Seasonality of *Oithona similis* and *Calanus helgolandicus* reproduction and abundance: contrasting responses to environmental variation at a shelf site

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Abstract

The pelagic copepods *Oithona similis* and *Calanus helgolandicus* have overlapping geographic ranges, yet contrast in feeding mode, reproductive strategy, and body size. We investigate how these contrasting traits influence the seasonality of copepod abundance and reproductive output under environmental variation, using time series data collected over 25 years at the Western Channel Observatory station L4. The proportional change in Egg Production Rate (EPR, eggs female\(^{-1}\) d\(^{-1}\)) over the annual cycle was ~10-fold and similar for both species, although EPR of *O. similis* was only ~ 11% that of *C. helgolandicus*. The timing of EPR maxima for *O. similis* coincided with increased Sea Surface Temperature (SST) in summer, likely due to a temperature-dependent brooding period. Conversely, EPR of broadcast spawning *C. helgolandicus* was more strongly related to Net Heat Flux (NHF) and diatom biomass, both parameters associated with the spring phytoplankton bloom. In both species, female body mass negatively correlated with SST, with a 7.5% reduction in body mass per °C in *C. helgolandicus* compared to just 2.3% in *O. similis*. Finally, seasonality of EPR and adult and copepodite abundance was strongly decoupled in both species, suggesting that optimum conditions for reproduction and abundance occur at different times of the year.

**Keywords**: functional trait, egg production rate, *Oithona similis*, *Calanus helgolandicus*, Western Channel Observatory.
Introduction

Functional traits are characteristic features of an organism that impact fitness by mediating growth, reproduction, and survival (Litchman et al., 2013). Such traits can be used to identify links between population responses and the processes that drive them (McGill et al., 2006). For major copepod species, much of our biological knowledge on their dynamics has been based on single species studies. Examples of such studies for the cyclopoid *Oithona similis* include Sabatini and Kiørboe (1994); Fransz and Gonzalez (1995); Castellani et al (2005a); Dvoretsky and Dvoretsky (2009a,b). The calanoid *Calanus helgolandicus* overlaps in range with *O. similis* but contrasts in several key traits. However, knowledge of these traits is again based heavily on autecological studies (e.g. Pond et al., 1996; Irigoien et al., 2000a,b; Irigoien and Harris, 2003; Rey-Rassat et al., 2004; Maud et al., 2015). Despite recent establishment of copepod trait databases (Benedetti et al., 2015; Brun et al., 2017) and meta-analyses (Horne et al., 2016), it remains difficult to identify the degree to which contrasts in feeding and egg production rates (Benedetti et al., 2015; Brun et al., 2016; 2017), or temperature-body size response (Horne et al., 2016), represent genuine contrasts in functional traits, or simply differences in environmental conditions between the respective studies.

To address this issue, we make a direct comparison of two dominant, co-existing species, *Oithona similis* and *Calanus helgolandicus*. Our study is based on the L4 time series site, a shallow, stratifying shelf site in the Western English Channel (Harris, 2010). *O. similis* is thought to exert minimal energy waiting for motile prey, such as ciliates and dinoflagellates, to enter detection range (Kiørboe, 2011). Conversely, *C. helgolandicus* is an active feeder, generating feeding currents suited to catching non-motile, diatom prey (Kiørboe, 2011). Egg Production Rate (EPR, eggs female$^{-1}$ d$^{-1}$) in brooding species such as *O. similis*, may become limited by the fact that a new clutch cannot be laid until the previous eggs hatch (Ward and Hirst, 2007). Increased temperature increases embryonic development rate, thus potentially decreasing the time from the production of one clutch to the next (Nielsen et al., 2002), and facilitating greater egg production rates in warmer
temperatures. In contrast, EPR in *C. helgolandicus*, a broadcast spawning species, is not restricted in the same way by the time interval between clutches, and therefore its fecundity may be less temperature dependent.

Temperature may also have a series of other direct and indirect effects on copepod population dynamics. One reason for this is that temperature impacts metabolism through its effects on rates of biochemical reactions (Gillooly *et al*., 2001). For example, increased respiration rate with temperature has been observed in *Oithona similis* (Castellani *et al*., 2005b) and *Calanus helgolandicus* (Hirche, 1983). Furthermore, ectothermic organisms generally mature to a smaller body size under increased temperature conditions (Atkinson, 1994; Forster *et al*., 2012), as has been observed for female *O. similis* (Castellani *et al*., 2007), and *C. helgolandicus* (Bonnet *et al*., 2009). The temperature range over which such effects occur, as well as the thermal optima for reproduction and development, vary between copepod species and geographic populations (Halsband-Lenk *et al*., 2002). The effects of temperature on copepod populations will indirectly effect their prey, by altering feeding rate (Dam and Peterson, 1988), and inducing phenological shifts in copepod populations (Atkinson *et al*., 2015). Overall, temperature is thus an important parameter to consider when investigating ecosystem dynamics.

Another physical variable connected both to temperature and plankton seasonality, is the Net Heat Flux (NHF) between the atmosphere and the ocean (Smyth *et al*., 2014). NHF incorporates air-sea temperature difference, alongside irradiance, wind speed, and water column stratification, all of which are major factors that can affect plankton community at the Western Channel Observatory (WCO) coastal station L4 (Smyth *et al*., 2014). Water column stratification in spring increases the residence time of phytoplankton in the euphotic layer (Taylor and Ferrari, 2011; Smyth *et al*., 2014), facilitating the spring phytoplankton bloom. The autumn transition to negative NHF is associated with the restriction in phytoplankton growth due to shortened day-length, lower irradiance, and turbulent mixing limiting residence times in the euphotic layer.
In measuring the response of copepods to this seasonality, Egg Production Rate (EPR) provides an index of female copepod performance, as it integrates energy uptake and assimilation. Meanwhile, changes in population abundance over time are driven by changes in both recruitment and mortality rates (Hirst and Kiørboe, 2002). *Calanus helgolandicus* EPR at station L4 has been monitored on a weekly basis since 1992, an extensive dataset to which our study contributes new data on the contrasting species *Oithona similis*. The strong seasonality at L4 makes it an ideal site for studying the impact of environmental variation on copepod population dynamics.

