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Biogeography of key mesozooplankton species in the North Atlantic and egg production of *Calanus finmarchicus*

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Abstract. Here we present a new, pan-North-Atlantic compilation of data on key mesozooplankton species, including the most important copepod, *Calanus finmarchicus*. Distributional data of eight representative zooplankton taxa, from recent (2000–2009) Continuous Plankton Recorder data, are presented, along with basin-scale data of the phytoplankton colour index. Then we present a compilation of data on *C. finmarchicus*, including observations of abundance, demography, egg production and female size, with accompanying data on temperature and chlorophyll. This is a contribution by Canadian, European and US scientists and their institutions: http://doi.pangaea.de/10.1594/PANGAEA.820732, http://doi.pangaea.de/10.1594/PANGAEA.824423, http://doi.pangaea.de/10.1594/PANGAEA.828393 (please also see Melle et al., 2013; Castellani and Licandro, 2013; Jónasdóttir et al., 2014).

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1 Introduction

In this *ESSD* we present recent spatial distribution data, based on Continuous Plankton Recorder (CPR) observations (Beaugrand, 2004) for key meso- and macrozooplankton taxa in the northern North Atlantic Ocean (Fig. 1a). A full listing of zooplankton species diversity from CPR samples is provided by the Continuous Plankton Recorder Survey Team (2004). The key zooplankton taxa collated here are the copepods *Calanus finmarchicus*, *C. helgolandicus*, *C. hyperboreus*, *Pseudocalanus* spp. and *Oithona* spp., the gastropod Thecosomata species, the euphausid species, and the gelatinous zooplankton in the phylum Cnidaria. These taxa are representative of the most important multicellular zooplankton groups in the northern North Atlantic based on their abundance and on the roles they play within food webs and biogeochemical cycles (see Melle et al., 2014, for more details).

The copepod *Calanus finmarchicus* is perhaps the most ecologically significant, and certainly the most-studied, of all of the zooplankton species in the North Atlantic. *C. finmarchicus* is the subject of over 1000 research articles since the revised edition of Marshall and Orr's book (1972), and it has been the target species of several previous basin-scale research programs, including Investigations of *C. finmarchicus* migrations between oceanic and shelf seas off northwest Europe (ICOS: e.g. Heath et al., 1999), Trans Atlantic Studies of *Calanus finmarchicus* (TASC: e.g. Tande and Miller, 2000) and the Global Ocean Ecosystem Dynamics program (GLOBEC: e.g. Gifford et al., 2010), as well as the ongoing EURO-BASIN program. By compiling cross-basin North Atlantic data sets, we aim to build the foundation for ongoing and future research on the influence of habitat change, including climate forcing, on the distribution and abundance of this species.

2 Materials and methods

2.1 Hydrography and chlorophyll measurements and analyses

CTD (conductivity–temperature–depth) probes were used to collect hydrographic data (temperature and salinity) at all sampling stations (Fig. 1b, c). Water samples for measurements of chlorophyll *a* concentration were collected using water bottles on a rosette on the CTD probe or on a hydrowire. At most sites the hydrographic and chlorophyll samples were taken in concert with the zooplankton net samples. CTD profiling depths and water bottle depths varied among sampling sites. Methodologies for the determination of chlorophyll *a* concentrations are described in publications or can be retrieved from the data provider associated with each station as shown in Table 1. Temperatures (°C) were averaged over various depth ranges, while chlorophyll concentrations were either integrated (mg m^{-2}) or averaged (mg m^{-3}) over various depth ranges, as indicated in Melle et al. (2014). At each site where time series measurements were made, temperatures and chlorophyll concentrations were first averaged over 14-day periods within a given year and then for each 14-day period for all years.

