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Life history characters and population dynamics of the boreal larvacean *Oikopleura vanhoeffeni* (Tunicata) in Conception Bay, Newfoundland

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We examined the population dynamics and life history characters of the boreal larvacean Oikopleura vanhoeffeni *in Conception Bay over two years and determined its role in secondary production. Based on the analysis of age structure inferred from statolith diameter, the generation time was approximately one year. Recruitment of new cohorts and maximum population growth rate occurred in the spring. Somatic growth rate was 0.017 d^{-1} from the year 2001 to 2002 and 0.043 d^{-1} from 2002 to 2003, with an acceleration in growth rate during April in response to the spring diatom bloom despite the coldest water temperatures. The annual production rate (i.e. somatic + house production) of 8.7 g C m^{-2} y^{-1} in 2001/2, and 3.8 g C m^{-2} y^{-1} in 2002/3, represented 2.9–6.7% of primary production and 37–87% of estimated mesozooplankton production, suggesting that* O. vanhoeffeni *is a major secondary producer in Conception Bay. Individuals matured at seasonally variable body size throughout the year and potential fecundity peaked as the individuals matured at their largest body size during the spring bloom, most likely resulting in maximum egg production and population growth rates at that time of year. Thus, a seasonal pulse of food is a major driving force that regulates the variation in life history characters and population dynamics of the boreal* O. vanhoeffeni.

Keywords: larvacean, life history, population dynamics, *Oikopleura vanhoeffeni*, spring bloom

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INTRODUCTION

Larvaceans are pelagic tunicates that are common and abundant in all oceans. Most species are found in the euphotic zone, however new species have also been described from mesopelagic and bathypelagic depths (Fenaux *et al.*, 1998; Hopcroft, 2005). They are important secondary producers in marine ecosystems. Although biomass of these gelatinous zooplankters is generally lower than that of copepods, because of their high growth potential (Hopcroft & Roff, 1995; Nakamura *et al.*, 1997; Hopcroft *et al.*, 1998), production of larvaceans can be 30–100% of copepod production in eutrophic environments (Hopcroft & Roff, 1995, 1998; Nakamura *et al.*, 1997). In favourable conditions, larvaceans can form dense patches that consume up to 50–66% of the standing crop of phytoplankton daily (Alldredge, 1981; Deibel, 1988; Maar *et al.*, 2004). These suspension feeders continuously secrete mucous houses containing a complex set of filters which are used to consume a wide size-range of particles, from colloidal organic matter and pico- and nanoplankton to large diatoms (Deibel & Turner, 1985; Flood *et al.*, 1992; Urban-Rich *et al.*, 2006). Because they are prey for many invertebrates and fish (Purcell *et al.*, 2005), larvaceans efficiently transfer energy within food webs, bypassing the microbial loop by directly transferring very small particulate organic matter to higher trophic levels (Azam *et al.*, 1983; Gorsky & Fenaux, 1998). Larvaceans are also an important part of the biological pump, in the form of faecal pellets and discarded mucous houses containing trapped organic matter (Alldredge, 2005; Robison *et al.*, 2005; Dagg *et al.*, 2008).

Life history, population dynamics, and production of larvaceans have been studied primarily in tropical and temperate regions, and little is known about species living in cold environments. Generation time and growth rates of larvaceans have been estimated in the laboratory (Paffenhöfer, 1976; Sato *et al.*, 1999; Lombard *et al.*, 2009) and in mesocosms where artificial cohorts were created and food particle size and predation effects controlled (Nakamura *et al.*, 1997; Hopcroft *et al.*, 1998). Estimation of production has been based on field biomass data combined with growth rates determined in the laboratory at simulated natural temperatures (Uye & Ichino, 1995; Tomita *et al.*, 1999). In this study, life history characters and production of the cold water larvacean *Oikopleura vanhoeffeni* was determined *in situ* to understand its population dynamics and role as secondary producer in Conception Bay, Newfoundland.

Oikopleura vanhoeffeni is a cryophilic and stenohaline species (Choe & Deibel, 2008) distributed in the Arctic Ocean, and boreal North Pacific and North Atlantic Oceans (Lohmann, 1895; Frost *et al.*, 1932; Galt, 1970; Shiga, 1993a, b). This large larvacean in the epipelagic zone is capable of

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ingesting food particles of a wide size-range (colloid to microplankton; Flood *et al.*, 1992; Acuña *et al.*, 1996) due to the largest inlet filter pore sizes yet reported for any larvacean (Deibel & Turner, 1985). A substantial portion of primary production is removed by this species in the Arctic Ocean and Newfoundland coastal waters (Acuña *et al.*, 2002). The feeding ecology of *O. vanhoeffeni* has been explored in depth, but information regarding its population biology and life history is lacking. In order to study the population biology, age structure needs to be defined by identifying cohorts based on age-related characters. Results from a previous study showed that statolith diameter is a more reliable age indicator than body size in *O. vanhoeffeni*, due to lower and constant variability in statolith diameter-at-age in comparison to the more variable body length-at-age (Choe & Deibel, 2009). Thus, in the present study age structure is determined from frequency distributions of statolith diameter for estimation of generation time and somatic growth rates of identifiable cohorts of *O. vanhoeffeni in situ*.