Our study tests two hypotheses: 1) EPR in *Oithona similis* has a stronger relationship with Sea Surface Temperature (SST), compared to *Calanus helgolandicus*, due to its temperature-dependent brooding period; and 2) *O. similis* EPR has a stronger relationship with the biomass of motile prey, while *C. helgolandicus* EPR has a stronger relationship with the biomass of non-motile prey. To test these hypotheses we used Generalised Additive Mixed Models (GAMMs) to examine and identify the non-linear relationships between the environment and EPR for *O. similis* and *C. helgolandicus*. This is an accurate identification approach that accounts for noise autocorrelation (Hastie and Tibshirani, 1990; Young *et al.*, 2001; Bruun *et al.*, 2017). We used these models to detect the threshold value of the independent variables (SST, NHF, and prey biomass), where it starts to show a significant effect on EPR. Further, we examined the seasonality of adult female and copepodite abundance, and female and egg carbon mass.
Methods

The Western Channel Observatory (WCO) station L4 is 13 km SSW of Plymouth, and has been sampled by Plymouth Marine Laboratory (PML) on a weekly basis since 1988 (Harris, 2010). There is a large amount of knowledge on the conditions at L4, with numerous publications in the literature on the L4 plankton community (e.g. Eloire et al., 2010; Highfield et al., 2010; Widdicombe et al., 2010; Atkinson et al., 2015; White et al., 2015, and references therein). The variables explored in this study, and the time period over which they have been measured, are summarised in Table I. Access to the most updated versions of the WCO time series data is available from Plymouth Marine Laboratory upon request (http://www.westernchannelobservatory.org.uk/). Original data for *Oithona similis* are provided in the Supplementary Material.

Physical parameters

Sea Surface Temperature (SST) and surface Chlorophyll *a* concentration [Chl *a*] were measured as part of the ongoing WCO time series. SST was measured with a mercury in glass thermometer until 1993. Between 1993 and 2002, SST was recorded electronically using CTD sensors. Since 2002, SST has been determined using a SeaBird SBE 19+ CTD, attached to a vertical profiler. [Chl *a*] was obtained by filtering 100 mL of surface seawater through 25 mm GF/F filters in triplicate, extracting in 90% acetone at 4°C, then analysing by Turner fluorometry, following Welschmeyer (1994). Datasets for water column temperature and surface [Chl *a*] at L4 are publicly available at the above mentioned WCO website.

Net Heat Flux (NHF) was determined between 1992 and 2016 using the methodology of Smyth *et al* (2014), as follows. Four processes control air-sea heat flux: shortwave radiation from the sun (Q$_{SW}$), outgoing longwave radiation from the sea surface (Q$_{LW}$), sensible heat transfer resulting from air-sea temperature differences (Q$_{SH}$), and latent heat transfer via evaporation of sea water (Q$_{LH}$). The Woods Hole Oceanographic Institution air-sea exchange Matlab tools (Fairall *et al*., 2003) were used to determine Q$_{SW}$, Q$_{LW}$, Q$_{SH}$ and Q$_{LH}$ (Pawlowicz *et al*., 2001), in units of W
Meteorological parameters were obtained from the European Centre for Medium Range Weather Forecasting (ECMWF) ERA-40 and Operational analyses, extracted for the grid point 50°N, 4°W. These parameters were: air temperature ($T_a$, °C), dew point ($T_d$, °C), wind-speed at 10 m (U$_{10}$, ms$^{-1}$), cloud fraction (CF, 0: clear; 1: overcast) and atmospheric pressure (P, mb). SST ($T_s$, °C), combined with the ECMWF data, was used to run the heat flux model for the period 1992–2016. Q$_{SW}$ was calculated as a function of date and position with correction for CF (Reed, 1977); Q$_{LW}$ as a function of $T_a$, $T_s$, $T_d$, CF using the Berliand bulk formula (Fung et al., 1984). Q$_{SH}$ and Q$_{LH}$ were calculated as a function of $T_a$, $T_s$, $T_d$, CF, P, U$_{10}$. The sum of all four components results in NHF, with the sign convention of positive NHF being heat flux into the water column.

**Plankton sampling**

Plankton samples were collected using vertical net hauls from 50 m (sea floor depth ~ 54 m) to the surface. *Oithona similis* data were from samples collected in 2003, and from November 2011 to December 2016. Samples from 2003 were collected using a 50 µm mesh, 50 cm diameter ring net, from which samples were fixed in 4% buffered formalin. Samples from 2011 - 2014 were collected using a 63 µm mesh, 57 cm diameter ring net, and the plankton fixed as described above. Samples from 2015 - 2016 were collected using the 63 µm mesh ring net, and 250 mL sub-samples were fixed in 2% acid Lugol’s solution. Samples for *Calanus helgolandicus* abundance were collected using a 200 µm mesh, 57 cm diameter, WP2 net (UNESCO, 1968). Live, non-quantitative net hauls for *C. helgolandicus*, for Egg Production Rate (EPR) incubations throughout the period 1992 – 2016, were collected with a 710 µm mesh ring net of 45 cm diameter, towed obliquely throughout the top 10 m layer at 1 - 2 knots.

Weekly sampling for phytoplankton and protozooplankton has also been undertaken at L4 since 1992. Samples were collected from 10 m with a 10 L Niskin bottle. For each sampling event, a 200 mL sub-sample was fixed with 2% acid Lugol’s solution, and another 200 mL sub-sample was
fixed in 4% neutral formaldehyde for enumerating coccolithophores. Further detail on the methods can be found in Widdicombe et al (2010).

**Plankton analysis**

All data on *Oithona similis* were derived separately from the WCO core time series datasets, as detailed information on this species had not been previously recorded at L4. The 63 µm net samples fixed in 4% buffered formalin were screened through a 50 µm mesh, and the retained organisms re-suspended in tap water, made up to a known volume. The re-suspended sample was then pipetted into a 3 mL Hydrobios® counting chamber. The 63 µm net samples fixed in 2% acid Lugol’s solution were settled, and the top 200 mL removed via a syringe. The remaining 50 mL sample was left to settle for 3 hours in the counting chamber. Highly concentrated Lugol’s samples were thoroughly mixed, before a 25 mL sub-sample was removed and settled for 1 hour. Prepared samples were then analysed under an Olympus IMT-2 inverted microscope at 40 x magnification, and the number of adult males and females, juvenile copepodites, and egg sacs, were enumerated. As most egg sacs were detached from the females in all samples, both detached and attached egg sacs were enumerated. Copepodite abundance may be slightly overestimated due to the presence of the congener *O. nana*, the copepodites of which are difficult to distinguish from *O. similis*. However, *O. nana* abundance made up only ~ 7% of total *Oithona* abundance. *O. similis* females typically carry two egg sacs, thus ovigerous female abundance was determined by halving egg sac abundance (Uye and Sano, 1995). The number of eggs per sac was recorded from a randomly selected subset of 10 egg sacs in each sample. Egg sacs were transparent, thus not requiring dissection (Drif et al., 2010). Regrettably, naupliar abundance could not be quantitatively determined from the net samples, thus our data do not include this component of the total *O. similis* population.