2.2 Mapping of key species with CPR

The CPR survey is an upper layer plankton monitoring program that has regularly collected samples, at monthly intervals, in the North Atlantic and adjacent seas since 1946 (Warner and Hays, 1994). Water from approximately 6 m depth (Batten et al., 2003a) enters the CPR through a small aperture at the front of the sampler and travels down a tunnel, where it passes through a silk filtering mesh of 270 µm before exiting at the back of the CPR. The plankton filtered on the silk is analysed in sections corresponding to 10 nautical miles (approx. 3 m^3 of seawater filtered) and is microscopically identified (Jonas et al., 2004). In the current *ESSD* we present CPR data that represent basin-scale distributions of *C. finmarchicus* (CV-CVI), *C. helgolandicus* (CV-CVI), *C. hyperboreus* (CV-CVI), *Pseudocalanus* spp. (CVI), *Oithona* spp. (CI-CVI), total euphausiida, total pteropoda and the presence or absence of Cnidaria (Fig. 2). Monthly data collected between 2000 and 2009 were gridded using the inverse-distance interpolation method (Isaaks and Srivastava, 1989), in which the interpolated values were the nodes of a 2° by 2° grid. The resulting 12-monthly matrices were then averaged within the year and the data log-transformed (i.e. $\log_{10}(x+1)$). The phytoplankton colour index (PCI), which is a visual assessment of the greenness of the silk, is used as an indicator of the distribution of total phytoplankton biomass across the Atlantic Basin (Batten et al., 2003b; Richardson et al., 2006). After comparing the distribution of *Calanus finmarchicus* by CPR and vertical-net sampling, Melle et al. (2014) concluded that maximum *C. finmarchicus* abundances are found in the deep basins of the Norwegian and Labrador seas somewhat north of the CPR sampling routes. For this reason, since 2008, the spatial coverage of CPR monitoring has been expanded to cover the core areas of *C. finmarchicus* distribution in the Norwegian Sea. These data are not included in the present *ESSD*.

2.3 Seasonal dynamics and demography of *Calanus finmarchicus* by net sampling

Seasonal abundances and the demography of *Calanus finmarchicus* were derived from samples taken at sites across the North Atlantic (Table 1, Fig. 1b). The sampling sites include both coastal and oceanic stations and vary from relatively cold to warm water locations. Sampling frequency also differs among sites; the more easily accessed coastal sites were generally visited more frequently than the offshore sites. An overview of sampling site characteristics, sampling gear and methods is provided in Table 1. At all sites abundances of developmental stages were averaged over 14-day

Table 1. Metadata for *Calanus finmarchicus* sampling stations and transects in the North Atlantic. The column "Analyses" refers to the usage of data in Melle et al. (2014).

