Seasonal abundance and egg production rates of *Oithona similis* and *Pseudocalanus elongatus* in the northern North Sea: a first comparison of egg-ratio and incubation methods

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ABSTRACT: In this study, we examined egg production rates (EPR), clutch sizes, numbers of spawning females and prosome lengths of 2 common marine egg carrying copepods, *Oithona similis* and *Pseudocalanus elongatus*, over an annual cycle in the northern North Sea. For both species, we determined EPR using the incubation method, with rates being assessed after 24 (EPR_{0–24}), 48 (EPR_{0–48}), and between 24 and 48 h (EPR_{24–48}) of incubation. For *Oithona similis*, EPR were also determined by applying the egg-ratio method EPR_p, allowing a first ever comparison between these 2 approaches. In both species, mean rates of egg production from EPR_{24–48} incubations were lower on average than from EPR_{0–24} and EPR_{0–48} incubations; however, paired *t*-tests showed these differences to be insignificant ($p > 0.05$). In *Oithona similis*, the egg-ratio method EPR_p gave higher rates (mean $\pm$ 95 % CI: 1.06 ± 0.476 eggs female⁻¹ d⁻¹) than the incubation method, but only the comparison with EPR_{24–48} (mean $\pm$ 95 % CI: 0.51 ± 0.337 eggs female⁻¹ d⁻¹) was significantly different ($p = 0.031$). Possible reasons for the differences are explored and recommendations made. EPR were significantly correlated with temperature in *P. elongatus* ($p < 0.05$), but the correlation was significant in *O. similis* only when using the egg-ratio method ($p < 0.05$). Applying a modified Michaelis-Menten relationship showed EPR to be significantly related to chlorophyll *a* in both species ($p < 0.001$). Changes in prosome lengths explained little of the variability in clutch size in the 2 species over the course of the year. Finally, seasonality in the abundance and biomass of nauplii, copepodites and adults was examined, together with adult female production and weight-specific fecundity rates, and these were compared across a variety of regions.

KEY WORDS: Egg production · Copepod · Egg ratio · Incubation · *Oithona similis* · *Pseudocalanus elongatus* · Clutch size · North Sea

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INTRODUCTION

Marine pelagic copepods play a pivotal role in the transfer of carbon and energy to higher trophic levels (Dam et al. 1993), and in the export of organic material as faeces and dead bodies from the upper mixed layer (Legendre & Rivkin 2002). If we are to predict population dynamics and production rates of copepods, we

need to understand their reproductive rates. Species of copepods living in mid to high latitudes typically show strong seasonality in their breeding cycles (Mauchline 1998). The timing of reproduction determines the annual productive cycle and the rate of supply of eggs and nauplii, which are important as prey items to many commercially important fish (Economou 1987, McLaren & Avendaño 1995, Munk 1997, Heath 2007).

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Copepod reproduction therefore has important implications for fish recruitment (Cushing 1975), and the success of other higher trophic levels.

Many studies have examined how copepod egg production rates (EPR) respond to environmental variability. These rates have been found to depend upon food quantity (e.g. Runge 1985, Peterson & Bellantoni 1987, Uye & Murase 1997, Koski et al. 2006) and quality, for example, expressed as specific fatty acids (Evjemo et al. 2008, Jónasdóttir et al. 2009). EPR are also commonly found to be strongly temperature dependent (Ward & Hirst 2007, Liu & Hopcroft 2008, Bonnet et al. 2009, Devreker et al. 2009). In addition to the combination of temperature and food (see review of Bunker & Hirst 2004), female size (e.g. Corkett & McLaren 1969, Halsband & Hirche 2001) can also be an important determinant of EPR.

The methods for assessing juvenile growth rates can be demanding in terms of effort (Hirst et al. 2005, Kimmerer et al. 2007), while egg production approaches can be more practical when assessing copepod growth and recruitment. Two methods are routinely used to estimate the EPR of marine pelagic copepods: the incubation and the egg-ratio methods (see Runge & Roff 2000), the former being more widely used. In the incubation method, adult females are collected and incubated in containers with natural seawater as food; as such, this is an *ex situ* method. Eggs produced are enumerated typically after a 24 or 48 h period of incubation (Runge & Roff 2000). In contrast, in the egg-ratio method, EPR are determined by combining estimates of the abundance of eggs and adult females with egg hatch times (e.g. Checkley 1980). The method can therefore be described as being broadly *in situ* (although the egg hatch times are commonly determined separately by incubation).

There are problems specific to each approach. Incubating animals can lead to container effects, including changes in the vertical migration ambit of the copepods and in the food regime experienced. The egg-ratio method does not rely on incubation, and hence does not suffer from these problems. The method, however, relies upon the accurate assessment of abundance, and hence may be liable to sampling and enumeration problems. The egg hatch time estimates are also critical to the accuracy of the results. Finally, the method also assumes a steady state, i.e. eggs 'removed' by hatching are replaced by the supply (production) of new eggs.

To date, the egg-ratio and incubation methods have never been compared against one another in sac spawning copepods. Yet, given the ubiquity of egg production measurements, and their importance in copepod dynamics, we need to be sure that the rates we measure are accurate and that the results from

these 2 methods are consistent. Although these methods have been applied simultaneously in broadcast spawning copepods, the results are not expected to be similar; indeed, their difference is used to solve for mortality rates of the free eggs (e.g. Peterson & Kimmerer 1994, Hirst et al. 2007). Sac spawners present the possibility to appropriately determine whether these 2 methods produce similar results. As eggs are carried by females, they should have a mortality rate similar to the adults, thus removing the main cause of divergence between the results of the two methods as seen in broadcast spawners.

The aims of this study are to (1) describe the seasonality of *Pseudocalanus elongatus* and *Oithona similis* in the northern North Sea including the seasonality in their EPR (and clutch size) off Stonehaven, Scotland, and the relationship of these rates to temperature, chlorophyll *a* (chl *a*) and prosome length, (2) compare EPR for different incubation periods (0–24, 24–48 and 0–48 h), and (3) compare EPR for both incubation and egg-ratio methods. To address the last objective, we examined the ubiquitous species *O. similis*, which is a true sac spawner that retains its eggs within a membrane.