Female prosome length and egg diameter of *Oithona similis* were measured under an Olympus IMT-2 inverted microscope at 100 x magnification using an eye-piece graticule. Prosome
length was taken from the anterior margin of the prosome to the posterior of the 4th thorax segment, 
where the articulation exists, following Uye (1982). Prosome length was measured for 10 females 
per sample, or for all females when less than 10 were present, and converted into female carbon 
mass (Cf, µg C female⁻¹) using length-mass relationships in Uye (1982). Egg diameter was 
measured from 2 - 3 eggs per sac, and converted to egg carbon mass (Ce, µg C egg⁻¹) (Uye and 
Sano, 1995). To calculate the percent change in Cf per °C, the slope of the linear regression plot of 
the natural Log (ln) Cf against SST was transformed using the equation of Forster et al (2012). All 
equations for O. similis carbon mass calculations are provided in Table II.

Female and copepodite abundance data for Calanus helgolandicus were obtained from the 
WCO time series from 1992 – 2016. C. helgolandicus is the dominant Calanus species at L4. 
Calanus copepodite abundance data may include C. finmarchicus, although considering C. 
finmarchicus comprises a median of just 4% of C. helgolandicus abundance throughout the water 
column at L4 (Maud et al., 2015), we therefore made the simplifying assumption that all counted 
individuals were C. helgolandicus. For the purpose of comparison, we used carbon mass data of 
Pond et al (1996) for C. helgolandicus females and eggs, at L4 as measured over the period March - 
September 1994. To calculate the percent change in female carbon mass per °C, we used the same 
equation as for O. similis (following Forster et al., 2012) (Table II). Once again, naupliar 
abundance could not be quantitatively measured from the 200 µm net samples, and so once again 
our data do not include these in our total C. helgolandicus population abundances.

Phytoplankton and protozooplankton time series data were available from 1992 – 2014, 
from which we derived biomass data for the following functional groups; diatoms, phyto- and 
zooflagellates, auto- and heterotrophic dinoflagellates, ciliates, and coccolithophores. All cells > 2 
µm were identified, to species level where possible, and enumerated at either 200 or 400 x 
magnification using an inverted microscope. Phyto- and zooflagellates are typically 2 - 10 µm, and 
were separated based on the presence or absence of chloroplasts. Cell measurements were used to
calculate taxa-specific mean cell biovolume according to appropriate geometric shapes (Kovala and Larrance, 1966) and converted to biomass using the equations of Menden-Deuer and Lessard (2000). For further detail we refer the reader to Widdicombe et al (2010).

**Egg Production Rate (EPR)**

*In situ* EPR (eggs female\(^{-1}\) d\(^{-1}\)) of *Oithona similis* was calculated from female and egg sac abundance, and the number of eggs per sac, using the egg ratio method (Edmondson et al., 1962; Checkley, 1980). To account for the effect of female body size, mass-specific EPR (SEPR, egg-C female-C\(^{-1}\) d\(^{-1}\)) was calculated utilising our measures of prosome length together with prosome length-mass equations (Uye, 1982) and egg diameter (Uye and Sano, 1995). All equations for *O. similis* EPR and SEPR are provided in (Table II).

*Calanus helgolandicus* EPR has been determined since 1992 using the following protocol. After each sampling event, live samples were transported to the laboratory in a cool box within 2 – 3 h of collection, and 25 mature females were picked from the sample and five replicates of five females were incubated. To prevent cannibalism of the eggs, females for each replicate were placed in a 500 µm mesh-bottom Plexiglas chamber inside a 2 L plastic beaker filled with 1.5 L of 0.2 µm filtered seawater, at ambient SST and constant darkness for 24 h. Eggs from each replicate were counted and EPR calculated (Maud et al., 2015). *C. helgolandicus* SEPR was calculated using the carbon mass data of Pond et al (1996) for *C. helgolandicus* at L4 during March - September 1994, by multiplying EPR by egg carbon content (µg C egg\(^{-1}\)), then dividing the product by female carbon mass (µg C female\(^{-1}\)), for all corresponding dates.

**Statistics**

Statistical analysis was performed in R (version 3.02.1, R Development Core Team, 2016). A *t*-test was run to test the difference between the full *Calanus helgolandicus* EPR dataset, and a dataset comprising just the dates compatible with the *Oithona similis* dataset. The strength of the
relationship between EPR and SEPR in both species was assessed using the Pearson’s correlation coefficient. Generalised Additive Mixed Models (GAMMs) were run using the function ‘gamm’ from the R package ‘mgcv’ (Wood, 2006), to determine the relationships between EPR and the physical environment and trophic interaction terms. GAMMs were chosen for their greater capacity to identify non-linear relationships compared to Generalised Linear Models (GLMs). The GAMM also accommodates Auto Regressive (AR) and Moving Average (MA) noise, and so together this approach provided an unbiased fit for our data. The models were selected based on Akaike Information Criterion (AIC), choosing the model with the lowest AIC value while maintaining a complete physical environment and trophic interaction model structure. Autocorrelation function (ACF) and partial autocorrelation function (PACF) plots of the raw and standardised residuals indicated that an AR of order 3 was required for the $C. helgolandicus$ time series to account for temporal autocorrelation. The GAMM was used to analyse the $O. similis$ dataset for the contiguous years of 2011 to 2016. The year 2003 was excluded to remove the gap in the time series. An autoregressive model was not selected for the $O. similis$ dataset as the ACF evidence was less certain: the relatively short duration record means the selection of ARMA noise terms would be less accurate. A white noise model was selected in this case. For further detail on this type of non-linear process identification and statistical analysis approaches, see Bruun et al (2017), Tarran and Bruun (2015), and Young et al (2001). Non-significant relationships between EPR and the environmental parameters analysed in this study are not presented.
Results

L4 dynamics

The environmental conditions at L4 varied inter-annually, but maintained general seasonal trends. Sea Surface Temperature (SST) increased from ~ 9°C in March to ~ 16°C in August (Fig. 1). From March – September there was a positive Net Heat Flux (NHF) into the water column, peaking in June at ~ 180 W m\(^{-2}\), followed by a transition to negative NHF, becoming most negative in December at ~ -115 W m\(^{-2}\) (Fig. 1). Pre-spring bloom total Chlorophyll \(a\) concentration [Chl \(a\)] was ~ 0.6 µg L\(^{-1}\), and increased during the spring bloom to ~ 2 µg L\(^{-1}\) (Fig. 2). Diatom blooms occurred predominantly in spring, sometimes continuing into autumn. Ciliate and phytoflagellate biomass was generally highest in late spring, followed by biomass peaks for heterotrophic dinoflagellates and zooflagellates in the summer, and autotrophic dinoflagellates and coccolithophores in autumn (Fig. 2).