Sampling site	Site no.	Location	Latitude	Longitude	Bottom depth (m)	Water mass	Shelf/slope/ oceanic	Max. sampling depth (m)	Gear	Mesh size (µm)	Years	No. stations	Analyses[b]	Data provider
Jeffreys Ledge	1	Gulf of Maine	42.83° N	70.31° W	50	Coastal	Shelf	45	0.75 m Ring net	200	2003–2008	1	M/D	BCO-DMO, USA
Wilkinson Basin	2	Gulf of Maine	42.86° N	69.86° W	250	Coastal	Shelf	240	0.75 m Ring net	200	2005–2008	1	M/D/S	BCO-DMO, USA
AZMP lines	3	Gulf of St. Lawrence, Scotian Shelf, Newfoundland Shelf	–	–	–	Coastal, Atlantic	Shelf	Btm. or 1000	0.75 m Ring net	200	1999–2009	108	M	DFO, Canada
AZMP Prince 5	4	Bay of Fundy	44.93° N	66.85° W	95	Coastal	Shelf	Btm. or 1000	0.75 m Ring net	200	1999–2009	1	D	DFO, Canada
AZMP Station Halifax 2	5	Scotian Shelf	44.27° N	63.32° W	155	Coastal	Shelf	Btm.	0.75 m Ring net	200	1999–2009	1	M/D/S	DFO, Canada
AZMP Rimouski Station	6	Lower St. Lawrence Estuary	48.67° N	68.58° W	340	Coastal	Shelf	320	1 or 0.75 m Ring net	333, 73, 200	1994–2008	1	M/D/S	DFO, Canada
AZMP Anticosti Gyre	7	Northwest Gulf of St. Lawrence	49.72° N	66.25° W	340	Coastal	Shelf	330	0.75 m Ring net	200	1999–2003	1	M/S	DFO, Canada
AZMP Gaspé Current	8	Northwest Gulf of St. Lawrence	49.24° N	66.20° W	185	Coastal	Shelf	180	0.75 m Ring net	200	1999–2003	1	M/S	DFO, Canada
AZMP Shediac	9	Southern Gulf of St. Lawrence	47.78° N	64.03° W	84	Coastal	Shelf	Btm.	0.75 m Ring net	200	1999–2009	1	D	DFO, Canada
AZMP Station 27	10	Newfoundland Shelf	47.92° N	52.98° W	175	Coastal, Atlantic	Shelf	Btm.	0.75 m Ring net	200	2000–2009	1	M/S	DFO, Canada
Labrador Shelf	11	Labrador Shelf	54.22° N	55.04° W	140–200	Arctic	Shelf	100	0.75 m Ring net	200	1995–2006	1-7	M/S	DFO, Canada
Labrador Slope	12	Labrador Slope	55.27° N	53.98° W	1000–3000	Arctic, Atlantic	Slope	100	0.75 m Ring net	200	1995–2006	< 7	M/S	DFO, Canada
Central Labrador Sea	13	Labrador Sea	57.37° N	51.80° W	3000–3700	Atlantic, Arctic	Oceanic	100	0.75 m Ring net	200	1995–2006	4–13	M/S	DFO, Canada
Eastern Labrador Sea	14	Labrador Sea	59.99° N	48.90° W	2800–3600	Atlantic, Arctic	Oceanic/Slope	100	0.75 m Ring net	200	1995–2006	0–9	M/S	DFO, Canada