MATERIALS AND METHODS

Site. This study was undertaken at the Stonehaven site in the northern northwestern North Sea (Fig. 1), which is located 3 km offshore from the coast (56° 57.80' N, 2° 06.20' W), and has a total water column depth of 45 m. This location is being studied as part of an on-going monitoring time series by the Marine Scotland Laboratories, Aberdeen. This site was originally chosen as an accessible location that is representative of the wider region of the northeast coast of Scotland. The northern North Sea at Stonehaven is under the influence of various water masses. One of these, a large tongue of saline water from the Atlantic Ocean (Otto et al. 1990, Fransz et al. 1991), is known as the 'Atlantic Water'. It has a salinity reaching over 35 and can extend from the Orkney Island to the Dogger Bank. Stonehaven is also under the influence of 'North Sea Water', which results from the mixing of the Atlantic Water with the less saline coastal waters, and has a salinity of 34 to 35. Circulation in the North Sea is classically presented as an anticlockwise gyre that is driven mainly by wind forcing. However, this may sometimes be reversed due to wind forcing, and may also split into 2 gyres in the north and in the south, or cease altogether (Kauker & von Storch 2000, ICES 2005). During the present study, the Stonehaven site was visited on a near fortnightly basis from February 2003 to February 2004.

Fig. 1. Location of the Stonehaven site in the northern North Sea

Egg production: incubation method. To determine egg production using the incubation method, we collected copepods by slow vertical tows from 45 m (near bottom) to the surface using 2 different sized mesh nets (95 or 200 μm) that were fitted with a non-filtering cod end. The contents of the cod end were gently emptied into a 15 l bucket that was freshly rinsed and partly filled with surface seawater. Buckets were topped up and tight fitting lids were used to exclude air and avoid mechanical damage in transit to the laboratory. Natural seawater for use in subsequent incubations was collected from a depth of 5 m and stored in a 15 l carboy for return to the laboratory.

Upon return to the laboratory (within 2 h of collection), live copepod samples were sorted in a controlled temperature room set at *in situ* seawater temperature ($\pm 1^\circ\text{C}$). Animals were transferred into a plastic petri dish, and non-ovigerous *Oithona similis* and *Pseudocalanus elongatus* females were randomly selected using a wide bore pipette. The seawater used for incubations was pre-screened through a 95 μm mesh to remove large metazoans while retaining food. Live undamaged females were placed individually in 70 ml plastic tissue flasks filled with incubation water. Flasks were completely filled, and cling film placed over the mouth to prevent the formation of air bubbles. We aimed to incubate >15 females of each species, but this was not achieved in 3 of 36 incubations because of the low densities of animals. Incubations began within 6 h

of collection and continued for up to 2 d. Bottles were placed on a plankton wheel that was set to revolve at 0.5 rpm, with the flasks rotating end over end. After 24 h, each flask was examined to see if any eggs had been produced. Eggs were counted using a stereomicroscope with variable illumination, without disrupting the sacs on the live animals; the transparent nature of the sac allowed this. Subsequent checks revealed this method to be accurate for the assessment of the number of eggs when compared with counts made by dissecting the egg sacs. After counting, the flasks were replaced on the plankton wheel for a further 24 h. The animals were removed after 48 h, and the eggs dissected from the sacs and counted. The incubation water was also filtered to ensure that any eggs that might have been dislodged (this occasionally occurred for *Pseudocalanus*) could be included in this count. No eggs hatched before the end of the 48 h. Prosome lengths of the females were also measured upon termination of the experiment using a microscope (Leica MZ75) with a fitted eyepiece graticule (lengths measured to the nearest 9.2 μm). On 28 July 2003, there was no reproduction in either species and animals suffered very high mortality rates; this data was therefore not included in this study. *Oithona similis* usually carries 2 sacs clutch⁻¹, so the value for clutch size reported here is the total number of eggs carried, i.e. combined from the 2 sacs. *Pseudocalanus elongatus* produces a single egg mass; hence, this is the value reported here.

The EPR (eggs female⁻¹ d⁻¹) from incubation experiments were calculated as follows:

$$\text{EPR} = \frac{E}{I \times F} \quad (1)$$

where E is the total number of eggs produced (estimated after 24 and 48 h of incubation), I is the incubation period in days (i.e. 1 or 2 d), and F is the number of females incubated. Daily EPR rates were determined for the period 0 to 24, 24 to 48 and 0 to 48 h (EPR_{0–24}, EPR_{24–48} and EPR_{0–48} respectively) to examine the impact of the incubation period on the results.

Egg production: egg-ratio method. The *in situ* abundance of eggs and adults were determined using collections made with bongo nets of 68 µm mesh size (mouth opening diameter 0.3 m). This mesh size was chosen to reduce clogging, while ensuring that egg sacs of *Oithona* would be retained (see Ward & Hirst 2007). One sample was collected on each visit by hauling the nets vertically over the entire water column (0 to 45 m depth). Samples were preserved in 4 % buffered formaldehyde solution and females and eggs were later counted in subsamples. Between 50 and 100 females of *O. similis* were enumerated and the number of eggs counted. Egg development times, i.e. the time from laying to hatching (HT, days), were predicted using the equation of Nielsen et al. (2002):

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

Temperature (T , °C) was measured using electronic reversing thermometers (SIS RTM 4002 X), and applied here as the average of surface (1 m) and bottom (45 m) temperatures, which rarely diverged by >1°C between these 2 depths (see Fig. 2). The egg-ratio method equation (Edmondson et al. 1962, Checkley 1980) was then applied to determine the daily egg production rates (EPR_p) as:

$$\text{EPR}_p = \frac{E_p}{(F_p \times \text{HT})} \quad (3)$$

where E_p is the abundance of eggs (ind. m⁻³), and F_p the abundance of females (ind. m⁻³).

Chl *a* concentration was determined from water collected using a Lund tube, sampling the top 10 m of the water column. Duplicate samples (1 l each) were GF/F filtered. Fresh or previously frozen (–80°C) filters were then soaked in 90 % buffered acetone in a centrifuge tube, covered with aluminum foil and placed in a refrigerator overnight. Fluorometer (Turner 10-AU) readings were done before and after acidification (0.1 M HCl).

Length–weight analyses. The prosome lengths of freshly caught specimens of *Oithona similis* and *Pseudocalanus elongatus* were measured as described above. Specimens were quickly rinsed in Milli-Q water or 3 % ammonium formate to remove salts, and placed

in an open pre-weighed tin capsule (Klein Breteler et al. 1982, Chisholm & Roff 1990). Capsule samples containing various numbers of copepodites of a specific stage were prepared. Between 1 to 6 ind. for *P. elongatus*, and 1 to 25 ind. for *O. similis* were pooled for each determination. Stages C1 to adults for *P. elongatus*, and C2 to adults for *O. similis* were examined. Prosome lengths of all copepodites within each capsule were measured, and the arithmetic mean applied when determining the length–weight regression. After drying samples at 60°C for 24 h, samples were allowed to cool at room temperature for 24 h in a desiccator before being weighed. The capsules were then analysed for carbon using an Elemental Analyser (Carlo Erba). Length–weight relationships were determined for both species using the equation:

$$\text{Log}_{10} W = a + [b (\text{Log}_{10} L)] \quad (4)$$

where a and b are constants, W is carbon mass (µg C) and L is prosome length (µm).