Physical and trophic effects on Oithona similis egg production

Egg Production Rate (EPR) and mass-specific EPR (SEPR) of Oithona similis were strongly correlated (Pearson’s correlation coefficient, \(\rho = 0.98\)). Maximum mean (± SE) EPR occurred in August (3.29 ± 0.95 eggs female\(^{-1}\) d\(^{-1}\)), and was lowest in December (0.35 ± 0.09 eggs female\(^{-1}\) d\(^{-1}\)) (Fig. 1). Thus, the proportional change of EPR over an annual cycle had an almost 10-fold range, and a coefficient of variation of 89.7%. EPR increased with SST, with this relationship becoming significant at ~ 15°C (Fig. 3, Table III), indicating rapid increase in EPR above this threshold temperature. The only other variable to show a clear significant relationship with O. similis EPR was NHF (Table III), with the positive relationship between EPR and NHF becoming significant above ~ 200 W m\(^{-2}\) (Fig. 3), at the point of maximum positive NHF into the water column (Fig. 1).

No significant relationship occurred between Oithona similis EPR and the biomass of any phyto- protozooplankton taxa that we considered. Therefore, in order to provide a trophic
interaction term, [Chl a] was included in the GAMM, although this term did not have an overall significant relationship with EPR (Table III). The GAMM plot shows [Chl a] had a large uncertainty interval, although it may have a marginally significant relationship with EPR at [Chl a] below ~ 0.9 µg L⁻¹ (Fig. 3).

**Oithona similis abundance**

Mean (± SE) female abundance was highest in March (286 ± 111 ind m⁻³), and lowest in December (49 ± 15 ind m⁻³) (Fig. 4). Similarly, mean egg sac abundance was highest in April (172 ± 28 ind m⁻³) and lowest in December (9 ± 3 ind m⁻³) (Fig. 4). Mean copepodite abundance had two peaks, the largest in March (737 ± 198 ind m⁻³) followed by a smaller peak in August, and abundance was again lowest in December (152 ± 32 ind m⁻³) (Fig. 4). The proportion of ovigerous females in the total female population ranged from ~ 9% in December to ~ 30% throughout February - September. Mean male abundance also peaked in March (42 ± 22 ind m⁻³), but was lowest in October (4 ± 2 ind m⁻³). There was a strong female-biased sex ratio, with a mean female: male abundance ratio of 10, although this varied considerably over time.

**Oithona similis body size variation**

Females were observed to have largest body sizes in May (0.41 ± 0.01 µg C female⁻¹), and were smallest in November (0.33 ± 0.004 µg C female⁻¹) (Fig. 5). Female carbon mass (Cf) negatively correlated with SST (Fig. 6), exhibiting a mean (± 95% CI) percent change of -2.33 ± 0.5% in Cf per °C increase in SST. Egg carbon mass (Ce) showed no clear seasonality, with a mean (± SE) of 0.014 ± 0.001 µg C egg⁻¹ throughout the year (Fig. 5), and was not significantly correlated with Cf, or the number of eggs per sac. The mean (± SE) values of these parameters are provided in Table IV.

**Physical and trophic effects on Calanus helgolandicus egg production**
The seasonality of EPR and SEPR were very similar (Pearson’s correlation coefficient, $\rho = 0.88$) (Fig. 1), at least during 1994, the year for which carbon data were available (Pond et al., 1996).

There was no significant difference in EPR seasonality between the full Calanus helgolandicus dataset and the one comprising just the dates compatible in time with the values for Oithona similis, thus we use the full dataset in our comparisons. Mean ($\pm$ SE) EPR was highest throughout April – June ($24.8 \pm 1.1$ eggs female$^{-1}$ d$^{-1}$), and lowest in December ($3.14 \pm 0.52$ eggs female$^{-1}$ d$^{-1}$) (Fig. 1).

The proportional change of EPR over the year therefore showed an approximate 8-fold range, and a coefficient of variation of 73.6%. There was a strong relationship between EPR and NHF (Table V), with a significant positive effect occurring for NHF above $\sim 50$ W m$^{-2}$ (Fig. 7). No significant relationship was found between C. helgolandicus EPR and SST. The C. helgolandicus EPR and diatom biomass analysis indicated a logarithmic relationship, which was significant at diatom biomass between 20 - 60 mg C m$^{-3}$ (Fig. 7, Table V). Once diatom biomass exceeded $\sim 60$ mg C m$^{-3}$, the relationship became non-significant. Analysis also showed a marginally significant relationship between EPR and heterotrophic dinoflagellates, which appeared to take a logarithmic form, with the relationship becoming positive after heterotrophic dinoflagellate biomass reached $\sim 5$ mg C m$^{-3}$ (Fig. 7, Table V). We note that the relationship between EPR and heterotrophic dinoflagellate biomass shows a significant non-linear effect with a wide uncertainty interval (Fig. 7). No significant relationship was found between C. helgolandicus EPR and [Chl a].

**Calanus helgolandicus abundance**

Mean ($\pm$ SE) female abundance was highest in June ($20 \pm 3$ ind m$^{-3}$) and lowest in November (2 $\pm$ 0.2 ind m$^{-3}$) (Fig. 4). Mean copepodite abundance was considerably higher, peaking in August ($176 \pm 37$ ind m$^{-3}$), with minimum values in December ($13 \pm 3$ ind m$^{-3}$) (Fig. 4). Mean male abundance was also highest in June ($6 \pm 3$ ind m$^{-3}$) and lowest in December ($0.3 \pm 0.07$ ind m$^{-3}$).

**Calanus helgolandicus body size variation**
Based on published carbon mass data at L4 extracted from Pond et al (1996) and measured between March and September in 1994, mean (± SE) female carbon mass (Cf) was highest in April (64 ± 2 µg C female\(^{-1}\)), and lowest in August (33 ± 1 µg C female\(^{-1}\)) (Fig. 5), and thus negatively correlated with SST (Fig. 6), with a mean (± 95% CI) percent change of -7.46 ± 1.6% in Cf per °C increase in SST. Egg carbon mass (Ce) peaked in April (0.64 ± 0.04 µg C egg\(^{-1}\)), with minimum values in September (0.23 ± 0.01 µg C egg\(^{-1}\)) (Fig. 5). The mean (± SE) values of these parameters are provided in Table IV.
Here we show that *Oithona similis* and *Calanus helgolandicus* exhibit contrasting responses to environmental variation at station L4, measured as differences in Egg Production Rate (EPR), adult female and egg carbon mass, and adult female and copepodite abundance. *O. similis* EPR appears to be more influenced by the physical environment, being significantly related to Sea Surface Temperature (SST) and Net Heat Flux (NHF), whereas physical and trophic parameters both seem to drive *C. helgolandicus* EPR, specifically Net Heat Flux (NHF), and diatom and heterotrophic dinoflagellate biomass. We also discovered a greater relative reduction in body mass with increasing SST over the season in *C. helgolandicus* compared to *O. similis*. Finally, we show that the timing of EPR and adult female and copepodite abundance maxima were decoupled in both species, a result that has implications for defining a single set of optimal conditions, or predictors, for maximum population fitness in either species.