West Greenland shelf	15	West Greenland	60.51° N	48.30° W	130	Arctic	Shelf	100	0.75 m Ring net	200	1995–2006	< 5	M/S	DFO, Canada
MarProd Program	16	Irminger Sea	62° N	32.20° W	> 3000	Atlantic	Oceanic	> 3000	ARIES	200	2001–2002	–	M	Heath et al. (2008)
Vestmannaeyjar	17	Southern Iceland	63.37° N	19.92° W	200	Atlantic	Shelf	190	Bongo	200	1997–1998	1	M/D/S	MRI, Iceland
Siglunes Section	18	Northern Iceland	67° N	18.83° W	80–1045	Atlantic, Arctic	Shelf/slope	100 or btm.	Bongo	335	1993–1994	8	M/S	MRI, Iceland
Langanes-NA	19	Northeastern Iceland	67.5° N	13.27° W	188–1860	Atlantic, Arctic	Shelf/oceanic	100	Bongo	200	1995–1996	6	M/S	MRI, Iceland
Faroe Shelf Station	20	Faroese Shelf	62.05° N	6.62° W	55	Atlantic	Shelf	50	WP-2/Bongo	100, 200	1997, 2004	1	M/D/S	FAMRI, Faroes
Faroe Oceanic Section	21	Southern Norwegian Sea	63.59° N	6.08° W	550–3300	Atlantic, Arctic	Oceanic	50	WP-2	200	1990–2009	11	M	FAMRI, Faroes
Foinaven	22	Faroe–Shetland Channel	60.32° N	4.23° W	500	Atlantic	Slope	330–500	Bongo	200	1997–1998	1	M/D/S	Heath et al. (2000)
Svinøy Section, Arctic	23	Central Norwegian Sea	64.51° N	0.36° E	2932	Arctic	Oceanic	200	WP2	180	1996–2006	1–2[a]	M/S	IMR, Norway
Svinøy Section, Atlantic	24	Eastern Norwegian Sea	63.52° N	2.66° E	1453	Atlantic	Slope/oceanic	200	WP2	180	1996–2006	7–8[a]	M/D/S	IMR, Norway
Weather Station Mike	25	Eastern Norwegian Sea	66° N	2° E	> 1600	Atlantic	Oceanic	200	Multinet/WP2	180	1997–1998	1	M/D/S	IMR, Norway
Svinøy Section, coastal	26	Eastern Norwegian Sea	62.82° N	4.21° E	501	Coastal	Shelf	200 or btm.	WP2	180	1996–2006	4–5[a]	M/D/S	IMR, Norway
Saltenfjorden	27	Northern Norwegian Shelf	67.23° N	13.65° E	400	Coastal	Shelf	370	WP2	200	1997–1998	1	M/S	Heath et al. (2000)
Stonehaven	28	North Sea, Scotland Shelf	57° N	2° W	47	Coastal	Shelf	45	Bongo	200	1997–2008	1	M/S	Heath et al. (2000)
Murchinson	29	North Sea	61.50° N	1.67° E	170	Atlantic	Oceanic	150	Bongo	200	1997–1998	1	M/D/S	Heath et al. (2000)
Arendal St. 2	30	Southern Norway Shelf	58.38° N	8.82° E	105	Coastal	Shelf	50	WP2	180	1994–2010	1	M/S	IMR, Norway
Station India	31	Northeast ATL	59° N	19° W	2000	Atlantic	Oceanic	600	LHPR	270	1971–1975	1	M	Irigoien (2000)