Abundance, biomass and adult production rates. To estimate the abundance of the copepods, samples were collected with both a 68 and a 200 µm mesh net (mouth diameters of 0.3 and 0.4 m respectively). Samples were preserved in 4 % formaldehyde solution for later identification in the laboratory using a dissecting microscope. The abundance of all stages of *Oithona similis* was determined from the analysis of samples from the 68 µm mesh net. For *Pseudocalanus elongatus*, nauplii and C1 stages were counted from the 68 µm mesh net samples, while the abundance of the C2 to adult stages was derived from the 200 µm mesh net. The choice of which net data to apply was made based on an examination of which net gave the greatest abundances of stages (data not shown).

Identification and staging of animals was based on published keys for *Pseudocalanus* and *Oithona* (Ogilvie 1953, Sazhina 1985, Frost 1989) including web resources (<http://copepodes.obs-banyuls.fr/en>). Prosome lengths of copepodite stages were measured using the 68 µm mesh samples. The mass of each copepodite stage (C1 to adult) was calculated by applying a monthly mean prosome length for each stage to our length–weight equation, and then multiplying this by the stage and sex-specific abundance to determine biomass. Total biomass (B , µg C m⁻³) was obtained by summing all copepodite stages excluding nauplii.

Weight-specific fecundity rates (WSFR, d⁻¹) were obtained as:

$$\text{WSFR} = \text{EPR}_{0-24} \times \frac{W_e}{W_f} \quad (5)$$

where W_e and W_f are the egg and adult female carbon weights respectively. We applied egg mass C of 0.014 and 0.14 µg C egg⁻¹ for *Oithona similis* and *Pseudo-*

calanus elongatus, respectively, as estimated from egg volume assuming a conversion factor of $0.14 \times 10^{-6} \mu\text{g C } \mu\text{m}^{-3}$ (Kiørboe et al. 1985, Huntley & Lopez 1992, Uye & Sano 1995). The adult weights were based on the arithmetic mean lengths of females in the incubation experiments, as predicted by our length–weight equations.

Adult female production rates (PR, $\mu\text{g C m}^{-3} \text{ d}^{-1}$) were obtained by multiplying the biomass of adult females (B_f , $\mu\text{g C m}^{-3}$) by the weight-specific fecundity rate (WSFR):

$$\text{PR} = B_f \times \text{WSFR} \quad (6)$$

We applied a modified Michaelis-Menten relationship to describe the relationship between egg production rates (EPR, eggs female $^{-1} \text{ d}^{-1}$) and chl *a* concentration (mg m^{-3}) (Ward & Hirst 2007):

$$\text{EPR} = y_0 + \frac{a \times (\text{Chl } a)}{b + (\text{Chl } a)} \quad (7)$$

where y_0 is the egg production rate when chl *a* is zero. This equation does not assume that egg production converges at 0 as chl *a* levels approach 0.

RESULTS

Temperature and chl *a* concentrations varied on a seasonal basis over the course of this investigation (Fig. 2). Temperature was lowest in February and March when surface and bottom waters were $\sim 6^\circ\text{C}$. Temperature rose steadily through spring and reached a peak at 16.1°C in July. From early July to late Sep-

tember, temperatures were between ~ 12 and 16°C . The difference in temperature between surface and bottom waters rarely exceeded 1°C , although there were isolated instances of a $>2^\circ\text{C}$ difference. Temperature fell, starting late September, reaching its minimum once again in February. Chl *a* demonstrated low values throughout the winter months of November to February, increasing greatly in April to a peak of 10.2 mg m^{-3} . From late May until late October, values rarely fell below 2 mg m^{-3} . A second peak was evident in August, again being $>10 \text{ mg m}^{-3}$.

Egg production

Copepod egg production rates (EPR_{0-24}) varied markedly with season (Figs. 3a & 4a), with maximum rates in early June for *Pseudocalanus elongatus* ($7.41 \text{ eggs female}^{-1} \text{ d}^{-1}$) and in July for *Oithona similis* ($4.00 \text{ eggs female}^{-1} \text{ d}^{-1}$). *P. elongatus* EPR rose sharply in May, falling back in June, and then somewhat varied over the remainder of the year, but remained $>0.7 \text{ eggs female}^{-1} \text{ d}^{-1}$ until late November. *O. similis* EPR were greatest in May and July, and stayed $>0.7 \text{ eggs female}^{-1} \text{ d}^{-1}$ from June until November.

Oithona similis annual average EPR_{0-24} and EPR_{24-48} values were $1.01 (\pm 0.532, 95\% \text{ CI})$ and $0.51 (\pm 0.337, 95\% \text{ CI})$ eggs female $^{-1} \text{ d}^{-1}$, respectively (Table 1, Fig. 5). *Pseudocalanus elongatus* annual average EPR_{0-24} and EPR_{24-48} rates were 1.79 and $1.23 \text{ eggs female}^{-1} \text{ d}^{-1}$, respectively (Table 1). In both species, average rates were lower on the second day of incubation than on the first. However, paired *t*-tests showed

Fig. 2. Surface (1 m) and bottom (45 m) water temperature and surface chlorophyll *a* concentration at the Stonehaven site in the northern North Sea

Fig. 3. *Pseudocalanus elongatus*. (a) Daily egg production rate calculated as EPR₀₋₂₄ and EPR₀₋₄₈; (b) clutch size of ovigerous females $\pm$ SD after 24 h; (c) proportion of ovigerous females after 24 h (* denote a value of 0); and (d) prosome length (μ m; $\pm$ 95 % CI) of adult females in the incubation experiment at the Stonehaven site (northern North Sea)

Fig. 4. *Oithona similis*. (a) Daily egg production rate calculated as EPR₀₋₂₄ and EPR₀₋₄₈; (b) clutch size of ovigerous females $\pm$ SD after 24 h; (c) proportion of ovigerous females after 24 h (* denote a value of 0); and (d) prosome length (μ m; $\pm$ 95 % CI) of adult females in the incubation experiment at the Stonehaven site (northern North Sea)

Table 1. *Oithona similis* and *Pseudocalanus elongatus*. Comparison of egg production rates (EPR, eggs female⁻¹ d⁻¹) for the incubation method over 0 to 24 (EPR₀₋₂₄), 0 to 48 (EPR₀₋₄₈) and 24 to 48 (EPR₂₄₋₄₈) h, and for the egg-ratio method (EPR_p). n = 18 paired observations for all methods. *p < 0.05; ns: not significant. See Fig. 5