### Seasonality of egg production, egg size, and female size

Egg-brooding, ambush feeding predators typically have lower fecundity than broadcast spawning, active feeders (Sabatini and Kiørboe, 1994; Nielsen and Sabatini, 1996; Hirst and Kiørboe, 2002). Our study supports this, reporting low mean EPR in *Oithona similis* (1.73 eggs female$^{-1}$ d$^{-1}$), compared to *Calanus helgolandicus* (15.11 eggs female$^{-1}$ d$^{-1}$). Indeed, the data (Table IV) suggest that *C. helgolandicus* contribute more carbon, as a proportion of female body mass, into their eggs (Pond et al., 1996). However, the proportional change of EPR over an annual cycle was broadly similar between the two species, with an approximate 8 to 10-fold range, and coefficients of variation of 73.6% and 89.7%, for *C. helgolandicus* and *O. similis*, respectively. The similarity in relative EPR variability between these species over the annual cycle contrasts with a series of papers suggesting that EPR of brooding species is more stable throughout the year, compared to that of broadcast spawners (Sabatini and Kiørboe, 1994; Nielsen and Sabatini, 1996). Although weak seasonality in *O. similis* EPR has previously been reported (Fransz and Gonzalez, 1995; Castellani...
et al., 2005a; 2007), these studies sampled over an incomplete annual cycle, hence the variation in the analysis could have had a seasonal bias. Seasonality in O. similis reproduction has indeed been reported in studies focused on a single site, in the Barents Sea (Dvoretsky and Dvoretsky, 2009a), the Arctic (Lischka and Hagen, 2005), and the North Sea (Drif et al., 2010). However, we acknowledge that studies on a single species and site, as in our present study, do not provide sufficient evidence to reject the general rule that EPR in egg brooding copepods is more stable relative to broadcast spawning species (see Fig. 2. in Bunker and Hirst, 2004). Previous studies at L4 provide evidence of seasonality in C. helgolandicus EPR (Pond et al., 1996; Irigoien et al., 2000a,b; Irigoien and Harris, 2003; Rey-Rassat et al., 2004; Maud et al., 2015).

For Oithona similis, neither egg carbon mass or diameter showed any clear seasonality at L4, which is similar to that reported for O. similis egg diameter in North Atlantic (Castellani et al., 2005a; 2007) and Greenland (Zamora-Terol et al., 2013) populations. However, in the Barents Sea, O. similis egg diameter correlated positively with female prosome length (Dvoretsky and Dvoretsky, 2009a) and negatively with clutch size (Dvoretsky and Dvoretsky, 2009a,b). Conversely, Calanus helgolandicus egg carbon mass and female carbon mass followed similar trends, both reaching maximum values in spring (Fig. 5).

Our results show a stronger percent change in female carbon mass (Cf) per °C of seasonal warming in Calanus helgolandicus compared to Oithona similis (Fig. 6), with mean (± 95% CI) values of -7.46 (± 1.6)% and -2.33 (± 0.5)% for C. helgolandicus and O. similis, respectively. Similarly, Horne et al (2016) report that on average calanoid copepods exhibit a 4-fold greater reduction in percent change in adult body mass per °C, with a mean (± 95% CI) of -3.66 (± 0.70)%, compared to cyclopoids with a mean of -0.91 (± 0.59)%. This difference in temperature induced body size responses between calanoid and cyclopoid species has been attributed to contrasting feeding modes, as opposed to reproductive strategy (Horne et al., 2016). With rates of food acquisition and resource use proposed to scale with body size differently between feeding strategies...
(Horne et al., 2016). Furthermore, feeding mode is associated with metabolic rate (Kiørboe and Hirst, 2014), which differs substantially between active feeders and passive feeders (Kiørboe, 2011), and may also be a factor determining temperature-induced body size responses.

**Physical effects on egg production rate**

Despite the proportional change in EPR over the year being similar for both species, we propose that different factors influence the timing of EPR maxima in each species. In support of our first hypothesis, we found a stronger relationship between EPR and SST in *Oithona similis* compared to *Calanus helgolandicus*. The relationship between *O. similis* EPR and SST may in part be due to a temperature-dependent brooding period, whereby EPR is limited by the delay in production of new egg clutches until previous eggs hatch (Ward and Hirst, 2007). Since embryonic development rate increases with temperature, the time from the production of one clutch to the production of the next should decrease with increasing temperature (Nielsen et al., 2002). This would result in the strong positive relationship between EPR and temperature that we observed, especially under food saturated conditions. Positive correlation between temperature and EPR has also been reported for *O. similis* populations in the Barents Sea (Dvoretsky and Dvoretsky, 2009a,b) and Greenland (Zamora-Terol et al., 2014). In a synthesis of such rates, Ward and Hirst (2007) show the significant positive correlation between EPR and temperature in natural populations of *O. similis* (see their Fig. 6).

In contrast, reproduction in broadcast spawning *Calanus helgolandicus* does not require a brooding period, as eggs are released directly into the sea. This could partially explain why SST is a poorer predictor of *C. helgolandicus* EPR, both in our study, and previous studies at L4 (Laabir et al., 1998; Bautista et al., 1994; Pond et al., 1996; Irigoien et al., 2000b; Bonnet et al., 2005). NHF explained more of the variation in *C. helgolandicus* EPR, which peaked following the transition to positive NHF in spring (Fig. 1). This relationship between EPR and NHF becomes significant at ~50 W m\(^{-2}\) (Fig. 7). At this time of year, SST is still relatively low, and the water column stratified.
The relationship between *C. helgolandicus* EPR and NHF could be due to the influence of NHF over the timing of the spring bloom (Smyth *et al.*, 2010; 2014), during which increased phytoplankton prey biomass could sustain maximum reproductive output. The same cannot be said for the relationship between *Oithona similis* EPR and NHF, considering this does not become significant until positive NHF into the water column has peaked at ~ 200 W m$^{-2}$ (Fig. 3). This peak is later in the year, and when water column stratification will be starting to breakdown. Water column stratification was found to be the only physical variable to correlate with *C. helgolandicus* population increase at L4 (Maud *et al.*, 2015). Eggs of broadcast spawning *Calanus* spp. die quickly upon contact with sediment (Uye, 2000). Therefore, water column stratification may also be important for retaining *C. helgolandicus* eggs in the upper mixed layer (Irigoien and Harris, 2003), although this could make the eggs more visible to predators (Eiane *et al.*, 2002). Furthermore, water column stratification may support *C. helgolandicus* prey detection and capture (Kiørboe and Saiz., 1995). The effect of turbulence on foraging efficiency in zooplankton has been well studied (Visser *et al.*, 2009), but further research into the effects of stratification on recruitment success in broadcast spawning copepods would be highly beneficial.