[a] Number of stations out of a total of 17, based on water mass distribution. [b] M: mortality; D: dormancy; S: seasonal dynamics.
AZMP: Atlantic Zone Monitoring Program; ATL: Atlantic; bt: bottom; BCO-DMO: Biological and Chemical Oceanography Data Management Office; DFO: Fisheries and Oceans Canada; MRI: Marine Research Institute; FAMRI: Faroe Marine Research Institute; IMR: Institute of Marine Research; ARIES: Autosampling and Recording Instrumented Environmental Sampling System; LHPR: Longhurst Hardy plankton recorder

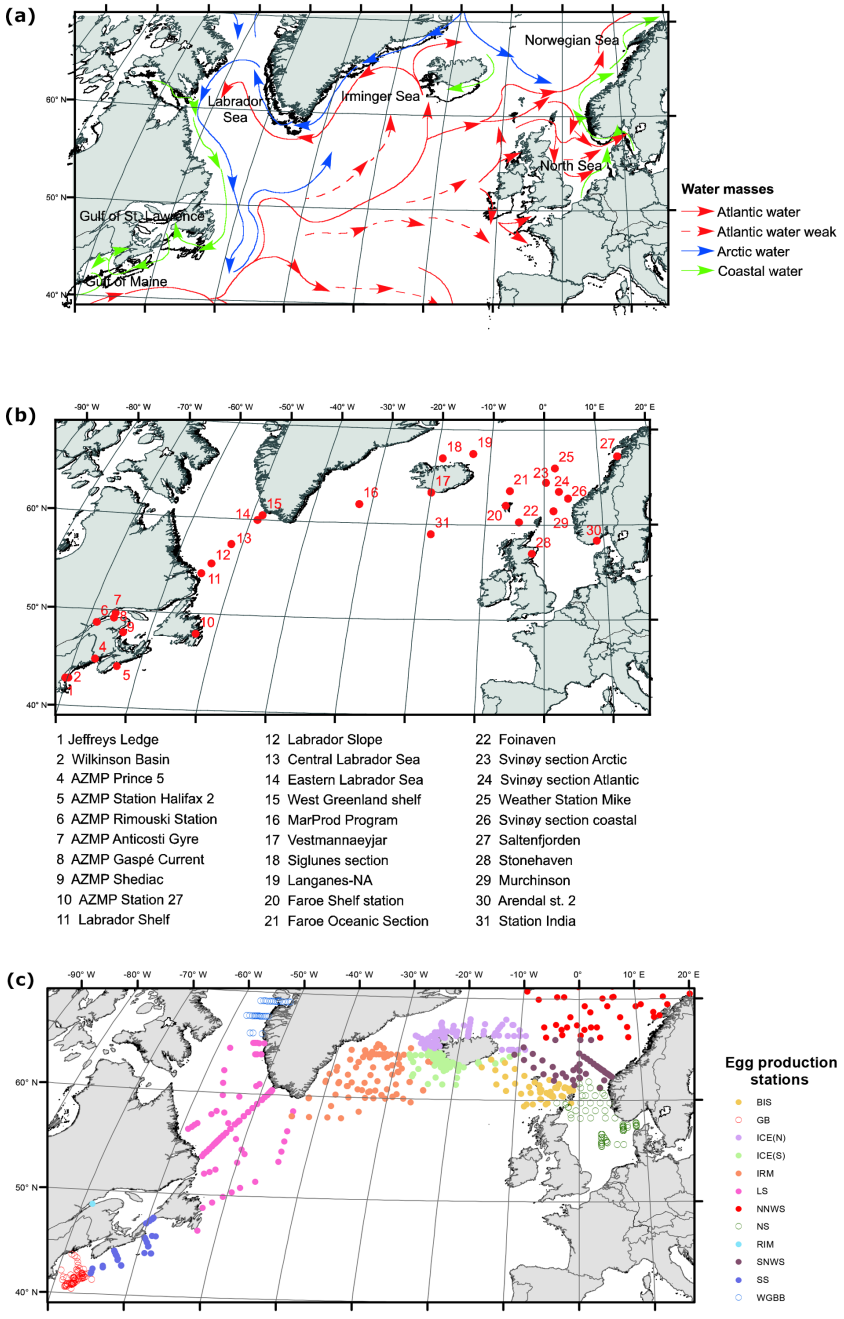

Figure 1. Panel **(a)**: the northern North Atlantic Ocean, major warm and cold water currents, and important seas. Panel **(b)**: locations of demographic stations and transects listed in Table 1. Panel **(c)**: locations of observations of *C. finmarchicus* egg production rates (and usually adult body size, chlorophyll *a* concentrations and temperature).

periods within the year and then for the same periods over all years.

2.4 *Calanus finmarchicus* egg production and female size

Observations of egg production rates (EPRs) for female *Calanus finmarchicus* were compared for different regions of the North Atlantic (Fig. 1c). The regions were diverse in size and sampling frequency, ranging from a fixed time series station in the Lower St Lawrence Estuary, off Rimouski (RIM), where nearly 200 experiments were carried out between May and December from 1994 to 2006, to a large-scale survey in the northern Norwegian Sea (NNWS), where about 50 experiments were carried out between April and June from 2002 to 2004. For this compilation the stations were grouped

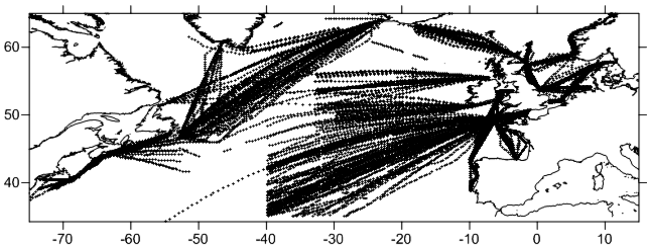

Figure 2. CPR data sampling routes, 2000–2009.

mostly along geographic lines, with only limited attention being paid to oceanographic features. There is some overlap between regions, however, where stations were sometimes kept together when they were sampled on the same cruise. Furthermore, some stations other than RIM were occupied more than once during different years and/or in different seasons, although not shown in Fig. 1c. Some of the data included here have appeared in published papers, and the citations are included. Previously unpublished data were also provided by C. Broms, E. Gaard, A. Gislason, E. Head and S. Jónasdóttir. Data have been submitted to PANGEA (Data Publisher for Earth & Environmental Science) as averages by area.