Species	Method (EPR)	Annual mean (95 % CI)	Annual range	— Paired <i>t</i> -test comparisons —		
				EPR ₀₋₄₈	EPR ₂₄₋₄₈	EPR _p
<i>Oithona similis</i>	EPR ₀₋₂₄	1.01 (0.532)	0.00–4.00	0.092 ns	0.092 ns	0.775 ns
	EPR ₀₋₄₈	0.76 (0.349)	0.00–2.25	–	0.092 ns	0.057 ns
	EPR ₂₄₋₄₈	0.51 (0.337)	0.00–2.53	–	–	0.031 *
	EPR _p	1.06 (0.476)	0.00–3.23	–	–	–
<i>Pseudocalanus elongatus</i>	EPR ₀₋₂₄	1.79 (0.896)	0.00–7.41	0.152 ns	0.152 ns	
	EPR ₀₋₄₈	1.51 (0.752)	0.00–6.35	–	0.152 ns	
	EPR ₂₄₋₄₈	1.23 (0.776)	0.00–5.29	–	–	

no significant differences between EPR₀₋₂₄ and EPR₂₄₋₄₈ ($p > 0.05$) for both species. EPR of *O. similis* in the egg-ratio method (EPR_p) averaged 1.06 eggs female⁻¹ d⁻¹ (± 0.476 , 95 % CI). Paired *t*-tests indicated EPR_p to be significantly different from EPR₂₄₋₄₈ ($p = 0.031$), but not from either EPR₀₋₂₄ or EPR₀₋₄₈. Results from the egg-ratio method therefore concurred with those obtained during the first 24 h of incubation (EPR₀₋₂₄) (Table 1).

The relationship between log_e EPR₀₋₂₄ and temperature was significant for *Pseudocalanus elongatus* ($p < 0.05$), but not for *Oithona similis* ($p > 0.05$), while log_e EPR_p was significantly related to temperature in *O. similis* (Fig. 6a,b). Further, the modified Michaelis-Menten relationships between both EPR₀₋₂₄ and EPR_p and chl *a* in *O. similis* were significant ($p < 0.001$) (Fig. 6d). The same is true in the case of EPR₀₋₂₄ in *P. elongatus* ($p < 0.001$) (Fig. 6c).

Clutch size

Our incubation results showed that the numbers of eggs in clutches were significantly correlated with the prosome lengths of the female *Pseudocalanus elongatus* that actually produced the eggs ($p = 0.036$), although the variability explained was very small (an r^2 of just 0.088; Table 2). The relationship was highly influenced by 4 values measured in the 31st March 2003 sample, which had very low clutch sizes given the prosome length of the females. This may be explained by the fact that temperature was low, food was scarce (chl *a* concentrations low), and many females had passed through winter conditions. Removing this date resulted in an r^2 of 0.294, which was highly significant ($p < 0.0001$) (Table 2). Comparing mean clutch sizes with mean prosome lengths of all females (i.e. data in Figs. 3b,d & 4b,d) over the annual cycle resulted in an insignificant relationship ($p = 0.136$).

Fig. 5. *Oithona similis*. Egg production rates (eggs female⁻¹ d⁻¹) obtained from the incubation (EPR₀₋₂₄, EPR₀₋₄₈ and EPR₂₄₋₄₈) and the egg-ratio method (EPR_p) at the Stonehaven site. (a) Rates plotted over the annual sampling period, (b) rates expressed as a percentage of the EPR₀₋₄₈ values (± 95 % CI)

Pseudocalanus elongatus:

$$\nabla \log_e \text{EPR}_{0-24} = (0.169T) - 1.376 \quad [r^2 = 0.216, p < 0.05]$$

$$\nabla \text{EPR}_{0-24} = -4.141 + \frac{8.084 \times \text{Chl } a}{0.217 \times \text{Chl } a} \quad [r^2 = 0.659, p < 0.001]$$

Oithona similis:

$$\nabla \log_e \text{EPR}_{0-24} = (0.079T) - 0.512 \quad [r^2 = 0.173, p < 0.05\text{ns}]$$

$$\circ \log_e \text{EPR}_p = (0.116T) - 1.077 \quad [r^2 = 0.256, p < 0.05]$$

$$\nabla \text{EPR}_{0-24} = -0.471 + \frac{2.076 \times \text{Chl } a}{0.243 \times \text{Chl } a} \quad [r^2 = 0.489, p < 0.001]$$

$$\circ \text{EPR}_p = -3.741 + \frac{5.669 \times \text{Chl } a}{0.101 \times \text{Chl } a} \quad [r^2 = 0.662, p < 0.001]$$

Fig. 6. *Pseudocalanus elongatus* and *Oithona similis*. Egg production rates versus (a,b) temperature and (c,d) chlorophyll a concentration. Triangles and solid lines denote EPR_{0-24} data, circles and broken lines denote EPR_p data

Table 2. *Pseudocalanus* spp. Comparison of the relationships between clutch size (C , eggs) and prosome length (L , μm). Values from this study are compared with published equations. Relationships are presented for this study with and without including the data from March 31 (see text for details). * $p < 0.05$, ** $p < 0.01$; ns: not significant

Species	Condition	Relationship	p	r^2	n	Source
Clutch producing females						
<i>P. elongatus</i>	Without 31 March	$C = 0.0000436 L^{1.847}$	$<0.0001^{**}$	0.29	46	Present study
<i>P. elongatus</i>	With 31 March	$C = 0.02 L^{0.940}$	0.036*	0.09	50	Present study
All females over seasonal cycle						
<i>P. elongatus</i>	—	$C = 0.0016 L^{1.291}$	0.136 ns	0.16	15	Present study
Published relationships						
<i>P. mimus</i>	—	$C = 18.17 + 50.56 \times \ln(L/1000)$	$<0.001^{**}$	0.347	—	Napp et al. (2005)
<i>P. newmani</i>	—	$C = 29.81 + 63.62 \times \ln(L/1000)$	$<0.001^{**}$	0.595	—	Napp et al. (2005)
<i>P. newmani</i>	—	$C = 22.391(L/1000)^{3.562}$	$<0.001^{**}$	0.903	7	Ban et al. (2000)
<i>P. minutus</i>	—	$C = 19.35(L/1000)^{3.939}$	—	0.951	—	McLaren (1963)
<i>Pseudocalanus</i> sp.	—	$C = 0.040L - 19.1$	$<0.0001^{**}$	0.66	—	Hopcroft & Kosobokova (2010)

The mean clutch size of *Pseudocalanus elongatus* had a clear seasonal cycle (Fig. 3b), generally increasing from 1 egg clutch⁻¹ in February to 20 eggs clutch⁻¹ in June, the maximum size observed being 28 eggs (Table 3). Mean clutch size then decreased with time after June, except for a somewhat higher mean value of 13.3 in October.

