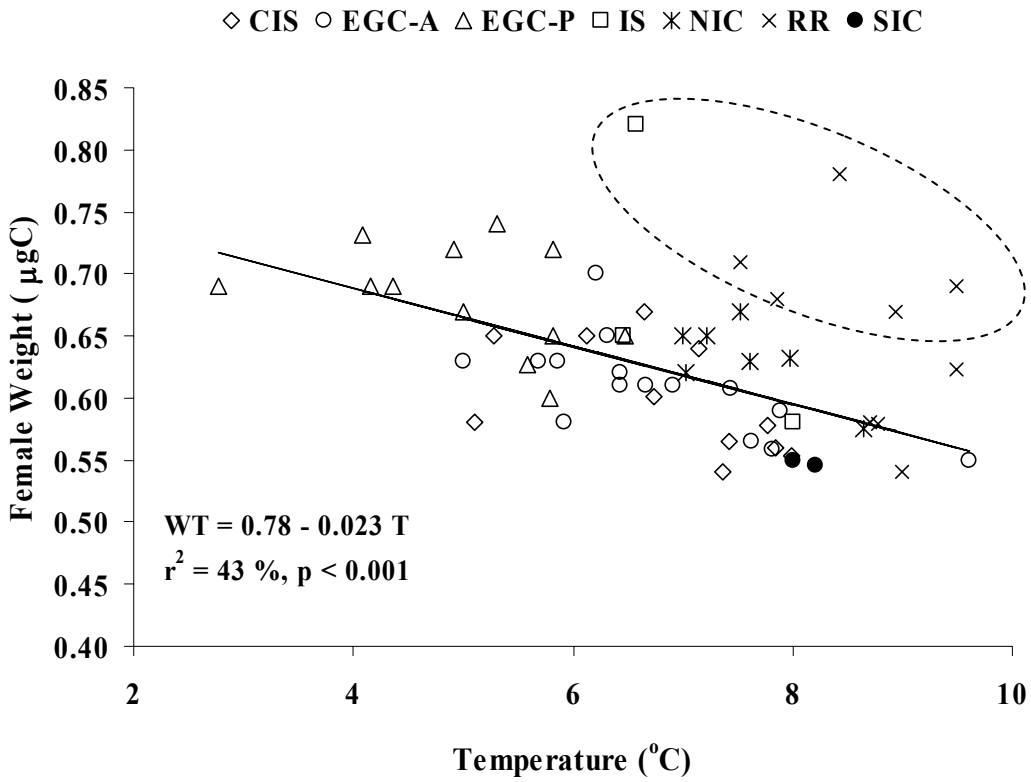

◇ CIS ○ EGC-A △ EGC-P □ IS ✳ NIC × RR ● SIC
Female Weight (µgC)
0.85
0.80
0.75
0.70
0.65
0.60
0.55
0.50
0.45
0.40
WT = 0.78 - 0.023 T
r2 = 43 %, p < 0.001
2
4
6
8
10
Temperature (°C)

Fig. 7:

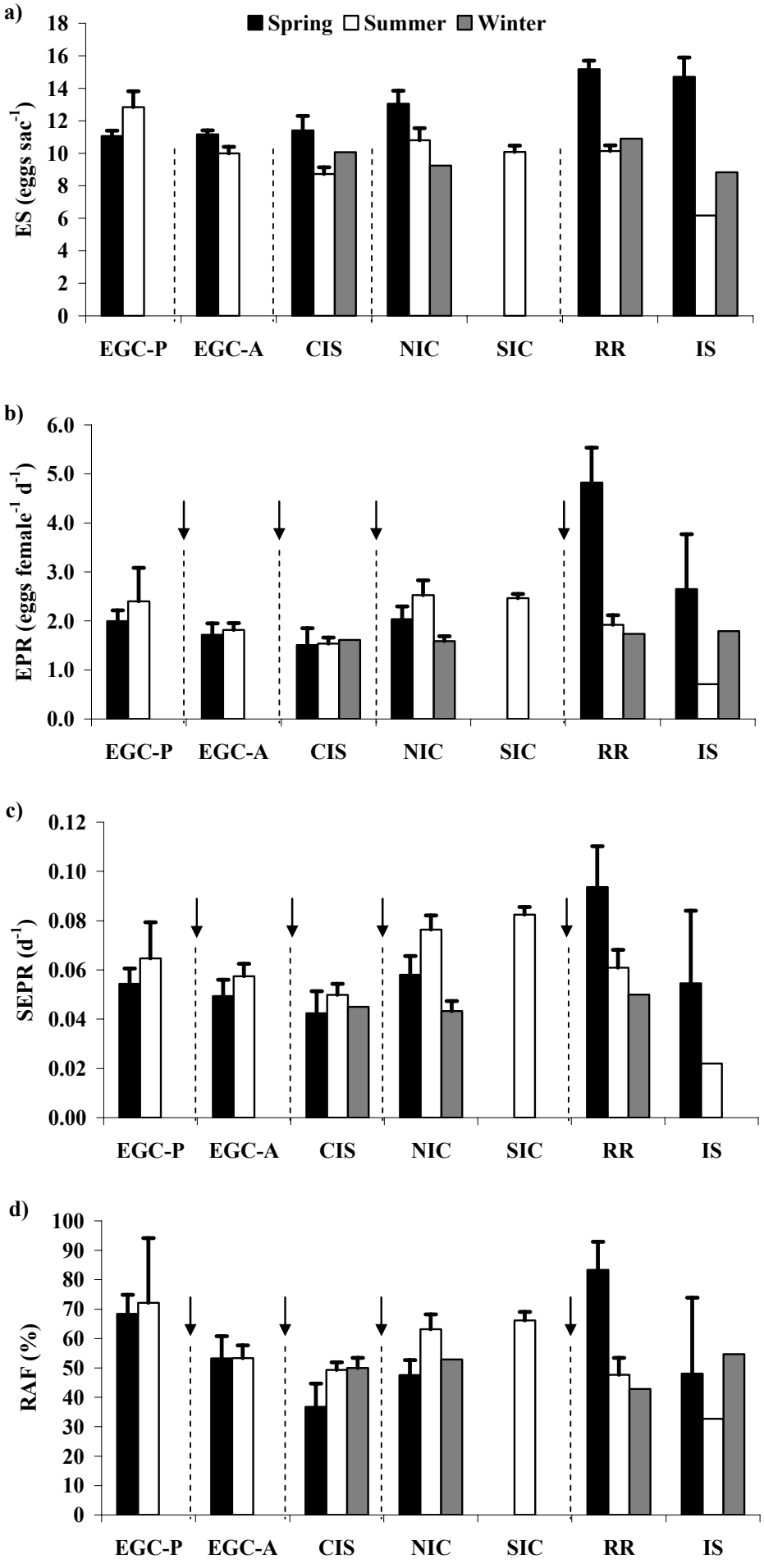

a)
Spring
Summer
Winter
ES (eggs sac-1)
18
16
14
12
10
8
6
4
2
0
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS
b)
EPR (eggs female-1 d-1)
6.0
5.0
4.0
3.0
2.0
1.0
0.0
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS
c)
SEPR (d-1)
0.12
0.10
0.08
0.06
0.04
0.02
0.00
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS
d)
RAF (%)
100
90
80
70
60
50
40
30
20
10
0
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS

Fig. 8:

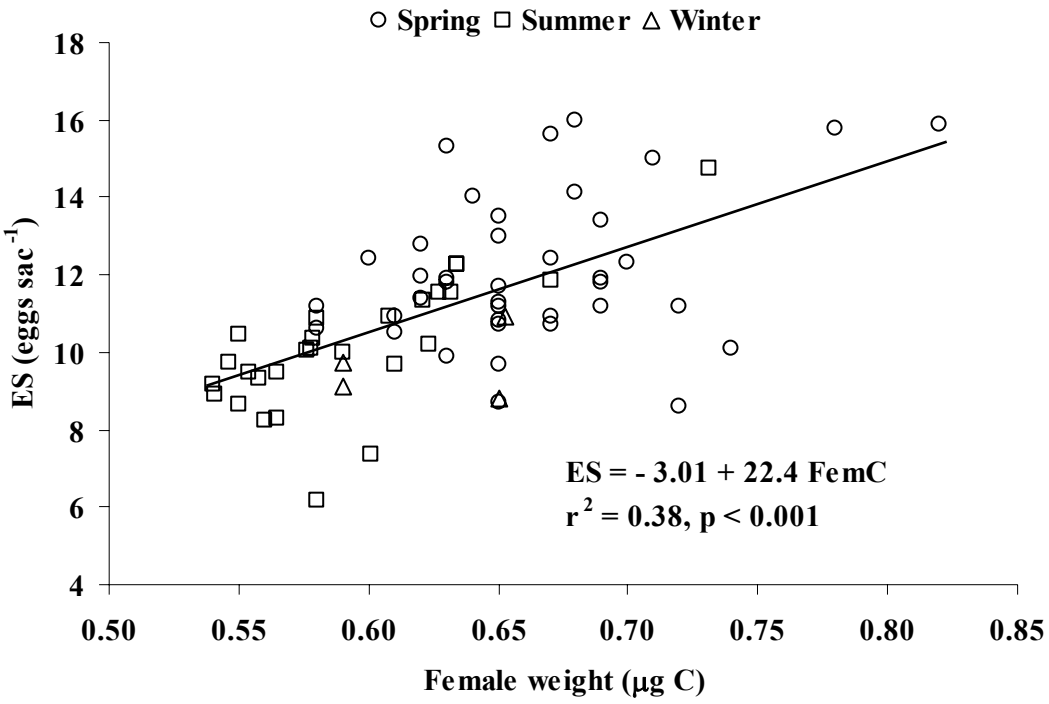

Spring Summer Winter
ES (eggs sac-1)
ES = - 3.01 + 22.4 FemC
r2 = 0.38, p < 0.001
Female weight (µg C)

Fig. 9:

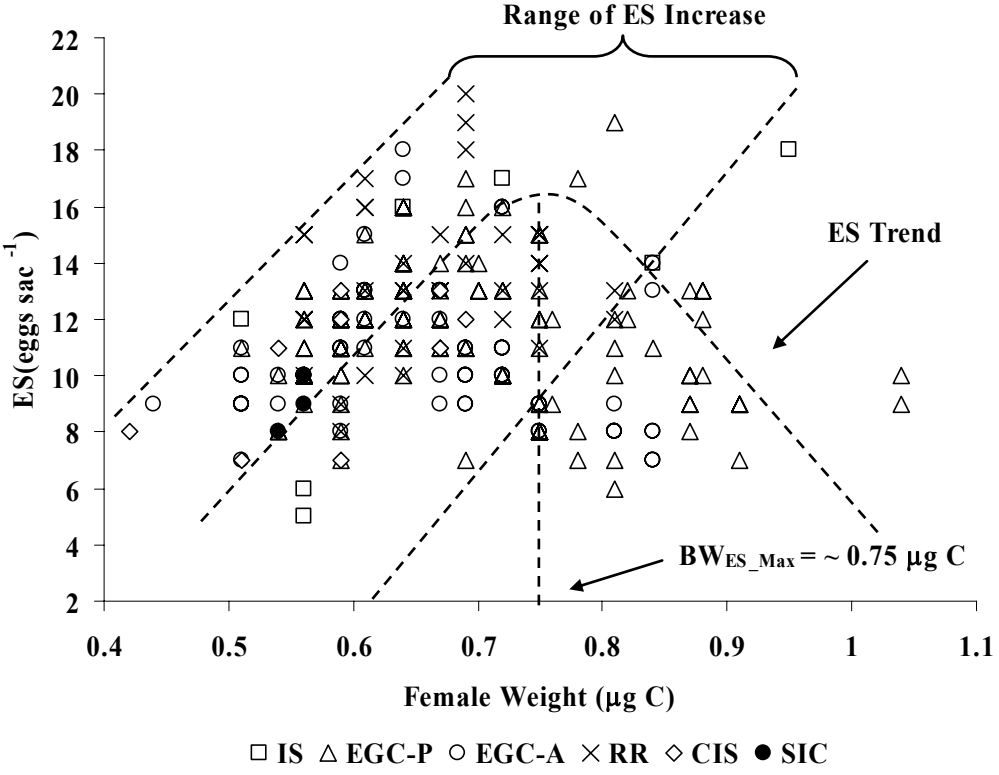

Range of ES Increase
ES Trend
BWES_Max = ~ 0.75 µg C
ES(eggs sac-1)
Female Weight (µg C)
IS EGC-P EGC-A RR CIS SIC

Fig. 10:

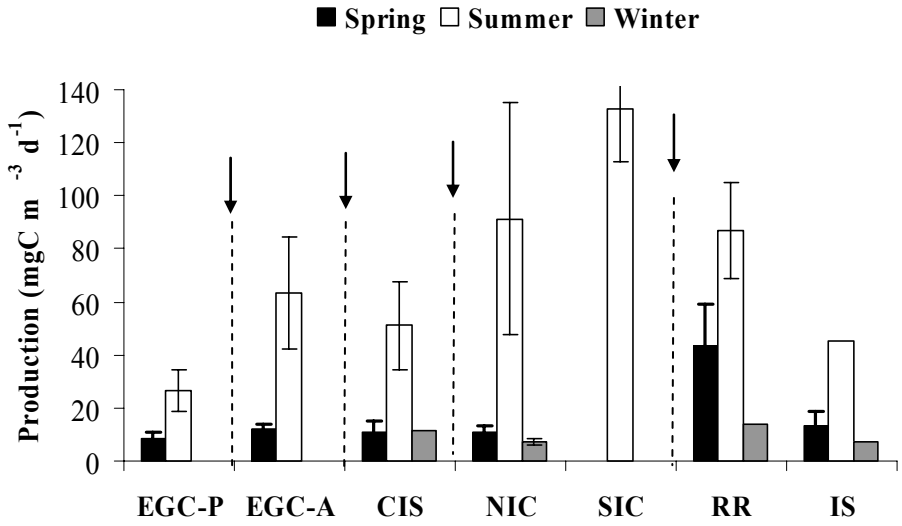

Spring
Summer
Winter
Production (mgC m -3 d-1)
140
120
100
80
60
40
20
0
EGC-P
EGC-A
CIS
NIC
SIC
RR
IS

Fig. 11:

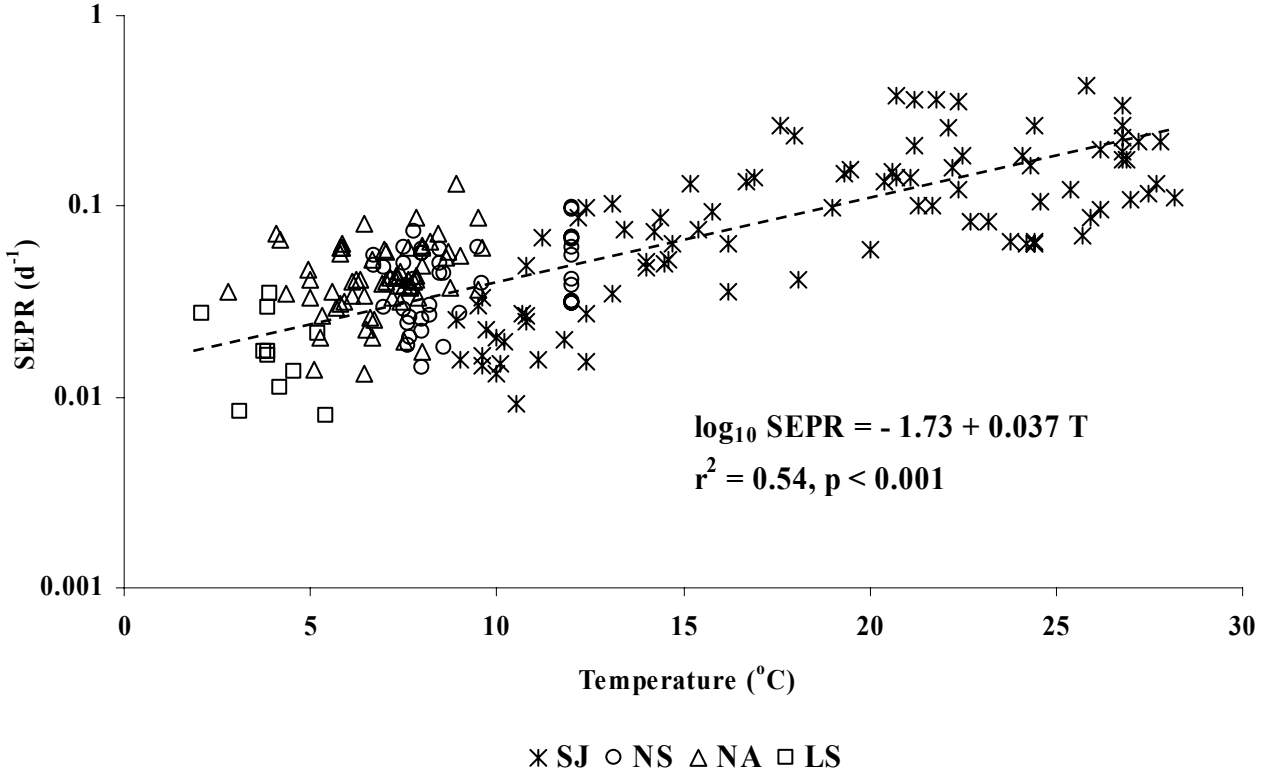
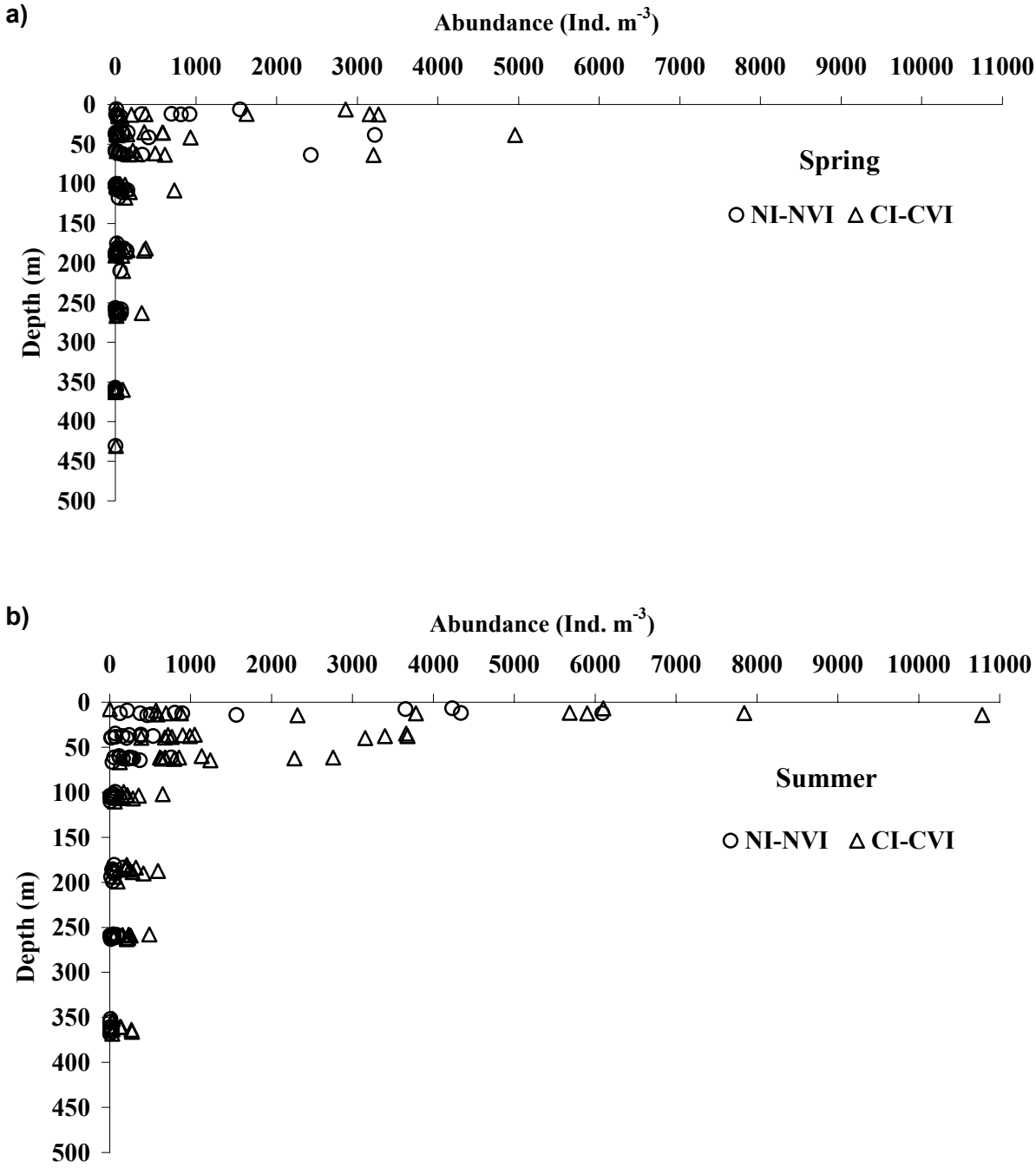

1
0.1
0.01
0.001
SEPR (d-1)
log10 SEPR = - 1.73 + 0.037 T
r2 = 0.54, p < 0.001
0
5
10
15
20
25
30
Temperature (°C)
SJ
NS
NA
LS

Fig. 12:


a)
Abundance (Ind. m-3)
0 1000 2000 3000 4000 5000 6000 7000 8000 9000 10000 11000
Depth (m)
0 50 100 150 200 250 300 350 400 450 500
Spring
NI-NVI CI-CVI
b)
Abundance (Ind. m-3)
0 1000 2000 3000 4000 5000 6000 7000 8000 9000 10000 11000
Depth (m)
0 50 100 150 200 250 300 350 400 450 500
Summer
NI-NVI CI-CVI