Egg production in *C. finmarchicus* occurs in spawning bouts, which are of relatively short duration and may occur once or more per day (Marshall and Orr, 1972; Hirche, 1996). While there is evidence for diel spawning periodicity in the sea (Runge, 1987; Runge and de Lafontaine, 1996), females incubated in dishes for the first 24 h after capture do not always show a consistent night-time release of eggs, as they did for *Calanus pacificus* (Runge and Plourde, 1996; Head et al., 2013). Because of the potential for diel egg-laying behaviour, the vast majority of egg production experiments have been carried out by incubating freshly caught females for 24 h. It has been shown that female *Calanus* that are kept and fed in vitro and then transferred to an incubation chamber lay the same number of eggs over the next 24 h whether or not they are fed (Plourde and Runge, 1993; Laabir et al., 1995). Thus, it has been assumed that average egg production rates of freshly caught females are the same during the 24 h following capture as they would have been in situ (Runge and Roff, 2000). In this study we include only results from such 24 h incubation experiments, and we term the eggs laid during these 24 h periods "clutches", even though they may originate from more than one spawning bout, and we refer to the number of eggs laid by one female during a 24 h period as the clutch size (CS). In most experiments 20–30 females were incubated individually in separate chambers, and the proportion of females that laid eggs over 24 h is referred to as the "spawning frequency" (SF), which is here expressed as a percentage per day. EPRs reported here were calculated by individual contributing investigators either simply as the sum of all of the eggs produced in an experiment divided by the number of females incubated and the average incubation time (generally 1 day) or as the average of the EPRs calculated for each experimental female individually, which takes account of differences in incubation times for individual females. For the WGBB (West Greenland–Baffin Bay) most experiments were carried out using prolonged incubation periods (e.g. 36–48 h), often with relatively few females ($\sim$ 10). For several of the analyses carried out here it was necessary to include the results of these prolonged incubations.

As batches of eggs are released into the water column in situ, they may hatch and develop or they may be consumed by local predators, including female *C. finmarchicus* themselves, which are sometimes the most abundant potential predators (Basedow and Tande, 2006). To avoid cannibalism, incubations are generally set up so as to minimize contact between the females and the eggs they are laying. This has been done by the investigators contributing to this work using one of five techniques. In Method A females are incubated individually in 45–50 mL of seawater in 6–10 cm diameter petri dishes. The eggs sink rapidly to the bottom surface, where they are unlikely to be caught up in the females' feeding currents. Method B involves incubating females individually in similar but smaller "multiwell" chambers, which have a volume capacity of 10–15 mL. In Method C females are placed individually (or in groups of two or three) in cylinders, fitted with mesh screens on the bottom, which are suspended in beakers of 400–600 mL capacity (Gislason, 2005). The eggs sink through the mesh and are thus separated from the females. Method D represents a modification of Method C, in that there is flow of seawater through the chamber (White and Roman, 1992). Finally, in Method E, individual (or groups of two or three) females are incubated in bottles or beakers (up to 1 L capacity), without screening (Jónasdóttir et al., 2005). For Method E the vessels are kept upright and it is assumed that the eggs will sink out and become unavailable to the females relatively rapidly.

There have been relatively few comparisons of these different experimental methods. Cabal et al. (1997) found that female *C. finmarchicus* from the Labrador Sea incubated individually in 50 mL petri dishes (Method A) or 80 mL bottles (Method E) produced similar numbers of eggs after 3 days, although only three experiments were done, and over the first 24 h, CSs were larger for Method A. They also found that over 24 to 72 h periods, groups of females in screened cylinders within large volume chambers (Method C) gave higher egg production rates than those in chambers without screens (Method E) did. Runge and Roff (2000) reported that egg laying in dishes (Method A) yielded similar egg production rates to the egg laying of groups of 10–15 females incubated in 1.5 L screened beakers (Method C). However, the beaker egg production estimates declined dramatically relative to dish estimates in rough weather, presumably due to increased mixing in beakers and therefore higher loss due to cannibalism. More recently, Plourde and Joly (2008) found that suspending a mesh screen within petri dishes 2 mm above the