**Prey effects on egg production rate**

Our second hypothesis was that due to the contrast in feeding mode, *Oithona similis* EPR would have a stronger relationship with the biomass of motile prey, whereas *Calanus helgolandicus* EPR would have a stronger relationship with non-motile, diatom prey. Our data provide mixed support for this hypothesis. What we actually find is that *O. similis* EPR was not significantly related with any of the prey taxa considered. In contrast, *C. helgolandicus* EPR was significantly related with diatom biomass and also, to a lesser extent, heterotrophic dinoflagellates. Diatoms, ciliates, and heterotrophic dinoflagellates have previously been shown to sustain *C. helgolandicus* EPR at L4 (Pond *et al.*, 1996; Irigoien *et al.*, 2000a,b; Fileman *et al.*, 2010). Thus, it is likely that this copepod species consumes both motile and non-motile prey throughout the year according to availability.
For example, *C. helgolandicus* have been shown to graze predominantly on diatoms during the spring bloom, but are more dependent on protozooplankton later in the year once diatom biomass decreases (Fileman *et al.*, 2007). As heterotrophic dinoflagellate biomass peaks in summer, following the spring diatom bloom (**Fig. 2**), *C. helgolandicus* may consume these dinoflagellates during times of the year when diatom biomass is low, as previously reported (Irigoin *et al.*, 2000a,b; Fileman *et al.*, 2010). Although we found no statistically significant relationship between *C. helgolandicus* EPR and [Chl *a*], EPR for this species increases during the spring peak in [Chl *a*] (**Fig. 2**), as has been found previously at L4 (Bautista *et al.*, 1994; Pond *et al.*, 1996; Laabir *et al.*, 1998; Bonnet *et al.*, 2005; Maud *et al.*, 2015). Overall, the longer *C. helgolandicus* time series suggested that food can be an important factor influencing fecundity, yet the shorter *O. similis* time series was unable to explain these dynamics.

Environmental seasonality can influence energy allocation in organisms, with the investment of energy under stressful conditions going towards survival, resulting in reduced fecundity (Kiørboe *et al.*, 2015). The fact that *Oithona similis* is reproductively active throughout the year is indicative of efficient energy uptake and assimilation. We retained [Chl *a*] in our model for *O. similis* EPR in order to maintain a trophic interaction term. In general, [Chl *a*] is a good proxy for phytoplankton biomass, and *O. similis* EPR did show a marginal relationship with [Chl *a*] (**Fig. 3**), a finding also reported in previous studies (Sabatini and Kiørboe, 1994; Castellani *et al.*, 2007; Ward and Hirst, 2007; Drif *et al.*, 2010). *O. similis* fecundity has been shown to remain relatively high at low [Chl *a*] (Ward and Hirst, 2007), and weight-specific fecundity and growth in *Oithona* spp. is saturated at low [Chl *a*] (Hirst and Bunker, 2003), which could potentially explain the marginal significance observed here between *O. similis* EPR and [Chl *a*] at low chlorophyll concentrations (**Fig. 3, Table III**).

**Decoupled seasonality in egg production and copepod abundance**
The annual timing of EPR and adult female and juvenile copepodite abundance maxima was decoupled in both species (Fig. 4). Decoupled EPR and abundance seasonality has previously been reported for *Calanus helgolandicus* at L4 (Pond et al., 1996; Irigoien and Harris, 2003; Rey-Rassat et al., 2004; Maud et al., 2015), and for *Oithona similis* in the Arctic (Lischka and Hagen, 2005).

Our observation of maximum *O. similis* female abundance in spring is consistent with a previous study of this species at L4 (Castellani et al., 2016), and contradicts the notion that ambush feeders thrive during periods when motile prey predominates (Kenitz et al., 2017). The decoupled seasonality of EPR and abundance could be explained by variation in mortality rates (Hirst and Kiørboe, 2002). Mortality rates of *C. helgolandicus* at L4 show strong seasonality, and are highest among early developmental stages (Hirst et al., 2007). Consequently, EPR is a poor predictor of abundance in later developmental stages. Mismatch between seasonality in egg production and egg viability can lead to eggs being produced in sub-optimal conditions for peak egg fitness (Varpe et al., 2007), with negative consequences on recruitment success. The fact that optimum conditions for reproduction and adult female and copepodite abundance maxima occur at different times of year, under different temperature and food conditions, has implications for niche modelling approaches which only use species abundance as a function of environmental parameters, to represent an ecological niche (Helouët et al., 2013).

Rate of maturation from eggs to adults should determine the time period between maximum reproductive output and increased adult abundance, assuming high recruitment success of the population. *Calanus helgolandicus* may take longer to develop than *Oithona similis*, as development time from egg to adult at 15°C was estimated at 24 - 40 days in *C. helgolandicus* (Bonnet et al., 2009), and ~ 20 days in *O. similis* (Sabatini and Kiørboe, 1994). The fact that adult female abundance did not increase until long after the period of maximum EPR, despite their relatively short development times, confirms that there are indeed other factors, such as mortality and advection (Irigoien and Harris, 2003; Hirst et al., 2007), influencing copepod abundance.

Ohman and Hirche (2001) present evidence for density-dependent mortality in an oceanic
population of *Calanus finmarchicus*, whereby egg mortality rates were a function of adult female and copepodite abundance. Likewise, density-dependence in egg mortality rates, with higher mortality rates observed at higher adult densities, have been reported for the *C. helgolandicus* population at station L4 (Hirst *et al.*, 2007). Thus predation, by cannibalism or from other species, combined with egg hatching success (Maud *et al.*, 2015), may also contribute to decoupled seasonality in egg production and copepod abundance.

**Statistical analysis and development of predictive models**

One limitation of our study was the shorter period over which we have data for *Oithona similis*, and the restrictions this imposed on including an autoregressive noise process as part of the Generalised Additive Mixed Model (GAMM). The benefit of having the longer *Calanus helgolandicus* record was that it represents the L4 physical and trophic interactions with EPR over a longer time scale. Whilst the *O. similis* record is short, this species has been exposed to the same physical environment as for *C. helgolandicus*, and so we can discuss both taxa in the longer term context. Further work can be pursued using these dynamic relationships to help establish a predictive model for *O. similis*. 
Conclusion

Contrasting traits of feeding mode, reproductive strategy, and body size, between *Oithona similis* and *Calanus helgolandicus*, appear to induce different responses in both reproduction and abundance to environmental variation at L4. The fact that optimum conditions for reproduction and abundance of these copepod species occurred at different times of year, under differing temperature and food conditions, is relevant to niche modelling approaches. Our results therefore demonstrate that optimum population performance cannot be defined by a single set of environmental conditions. Overall, understanding how contrasting functional traits translate into seasonality of reproduction, abundance, and body size can enhance our ability to predict how species might perform under different climatic scenarios.
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Dvoretsky, V. G. and Dvoretsky, A. G. (2009b). Spatial variations in reproductive characteristics of