In 8.3% of cases, individual *Oithona similis* only produced 1 sac during their incubation, in which cases we reported the clutch size from this single egg sac. *O. similis* did not produce eggs from late November through February; during the rest of the year, there was no clear seasonal pattern in the number of eggs in the clutches produced (Fig. 4b). The average size of the clutch ranged from 7.5 to 20.0 eggs clutch⁻¹. The relationship between clutch size and prosome length in *O. similis* was not significant either when assessed by examining those females that actually produced the clutches in incubations ($p = 0.772$), or by examining the mean size of females (regardless of whether they produced a clutch or not) against mean clutch size ($p = 0.601$).

Ovigerous females

The highest number of ovigerous females after 24 h of incubation occurred in May for *Pseudocalanus elongatus*, and in July for *Oithona similis* (Figs. 3c & 4c). The percentage of ovigerous females was highly correlated with EPR_{0-24} in both *P. elongatus* ($r^2 = 0.832$, $p < 0.0001$) and *O. similis* ($r^2 = 0.958$, $p < 0.0001$), while no significant relationship was noted between clutch size and EPR_{0-24} in both species.

Prosome length and length–weight relationship

Seasonal changes in the prosome lengths of both *Pseudocalanus elongatus* and *Oithona similis* were observable at the Stonehaven site (Figs. 3d & 4d, respectively), with lengths changing by >25% over the year in both species. The small adults that were present in February 2003 were likely to be individuals that survived the winter (and which were in effect produced around the late-autumn period of the previous year). The rapid increase in prosome length that was observed in February to March might be due to the recruitment of a new generation, which could have developed in the cold temperatures recorded in these early months (there were nauplii and copepodites in this period, confirming recruitment, see Figs. 7 & 8). The decline in prosome lengths from April until June/July was likely caused by continual recruitment of smaller adults, which probably developed at warmer

Table 3. *Oithona similis* and *Pseudocalanus elongatus*. Comparison of total clutch size, absolute ranges (across individual animals) and means (seasonal). Clutch size is for the single egg sac/mass for *Pseudocalanus*, and for the pair of sacs combined for *Oithona*. For laboratory kept animals (Lab.), only experiments using saturated food conditions are included here. Incub. refers to the sampling of females at sea and subsequent incubation in natural seawater at site temperature for up to 48 h. Mesh results are based on field collected females with 2 sacs still attached after collection

Species (n)	Clutch size		Condition		Location	Period	Source
	Range	Mean (95% CI)	Type	T (°C)			
<i>P. elongatus</i> (50)	1–28	12.2 (1.78)	Incub.	6.3–14.7	Northern North Sea	Feb 03–Feb 04	Present study
<i>P. elongatus</i>	1–41	–	Incub.	5–18	Southern North Sea	Feb 04–May 05	Renz et al. (2008)
<i>P. elongatus</i>	3–31	18.3	Lab.	12.5	Southern North Sea	–	Paffenhöfer & Harris (1976)
<i>P. elongatus</i>	–	11.3	Lab.	4	Southern North Sea	–	Corkett & Zillioux (1975)
<i>P. elongatus</i>	–	13.8	Lab.	8.4	Southern North Sea	–	Corkett & Zillioux (1975)
<i>P. elongatus</i>	–	11.5	Lab.	16.2	Southern North Sea	–	Corkett & Zillioux (1975)
<i>Pseudocalanus</i> spp.	2–25	–	Incub.	4–20 ^a	Central Baltic Sea	Mar 02–May 03	Renz et al. (2007)
<i>Pseudocalanus</i> spp.	5–38	–	Incub.	–0.5–20	Southern North Sea	Jul 95–Aug 96	Halsband & Hürche (2001)
<i>O. similis</i> (24)	5–22	14 (1.69)	Incub.	6.3–14.7	Northern North Sea	Feb 03–Feb 04	Present study
<i>O. similis</i>	18–29	–	Mesh	1.5–8	Kola Bay, Barents Sea	1999–2006	Dvoretsky & Dvoretsky (2009a)
<i>O. similis</i>	14–32	21.5	Mesh	–1.6–10	Barents Sea	Aug 2006, Aug–Sep 2007	Dvoretsky & Dvoretsky (2009b)
<i>O. similis</i>	–	13.7	Lab.	15	Danish Straits	–	Sabatini & Kjørboe (1994)
<i>O. similis</i>	–	16.7	Lab.	10	Nova Scotia, Atlantic	–	Eaton (1971)

^(a) Maximum temperature of highly stratified waters

temperatures (Fig. 2). Between June and October, sizes varied little, but declined sharply again in late October in *Oithona*. This sharp decline might partly be related to poor feeding and the highest temperatures in the preceding month, i.e. September, when some of these adults might have been developing as juveniles. Although there was also a slight decline in prosome length in October to November in *Pseudocalanus*, this was not as dramatic as in *Oithona*.

The length–weight regressions for *Oithona similis* and *Pseudocalanus elongatus* were highly significant ($p < 0.0001$). Our values are very similar to published

length–weight regressions (*Pseudocalanus* spp.: Klein Breteler et al. (1982), Hay et al. (1988) and Liu & Hopcroft (2008); *Oithona similis*: Uye (1982) and Sabatini & Kiørboe (1994).

Abundance, biomass and weight-specific fecundity rates

Pseudocalanus elongatus density (nauplii to adults inclusive) ranged between 9 and 2039 ind. m^{-3} over the period of study (Fig. 7a). Copepodite density (C1 to

Fig. 7. *Pseudocalanus elongatus*. (a) Abundance of nauplii, copepodites (C1–C5), and adult females and males; (b) biomass of copepodites (C1–C5), and adult males and females, and (c) production rate and weight-specific fecundity rate (WSFR) of adult females over the period Dec 2002 to Feb 2004 at Stonehaven

Fig. 8. *Oithona similis*. (a) Abundance of nauplii, copepodite (C1–C5), and adult females and males; (b) biomass of copepodites (C1–C5), and adult females and males, and (c) production rate and weight-specific fecundity rate (WSFR) of adult females over the period Dec 2002 to Jan 2004 at Stonehaven

adults inclusive) ranged between 9 and 1138 ind. m^{-3} , and C1 to adult biomass between 19 and 2696 $\mu\text{g C m}^{-3}$ (Fig. 7b). A peak in the biomass of copepodites and females was noted at the end of April, with a second peak in July. The maximum adult female production rate ($27.1 \mu\text{g C m}^{-3} \text{d}^{-1}$; Fig. 7c) occurred at the end of April, with secondary peaks in production occurring in July and September. The weight-specific fecundity rate reached its maximum of 0.22d^{-1} in early June, with rates exceeding 0.1d^{-1} from May to July. Adult males were typically less abundant than adult females, with a sex ratio (male:female) across all sampling dates of $0.40 (\pm 0.37 \text{SD})$.