bottom made no difference to the number of eggs produced by female *C. finmarchicus* over 24 h, although it did increase the number of eggs recovered from *Metridia longa* females, which could be seen swimming actively and sweeping the bottom with their mouthparts in the unscreened dishes. In the northeast Atlantic, at Ocean Weather Station M (included in our southern Norwegian Sea (SNWS) region), B. Niehoff (personal communication, 2013) found that females incubated for 24 h in multiwells (Method B) had similar CSs to those incubated according to Method C. None of these studies compared all methods and the fact that the NW Atlantic groups have used Method A, while the central and NE Atlantic groups have used mainly Methods C, D or E introduces a question as to whether methodological differences might have contributed to the differences found among the CSs and EPRs in the different regions. Such an analysis is not possible based on the data currently available, however, and the topic will not be considered further in this work, although it merits further attention.

Another point on which investigators differed is how they dealt with small clutches. For the Georges Bank (GB), Rimouski station (RIM) and Scotian Shelf (SS) regions and for the Labrador Sea (LS) data, provided by R. Campbell, clutches of < 6 eggs were routinely not included in the data sets on CSs, since they were regarded as being the result of interrupted spawning events. These small clutches were apparently very rare (J. Runge, personal communication, 2013), and indeed for the LS data reported by Head et al. (2013) clutches of < 6 eggs accounted for only 32 of the 1324 clutches observed, i.e. 2 %. For regions farther east, however, the proportions of clutches of < 6 eggs were generally larger: between 13 % (SNWS) and 33 % (northern Norwegian Sea, NNWS). Because of this difference in data reporting, CSs of < 6 eggs were excluded from the calculations of average CSs for all regions. Small clutches were, however, included by all investigators in their calculations of EPRs.

Previous studies of egg production have shown a significant link between clutch size and female size (Runge and Plourde, 1996; Campbell and Head, 2000; Jónasdóttir et al., 2005; Runge et al., 2006), and most of the data sets provided for this work included measurements of the prosome lengths for each individually incubated female for each egg production experiment, along with each corresponding individual clutch size (Melle et al., 2014). One exception to this was in the SNWS region (data from Ocean Weather Station M), for which average female prosome lengths were determined for groups of females that had not been used in experiments but that had been collected on the same day. In addition, there were no measurements of prosome lengths for some data from the region "Between Scotland and Iceland" (BIS) and the SNWS and NNWS regions. Furthermore, prosome lengths were not measured for all clutch sizes enumerated at RIM.

Egg production rates for the experiments carried out within a given region were averaged seasonally. The rationale for the grouping of months into seasons within each region was based partly on observations of seasonal cycles of temperature and chlorophyll concentration, partly on what could be ascertained from the literature about the timing of the appearance of females at the surface after overwintering, and partly on the availability of data. The spring months cover the period when water temperatures are increasing, when the spring bloom is starting or is in progress, when diatoms dominate the female diet, and when the overwintered (G0) generation of females is abundant in the surface layers. Spring is the time when community egg production rates, although maybe not individual rates, are expected to be highest. In summer, temperatures are higher and the bloom may still be in progress, but the female diet may be more varied and some females of the new year's generation may be present. In autumn and winter relatively few females are in the near-surface layers and phytoplankton levels are generally low.

Observations of in situ temperature and chlorophyll concentration were made at nearly all experimental stations. The original aim had been to use in situ temperatures from 5 m and chlorophyll concentrations integrated to 30 m in this study. Not all data were provided in this form, however. For example, in some data sets temperature data were surface values or 0–10 or 0–20 m averages, and chlorophyll concentrations were sometimes values integrated to 50 m. The data were standardized to a comparable format by assuming that surface, 0–10 or 0–20 m average temperatures were the same as 5 m temperatures and that the chlorophyll concentrations were uniform throughout the 0–50 m depth range. These assumptions are likely to be most appropriate in spring and winter, when mixed layers are relatively deep.

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