**Figure Legends**


**Fig. 2:** Mean (± SE) for (a) Phytoplankton biomass seasonality over the period of the *Oithona similis* dataset (2003; 2011 – 2014) (b) Zooplankton biomass seasonality over the period of the *O. similis* dataset (2003; 2011 – 2014) (c) *O. similis* EPR and Chlorophyll *a* concentration ([Chl *a*]) (2003; 2011 – 2016) (d) Phytoplankton biomass seasonality over the period of the *Calanus helgolandicus* dataset (1992 – 2014) (e) Zooplankton biomass seasonality over the period of the *C. helgolandicus* dataset (1992 – 2014) (f) *C. helgolandicus* EPR and [Chl *a*] (1992 – 2016). Aut.dino = Autotrophic dinoflagellate, Pflag = Phytoflagellate, Het.dino = Heterotrophic dinoflagellate, Zflag = Zooflagellate. Coccolithophores were excluded from this figure due to their low biomass at L4.

**Fig. 3:** Plots showing the non-parametric contributions for each environmental factor included in the Generalised Additive Mixed Model (GAMM) on Egg Production Rate (EPR) for the *Oithona similis* dataset (2011 - 2016). (a) Sea Surface Temperature (SST, °C) (b) Net Heat Flux (NHF, W m⁻²) (c) Chlorophyll *a* concentration ([Chl *a*], µg L⁻¹). Horizontal line at y = 0 marks where there is no ‘non-linear effect’ of the ‘x’ variable on EPR. Both solid and dashed lines above the y = 0 line indicates a significant positive relationship. Dashed lines represent uncertainty interval.

**Fig. 4:** Mean (± SE) for (a) *Oithona similis* female abundance (Female Ab) and Egg Production Rate (EPR) (2011 – 2016) (b) *O. similis* copepodite abundance (Copepodite Ab) and egg sac abundance (Egg sac Ab) (2011 – 2016) (c) *Calanus helgolandicus* female abundance (Female Ab)

**Fig. 5:** Mean (± SE) for (a) *Oithona similis* female carbon mass (Cf) and Sea Surface Temperature (SST) (2011 – 2016) (b) *O. similis* Cf and egg carbon mass (Ce) (2011 – 2016) (c) *Calanus helgolandicus* Cf and SST (March – September 1994) (d) *C. helgolandicus* Cf and Ce (March – September 1994). Carbon mass data for *C. helgolandicus* was derived from Pond *et al* (1996).

**Fig. 6:** Female body carbon (Cf) of *Oithona similis* and *Calanus helgolandicus* against Sea Surface Temperature (SST). Note the y-axes are both Log$_{10}$ scales. Carbon mass data for *C. helgolandicus* from Pond *et al* (1996), measured over March – September, 1994. *O. similis* carbon mass data from the present study over 2011 – 2016. The regressions of body size are described by the equations:

\[
\text{Log}_e O. similis \text{ Cf} = -0.0236 \text{ SST} - 0.7197 \quad (R^2_{\text{adj}} = 0.35, \quad P < 0.0001, \quad n = 132),
\]

\[
\text{Log}_e C. helgolandicus \text{ Cf} = -0.0775 \text{ SST} + 4.8021 \quad (R^2_{\text{adj}} = 0.76, \quad P < 0.0001, \quad n = 28).
\]

**Fig. 7:** Plots showing the non-parametric contributions for each environmental factor included in the Generalised Additive Mixed Model (GAMM) on the Egg Production Rate (EPR) for the *Calanus helgolandicus* dataset (1992 - 2016). (a) Net Heat Flux (NHF, W m$^{-2}$) (b) Diatom biomass (mg C m$^{-3}$) (c) Heterotrophic dinoflagellate biomass (Hetdino, mg C m$^{-3}$). Horizontal line at y = 0 marks where there is no ‘non-linear effect’ of the ‘x’ variable on EPR. Both solid and dashed lines above the y = 0 line indicates a significant positive relationship. Dashed lines represent uncertainty interval.
Tables

Table I: Western Channel Observatory (WCO) time series data 1992 – 2016; length of datasets available and analysed for each parameter, and the sampling method used to obtain the data.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Years analysed</th>
<th>Sampling method</th>
</tr>
</thead>
</table>
| Oithona similis abundance        | Nov 2011 – Dec 2016.            | 2011 – 2014: ring net (63 µm mesh, 57 cm diameter), 0–50 m, fixed in 4% buffered formalin.  
|                                  | Excluding Mar 2014 - Jun 2015   | 2015 – 2016: ring net (63 µm mesh, 57 cm diameter), 0 – 50 m, fixed in 2% acid Lugol’s solution. |
| Oithona similis egg production   | 2003; Nov 2011 – Dec 2016.      | 2003: ring net (50 µm mesh, 50 cm diameter), 0 – 50 m, fixed in 4% buffered formalin. |
|                                  | Excluding Mar 2014 - Jun 2015   | 2011 – 2014: ring net (63 µm mesh, 57 cm diameter), 0 – 50 m, fixed in 4% buffered formalin.  
|                                  |                                 | 2015 – 2016: ring net (63 µm mesh, 57 cm diameter), 0 – 50 m, fixed in 2% acid Lugol’s solution. |
|                                  |                                 | 2002 – 2016: SeaBird SBE 19+ CTD.                                              |
| Sea Surface Temperature          | Feb 1992 – Dec 2016.            | 100 mL surface seawater filtered through 25 mm GF/F filters in triplicate, extracted in 90% acetone at 4 °C. Analysed by Turner fluorometry following Welschmeyer (1994) protocol. |
| Net Heat Flux                    | Feb 1992 – Dec 2016.            | Meteorological parameters obtained from the European Centre for Medium Range Weather Forecasting (ECMWF) operational and ERA-40 datasets, provided by the British Atmospheric Data Centre. |
| Surface Chlorophyll a Concentration | Feb 1992 – Dec 2016.            | 10 L Niskin bottle, 10 m, 200 mL sub-sample fixed in 2% acid Lugol’s solution. |
|                                  | Excluding Oct 1994 – May 1995   |                                                                                 |
Table II: *Oithona similis* egg production and carbon mass equations. E = Egg abundance (ind m$^{-3}$), F = Female abundance (ind m$^{-3}$), HT = Time from laying to hatching (days), T = Temperature (°C), PL = Prosome Length (µm), ED = Egg Diameter (µm). The ‘slope’ in the equation of Forster *et al* (2012) is that from the relationship between Log$_e$ mass and temperature (°C).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Equation</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg Production Rate (EPR, eggs female$^{-1}$ d$^{-1}$)</td>
<td>EPR = E / (F * HT)</td>
<td>Edmondson <em>et al</em> (1962); Checkley (1980)</td>
</tr>
<tr>
<td>Hatch Time (HT, d$^{-1}$)</td>
<td>HT = 1504.5 (T + 7.6998)$^{-2.05}$</td>
<td>Bělehrádek equation using parameters described for <em>O. similis</em> by Nielsen <em>et al</em> (2002).</td>
</tr>
<tr>
<td>Hatching Rate (HR, d$^{-1}$)</td>
<td>HR = 1 / [1504.5 (T + 7.6998)$^{-2.05}$ ]</td>
<td>Bělehrádek equation using parameters described for <em>O. similis</em> by Nielsen <em>et al</em> (2002).</td>
</tr>
<tr>
<td>Female carbon mass (Cf, µg C female$^{-1}$)</td>
<td>Cf = $10^{1.45 * (\log PL) - 4.25}$</td>
<td>Uye (1982)</td>
</tr>
<tr>
<td>Egg carbon mass (Ce, µg C egg$^{-1}$)</td>
<td>Ce = $5.32 \times 10^{-8} \times ED^{3.334}$</td>
<td>Uye and Sano (1995)</td>
</tr>
<tr>
<td>Mass-specific Egg Production Rate (SEPR, egg-C female-C$^{-1}$ d$^{-1}$)</td>
<td>SEPR = (E/F) HR (Ce/Cf)</td>
<td>Sabatini and Kiørboe (1994)</td>
</tr>
<tr>
<td>Percent change in female carbon mass per °C (% °C$^{-1}$)</td>
<td>$(e^{(slope)} - 1) \times 100$</td>
<td>Forster <em>et al</em> (2012)</td>
</tr>
</tbody>
</table>
Table III: Generalised Additive Mixed Model (GAMM) outputs for *Oithona similis* Egg Production Rate (EPR). SST = Sea Surface Temperature (°C), NHF = Net Heat Flux (W m⁻²), Chl *a* = Chlorophyll *a* (µg L⁻¹).