The density of *Oithona similis* ranged between 73 and 5540 ind. m^{-3} (Fig. 8a). Copepodite (C1 to adults inclusive) density was between 51 and 1975 ind. m^{-3} . Biomass (Fig. 8b) reached a maximum of $590 \mu\text{g C m}^{-3}$ in September. The maximum weight-specific fecundity rate was noted in July (0.12d^{-1}), and rates exceeded 0.02d^{-1} from May until October (except on a single date in June when values were very low). Production rates of adult females showed a first peak in May ($5.4 \mu\text{g C m}^{-3} \text{d}^{-1}$) and maximum values in early September ($10.6 \mu\text{g C m}^{-3} \text{d}^{-1}$). Adult males were much less abundant than adult females, with a mean sex ratio (male:female) across all sampling dates of $0.11 (\pm 0.19 \text{SD})$; male abundance never exceeded 61.2ind. m^{-3} .

The biomass of *Oithona similis* (Fig. 8b) was lower than that of *Pseudocalanus elongatus* (Fig. 7b). In contrast, *P. elongatus* was commonly less abundant, these differences being a consequence of the much smaller body size of *O. similis*. Both species had lower overall biomass during parts of May and June compared to the other spring and summer months. Adult female production rates in both species were rather variable over the course of the year, but highest in May and September in *O. similis*, and highest in April and then from June to September in *P. elongatus*. The production rates of females did not always closely follow the seasonal pattern in weight-specific fecundity rates, this mismatch being a result of the great variability in adult female abundance and biomass (production being the product of biomass and weight-specific fecundity).

DISCUSSION

Egg production

In this study, the EPR of *Pseudocalanus elongatus* (EPR_{0-24}) reached a maximum of $7.4 \text{eggs female}^{-1} \text{d}^{-1}$. This is comparable to the maximum of $8 \text{eggs female}^{-1} \text{d}^{-1}$ found for *Pseudocalanus* spp. at Helgoland Roads in the North Sea (Halsband & Hirche 2001), and a

maximum of $9.1 \text{eggs female}^{-1} \text{d}^{-1}$ in the southern North Sea (Renz et al. 2008). Halsband & Hirche (2001) found that egg production largely ceased between December and January, and we observed little to no egg production between December and February at our more northerly location. The range of average *Oithona similis* EPR we observed (0 to $4.0 \text{eggs female}^{-1} \text{d}^{-1}$) are comparable to literature data (Table 4). For example, in various locations in the North Sea, Nielsen & Sabatini (1996) found that rates of *Oithona* sp. egg production in spring ranged from 0.83 to $5.65 \text{eggs female}^{-1} \text{d}^{-1}$.

The EPR_{0-24} values for *Pseudocalanus elongatus* were significantly correlated with temperature in our study (Fig. 6). This was not the case in *Oithona similis*, although the egg-ratio method results were significantly correlated with temperature. Comparisons over a wider range of temperatures and environments suggest that temperature has an important control on *Oithona* EPR (Ward & Hirst 2007, see their Fig. 6), and the EPR we observed fell close to the global temperature-dependent patterns previously reported for this genus (Ward & Hirst 2007). However, when one examines just a narrow temperature range, the variability resulting from seasonal changes in food or other conditions may be too large to observe any significance.

Our results demonstrated a significant relationship between *Pseudocalanus* egg production and chl *a*, with patterns being very similar to those found in the global synthesis of these rates in *Pseudocalanus* spp. by Bunker & Hirst (2004). These authors found no significant relationship for *Oithona* spp. egg production versus chl *a* when using a Michaelis-Menten relationship. In contrast, in the current study, we used the modified equation and found the relationship to be significant. Interestingly, Ward & Hirst (2007) also reported a significant relationship between EPR and chl *a* for *O. similis* in the Scotia Sea using the same equation used here. We suggest this modified Michaelis-Menten equation is a better approach to describing egg production as it allows for a nonzero 0 intercept, i.e. the consumption of non-chlorophyll bearing prey fueling egg production. This is common in *Oithona similis* (Nakamura & Turner 1997) and in *Oithona* spp. more generally (see review in Castellani et al. 2008).

The significant correlation between the percentage of ovigerous females and the EPR_{0-24} as well as the insignificant relationship between clutch size and EPR_{0-24} in both *Pseudocalanus elongatus* and *Oithona similis* suggest that changes in the percentage of ovigerous females may be more important in driving changes in EPR_{0-24} for these species in the northern North Sea.

Table 4. *Pseudocalanus* spp. and *Oithona* spp. Comparison of the ranges (unless otherwise stated) of field rates of egg production (EPR), weight-specific egg production rates (WSFR) and production rates of adult females. Incub. refers to the incubation of females for a maximum of 48 h in screened or filtered natural sea water

Species	Location	T (°C)	Method	EPR (eggs fem ⁻¹ d ⁻¹)	WSFR (d ⁻¹)	Adult female production (µg C m ⁻³ d ⁻¹)	Source
<i>P. elongatus</i>	Northern North Sea	6.3–14.7	Incub.	0–7.4	0–0.22	0–27.1	Present study
	Southern North Sea	5–18	Incub.	0–9.1	0–0.13	–	Renz et al. (2008)
	Northern North Sea	9–12	Incub.	0–2.0	max 0.055	–	Kjørboe & Johansen (1986)
<i>Pseudocalanus</i> spp.	Chukchi Sea, Alaska ^a	–1–6	Incub.	2–9.5	0.015–0.41	–	Hopcroft & Kosobokova (2010)
	Central Baltic Sea	4–20	Incub.	max 3.6	0.01–0.13	–	Renz et al. (2007)
	Northern North Pacific	5–15	Incub.	1–9.3	–	–	Napp et al. (2005)
	Southern North Sea	–0.5–20.2	Incub.	0–8	–	–	Halsband & Hirche (2001)
<i>O. similis</i>	Northern North Sea	6.3–14.7	Incub.	0–4	0–0.12	0–10.6	Present study
	Northern North Sea	6.3–14.7	Egg ratio	0–3.2	0–0.10	0–13.2	Present study
	Barents Sea, Kola Bay	2–8	Egg ratio	0.04–2.2	0.0006–0.046	0.001–3.58	Dvoretsky & Dvoretsky (2009a)
	Barents Sea	–1.6–10	Egg ratio	0.2–1.8	0.005–0.04	mean: 1.24	Dvoretsky & Dvoretsky (2009b)
<i>Oithona</i> spp.	Southern Ocean	–1.5–3.3	Egg ratio	0–1.2	0–0.022	–	Ward & Hirst (2007)
	North Atlantic	3–11.1	Egg ratio	0.7–6	0.017–0.13	0.09–23.5	Castellani et al. (2007)
	North Sea	7–12	Egg ratio	0.83–5.65	0.014–0.095	–	Nielsen & Sabatini (1996)

^aResults shown for all species: *P. acuspes*, *P. newmani* and *P. minutus* at 24 h

Comparing egg production methods

Our results are the first to directly compare these 2 commonly applied egg production methods. Egg-ratio method (EPR_p) results for *Oithona similis* did not significantly differ from EPR_{0–24} or EPR_{0–48} incubations. However, they were significantly different from EPR_{24–48} values (paired *t*-tests, Table 1). The egg-ratio method produced the highest rates on average, with the lowest rate being from EPR_{24–48}.

Results from incubations for the 3 different periods (0–24, 24–48 and 0–48 h) were not significantly different from one another in either *Pseudocalanus elongatus* or *Oithona similis*, although rates were on average lower on the second day (24–48 h) than on the first (0–24 h). Hopcroft & Kosobokova (2010) incubated several species of *Pseudocalanus* in the sub-Arctic Chukchi Sea, and found a significant reduction in EPR between the first and second day of incubation. In their study, and in ours, females were incubated individually in 70 ml tissue culture flasks. This leads to the question: might food be significantly reduced during incubations when using such volumes? A comparison of published clearance rates for *Oithona* and *Pseudocalanus* shows that rates typically vary between ~2 to 10 ml ind.⁻¹ d⁻¹ for *Oithona* spp. (Lampitt and Gamble 1982, White & Roman 1992, Nakamura & Turner 1997, Svensen & Kjørboe 2000), and from 3 to 95 ml ind.⁻¹ d⁻¹ in *P. elongatus* (Paffenhöfer & Turner 1976, Koski et al. 1998, Schultz & Kjørboe 2009). It seems likely that <30% of the food may be cleared in 48 h by *Oithona* at temperatures similar to that in our study, while the maximum clearance of *Pseudocalanus* suggests that a much greater proportion of the food could be cleared. Combining this fact with the apparent reduction in EPR with time (albeit this was not significant in our study), we recommend that larger volumes be used for these species in future studies, especially if the incubation period exceeds 24 h.

Both the egg-ratio and incubation methods have problems. Incubations involve containment, which can change vertical migration habits, diel feeding and the food regime with time, as well as the turbulence experienced. This is important as *Oithona*, unlike many calanoids, does not create feeding currents (Paffenhöfer 1993). It is a raptorial ambush feeder in which levels of turbulence can impact feeding rates (Saiz et al. 2003). While the egg-ratio method overcomes many of the concerns with incubations, it requires accurate collection of adults and eggs, their correct identifi-

cation, and is generally more time consuming. Fortunately, *Oithona* spp. egg sacs were relatively easy to recognise, and typically do not break apart at collection (authors' pers. obs.). However, in other species, the sac may be too fragile or conspecifics may be too difficult to differentiate. *Pseudocalanus elongatus* eggs can be easily dislodged from the egg mass (authors' pers. obs.), and there is no true egg sac membrane. Thus, we did not apply the egg-ratio method to this species in our study.

The female copepods' feeding history prior to capture can determine egg laying rate in the first 24 h of incubation (e.g. Plourde & Runge 1993), and this incubation period is often selected when studying broadcast spawners collected from the wild. However, for egg carrying copepods, the inter-clutch time should also be considered (Hirst & McKinnon 2001). Females that are free of egg sacs are usually selected for incubations. Incubations will include both females that are between clutches at the time of collection, and those females that have lost their eggs during the net collection. The 2 groups will be at different stages in their reproductive cycles, the latter group being likely unable to produce another batch for a considerable period. Extending the incubation period for sac spawners partly counters this problem. Clearly, there should be a balance between incubating for a long enough period to ensure clutches are produced, and minimising incubation artefacts. The lack of any significant difference between EPR_{0-24} and EPR_p in *Oithona* gives us confidence that 24 h incubations were sufficient in this study. The lower average EPR_{24-48} indicates that care needs be taken when incubating animals for >24 h.

Clutch size and prosome length

The average clutch size in *Pseudocalanus elongatus* in the first 24 h of incubation ranged between 1 and 28 eggs (egg mass)⁻¹ in the present study. Other North Sea studies have reported clutch sizes to vary between 5 and 38 (Halsband & Hirche 2001) and 1 to 41 (Renz et al. 2008) (Table 3). There was a clear seasonal signal in the clutch size of *P. elongatus* in our study, which increased through much of February to June and then declined until November. Clutch size in *Oithona similis* had no clear seasonal pattern at Stonehaven, other than being 0 from late December until February, and then >11 eggs clutch⁻¹ through much of the remainder of the year (Fig. 4b). The relationship between clutch size (C) and prosome length (L) ($C = aL^b$) was not significant in this species when assessed by examining either those females that actually produced the clutches in incubations, or the mean size of females

(regardless of whether they produced a clutch or not) against mean clutch size over the course of the study.

The body size of ectotherms (including copepods) has been shown to be related to developmental temperature (temperature size rule; Atkinson 1994), and to a lesser extent to food (Vidal 1980, Dam & Peterson 1991); higher temperatures and lower food concentrations both result in smaller adults. Temperature during development and the changing pattern of recruitment to the adult stage may explain much of the observed change in prosome length over the year. This has additional importance as clutch sizes and reproductive effort have also often been linked to adult female size. A comparison between published relationships between clutch size and prosome length in *Pseudocalanus* are given in Table 2. Corkett & McLaren (1969) found the total volume and/or number of eggs in *Pseudocalanus* spp. clutches to be highly predictable from the female size. Halsband & Hirche (2001) found at the Helgoland Roads site in the North Sea, that the majority of the seasonal variation in mean clutch size (and egg production) over their year long study was explained by changes in mean prosome length in the broadcast spawners *Acartia clausi*, *Temora longicornis* and *Centropages hamatus*. This is an important outcome, suggesting that adult body size is critical to clutch size changes. In the same study, the amount of variability explained by changes in mean prosome length in *Pseudocalanus* was much lower ($r^2 = 0.247$), although still significant. When clutch size was related to female prosome length, the relationship somewhat varied across studies (Table 2), with r^2 values varying from 0.09 to 0.951. However, samples spanning the entire year were included only in Halsband & Hirche (2001), Napp et al. (2005), and the present study. These are also the studies that show a comparatively lower explained variance. While we found a significant relationship when we considered only those females that produced the clutch (Table 2), little of the variation was explained by changes in mean prosome length (<9%), and this relationship improved when we considered other seasonal factors and removed early season data (variation explained then became 29%). This might be because in seasonal studies, females in autumn and spring may have similar sizes, but experience vastly different food quantities and qualities. In addition, mean prosome lengths are the product of various overlapping generations and of adults of different ages. The age of an adult has a profound impact on its EPR (Kimoto et al. 1986). Neither the study of Halsband & Hirche (2001) nor ours support body size as the primary driver of clutch size or EPR in *Pseudocalanus* in the North Sea, and our study further demonstrate the lack of importance of body size in *Oithona*. It is interesting that the broadcast spawners in Halsband &

Hirche (2001) produced strong relationships, while the sac spawners did not. Whether these differences are genuinely related to the spawning strategies is not clear at this stage.