Each covariate is represented as a smooth function, s(x). EDF = Estimated Degrees of Freedom, Ref.df = Residual Degrees of Freedom. n = sample size.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>EDF</th>
<th>Ref.df</th>
<th>F</th>
<th>P</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>s(SST)</td>
<td>1.958</td>
<td>1.958</td>
<td>2.871</td>
<td>0.0438</td>
<td>217</td>
</tr>
<tr>
<td>s(NHF)</td>
<td>2.016</td>
<td>2.016</td>
<td>2.921</td>
<td>0.0622</td>
<td>217</td>
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<tr>
<td>s(Chl a)</td>
<td>1.485</td>
<td>1.485</td>
<td>1.421</td>
<td>0.1619</td>
<td>217</td>
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<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>Female PL (µm)</th>
<th>Cf (µg C female⁻¹)</th>
<th>Egg diameter (µm)</th>
<th>Ce (µg C egg⁻¹)</th>
<th>ES (eggs sac⁻¹)</th>
<th>EPR (eggs female⁻¹ d⁻¹)</th>
<th>SEPR (egg–C female–C⁻¹ d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Oithona similis</em></td>
<td>Spring</td>
<td>456 ± 3.29 (30)</td>
<td>0.40 ± 0.004 (30)</td>
<td>61 ± 0.84 (30)</td>
<td>0.015 ± 0.001 (30)</td>
<td>9.77 ± 0.33 (30)</td>
<td>1.66 ± 0.18 (33)</td>
<td>0.057 ± 0.008 (30)</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>425 ± 3.17 (37)</td>
<td>0.36 ± 0.004 (37)</td>
<td>59 ± 0.71 (37)</td>
<td>0.013 ± 0.001 (37)</td>
<td>9.28 ± 0.21 (37)</td>
<td>2.67 ± 0.37 (42)</td>
<td>0.113 ± 0.018 (31)</td>
</tr>
<tr>
<td></td>
<td>Autumn</td>
<td>403 ± 3.32 (37)</td>
<td>0.34 ± 0.004 (37)</td>
<td>60 ± 0.63 (37)</td>
<td>0.014 ± 0.0004 (37)</td>
<td>6.93 ± 0.25 (37)</td>
<td>1.56 ± 0.28 (39)</td>
<td>0.061 ± 0.011 (35)</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>420 ± 4.33 (28)</td>
<td>0.36 ± 0.005 (28)</td>
<td>59 ± 0.92 (28)</td>
<td>0.013 ± 0.001 (28)</td>
<td>6.8 ± 0.36 (28)</td>
<td>0.78 ± 0.17 (32)</td>
<td>0.032 ± 0.007 (27)</td>
</tr>
<tr>
<td><em>Calanus helgolandicus</em></td>
<td>Spring</td>
<td>59.57 ± 2.54 (10)</td>
<td>0.468 ± 0.04 (10)</td>
<td>0.468 ± 0.04 (10)</td>
<td>21.38 ± 0.71 (244)</td>
<td>0.167 ± 0.02 (10)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>36.92 ± 1.29 (14)</td>
<td>0.311 ± 0.01 (13)</td>
<td>0.311 ± 0.01 (13)</td>
<td>21.08 ± 0.64 (256)</td>
<td>0.189 ± 0.02 (13)</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Autumn</td>
<td>9.74 ± 0.45 (230)</td>
<td></td>
<td></td>
<td></td>
<td>9.74 ± 0.45 (230)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>5.77 ± 0.44 (200)</td>
<td></td>
<td></td>
<td></td>
<td>5.77 ± 0.44 (200)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table V: Generalised Additive Mixed Model (GAMM) outputs for *Calanus helgolandicus* Egg Production Rate (EPR). NHF = Net Heat Flux (W m$^{-2}$), Diatom = Diatom Biomass (mg C m$^{-3}$), Hetdino = Heterotrophic Dinoflagellate Biomass (mg C m$^{-3}$). Each covariate is represented as a smooth function $s(x)$. EDF = Estimated Degrees of Freedom, Ref.df = Residual Degrees of Freedom. n = sample size.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>EDF</th>
<th>Ref.df</th>
<th>$F$</th>
<th>$P$</th>
<th>n</th>
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<tbody>
<tr>
<td>s(NHF)</td>
<td>2.522</td>
<td>2.522</td>
<td>9.985</td>
<td>&lt; 0.0001</td>
<td>1081</td>
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<tr>
<td>s(Diatom)</td>
<td>3.644</td>
<td>3.644</td>
<td>4.454</td>
<td>0.00304</td>
<td>1081</td>
</tr>
<tr>
<td>s(Hetdino)</td>
<td>2.613</td>
<td>2.613</td>
<td>3.288</td>
<td>0.05366</td>
<td>1081</td>
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</table>