Although we found that clutch size generally increased with chl *a* and then leveled off in *Pseudocalanus elongatus*, there was no clear pattern in *Oithona similis*. Ward & Hirst (2007) also found no observable relationship between clutch size and chl *a* in *O. similis* across the Scotia Sea. *Oithona* are omnivorous species, and microzooplankton can play a greater role in their diets (Castellani et al. 2008), which may explain the lack of a relationship. Hopcroft & Roff's (1996) study on various species of egg carrying copepods in tropical waters also found no significant difference in clutch sizes between locations with contrasting chl *a* concentrations. Although food levels can impact overall EPR in egg carriers, this may act in *Oithona* primarily by altering the interval at which clutches are produced and the numbers of ovigerous females, rather than through clutch size itself.

Ovigerous females

The maximum number of ovigerous *Oithona similis* females found at Stonehaven was 32 %, which compares well with the value of 23 to 41 % in the Barents Sea (Dvoretzky & Dvoretzky 2009a). In the Southern Ocean, Ward & Hirst (2007) found that the proportion of females of *O. similis* carrying eggs varied from 0 to 67 %, but with most values falling between 20 and 40 %. Castellani et al. (2007) found that from 33 to 82 % of females were ovigerous across spring and summer in the Irminger Sea in the northwestern Atlantic. We need to emphasise that while the ovigerous population was defined in the present study as that which produced eggs within 24 h, this was determined directly from the egg sacs collected using nets in Castellani et al. (2007), Ward & Hirst (2007), and Dvoretzky & Dvoretzky (2009a). The percentage of ovigerous females obtained from preserved net samples is the result of the balance between those females that were incapable of producing eggs at all, those females that were actively reproducing and were carrying a clutch, and those females that were actively reproducing but were between clutches. In contrast, the balance between these when incubating females, especially given the synchronised nature of incubating non-egg bearing females to begin an experiment, means that a different balance of egg carrying (ovigerous) females may be reached after incubating for 24 or 48 h. Comparisons between percentages of ovigerous females from incubations versus fixed net samples are therefore not straightforward.

On 8.3 % of occasions in our incubations, individual females of *Oithona similis* produced a single egg sac. Sabatini & Kiørboe (1994) reported a comparable value of 10 %. An assumption of 2 egg sacs female⁻¹ is commonly made when reconstructing data using the egg-ratio method. This is necessary because egg sacs commonly become detached during sampling. Although this is a potential problem with the egg-ratio method (since net samples are in effect used to determine the numbers of egg sacs and the numbers of females these sacs are attributable to, the usual assumption being that each female has produced 2 sacs), it only impacts estimates of the number of ovigerous females and not the average EPR.

In *Pseudocalanus elongatus*, the maximum percentage of ovigerous females was much greater than was achieved in *Oithona similis*, being >40 % after 24 h of incubation and 75 % after 48 h in late May. Our values are broadly similar to those observed by Halsband & Hirche (2001) for *Pseudocalanus* spp. at the Helgoland Roads site in the North Sea, and by Renz et al. (2008) for *Pseudocalanus elongatus* in the southern North Sea (they observed that the percentage of ovigerous females after 24 h of incubation was typically between ~10 and 40 %). Our results show that using a 24 h incubation period commonly gives a much lower value for the percentage of ovigerous females than using a 48 h incubation period, with 48 h values being >3× of the values after 24 h. As already discussed, incubation approaches may present a problem when determining the percentage of ovigerous females in a natural population.

Biomass, weight-specific fecundity and secondary production

At Stonehaven, the biomass of *Pseudocalanus elongatus* was generally higher than that of *Oithona similis*, except in September and November. The *P. elongatus* biomass had peaks in April and July to August, whereas the biomass of *O. similis* had peaks in April, but also in August to September (Figs. 7 & 8). In the southern Kattegat, *Pseudocalanus* spp. biomass was greatest from April to June, while *Oithona* spp. biomass was greatest from late May through September (Kiørboe & Nielsen 1994). Averaged across the whole year, mean copepodite (C1 to adult) biomass was 0.5 mg C m⁻³ (20.7 mg C m⁻² when integrated over the water column) for *P. elongatus*, and 0.1 mg C m⁻³ (integrated = 4.7 mg C m⁻²) in *O. similis* in our study. Nielsen & Sabatini (1996) found that *Oithona* spp. copepodite biomass in the North Sea varied from 0 to ~200 mg C m⁻² over the course of a 10 d spring cruise. Castellani et al.'s (2007) study on *Oithona* spp. in the North

Atlantic gave a mean biomass (including nauplii) of 0.2 mg C m^{-3} in the spring, and 1.1 mg C m^{-3} in the summer. In *O. similis*, the highest seasonal mean in our study was in the summer, at 0.2 mg C m^{-3} .

Weight-specific fecundity rates of both *Pseudocalanus* sp. and *Oithona similis* are compared across a range of locations in Table 4. In *Pseudocalanus elongatus*, the maximum weight-specific fecundity rate was observed in June, at 0.22 d^{-1} , which is almost twice the maximum reported by Renz et al. (2008) of 0.13 d^{-1} in February in the southern North Sea. Kiørboe & Johansen (1986) reported a weight-specific fecundity rate of 0.055 d^{-1} in September in the northern North Sea, stemming from a much lower egg production rate of just $2.0 \text{ eggs female}^{-1} \text{ d}^{-1}$.

Mean production rates for adult females over the year at Stonehaven were $8.9 \mu\text{g C m}^{-3} \text{ d}^{-1}$ in *P. elongatus*, and $1.9 \mu\text{g C m}^{-3} \text{ d}^{-1}$ in *O. similis*, the lower production rates of the latter reflecting the lower weight-specific fecundity and biomass of this species. Changes in population abundance and biomass between sampling dates for both species are not simply a consequence of mortality and growth rates of the populations. Biomass and weight-specific fecundity display strikingly different patterns over the course of the year and, as production is a composite of these 2 factors, this explains why production shows a different temporal pattern from weight-specific fecundity.

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