MATERIALS AND METHODS

Sample collection

Samples were collected from 11 June 2001 to 25 June 2003 at a site in Conception Bay (47°32.2′N 53°07.9′W; Figure 1). The description of the study site can be found in Choe & Deibel (2008). Triplicate, vertical hauls from a near bottom depth of 225 m to the surface were made using a WP-2 ring net with a mesh size of 110 μm. The speed of retrieval was 0.13 m s^{-1} and the volume of water filtered was measured with a mechanical flowmeter (Model 2030 R6, General Oceanics, Inc.) An additional tow was made on each sampling day using a large ring net (1 m mouth diameter) with a 10 l cod end to collect mature individuals without damaging their gonads. Upon retrieval of the nets, samples were immediately fixed in 95% ethanol for statolith analysis and in 2% Bouin's solution for histological analysis of gonads. Samples were collected biweekly except during winter, when harsh weather conditions precluded sampling. A Seabird SBE25 CTD equipped with a SeaTech fluorometer was deployed before each tow to measure temperature and chlorophyll-*a* concentration. A detailed description of conductivity–temperature–depth data analysis is available in Choe & Deibel (2009).

Cohort analysis and generation time

Oikopleura vanhoeffeni were sorted from the samples which had been preserved in 95% ethanol. It was important to rinse the samples with 95% ethanol instead of water before sorting because addition of distilled water to the tow samples decreases the pH and dissolves the statolith. Trunk lengths of larvaceans were measured from the tip of the mouth to the posterior tip of the stomach, excluding gonads, to the nearest 25 μm under a Zeiss stereo microscope at ×40 magnification. After trunk length measurements, the individuals were cleared in 1% KOH and mounted on microscope slides in glycerol. The diameters of statoliths were measured to the nearest 0.5 μm using a Zeiss Axiovert 35 inverted microscope under transmitted light and bright field optics at ×1000 magnification. Location and morphology of statolith in larvaceans are described in Choe & Deibel (2009).

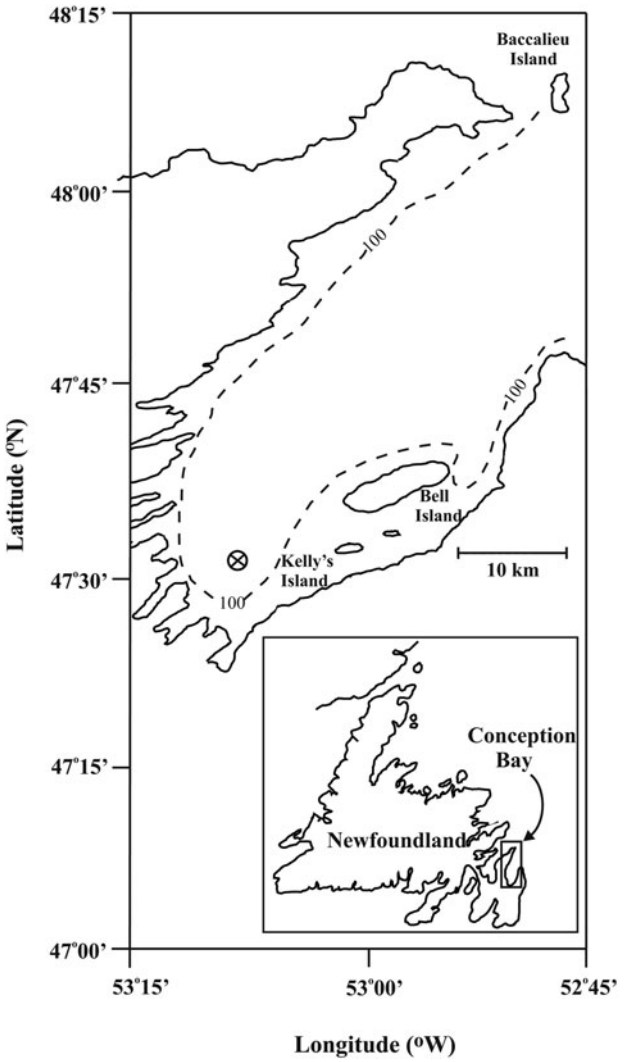

Fig. 1. Map of Conception Bay, Newfoundland (Choe & Deibel, 2008). 'X' indicates the sampling site at which *Oikopleura vanhoeffeni* were collected, and the dotted line indicates the 100 m isobath. The bottom depth at the sampling site was ~250 m.

Cohorts of *O. vanhoeffeni* were identified using the Bhattacharya method (Bhattacharya, 1967) on statolith diameter frequency distributions binned at 1 μm intervals. The FiSAT II software package (FAO-ICLARM Fish Stock Assessment Tools, Version 1.2.0) was used to separate the components of the normal distributions of statolith diameter from the total frequency distribution, starting on the left-hand side. Component normal distributions were removed iteratively until they could no longer be distinguished using the separation index $SI = \Delta L_k/\Delta\delta_k$, where ΔL_k is the difference between two successive means of component curves and $\Delta\delta_k$ is the difference between their estimated standard deviations (Sparre & Venema, 1998). The separation of cohorts was statistically reliable when the SI value was above 2 (Hasselblad, 1966; McNew & Summerfelt, 1978; Clarke, 1981).

Generation time of each cohort was estimated as the number of elapsed days between its appearance and disappearance. The elapsed time from egg release until the juveniles

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reach sufficient size to be quantitatively collected in the plankton tow at 0–1°C is approximately 7 days (laboratory observations), which may be the maximum underestimation of generation time in this study.

Population growth rate

For determination of population growth rate, animals from the triplicate net tow samples were counted. Larvacean abundance was determined from subsamples produced using a Motoda zooplankton sample splitter (Motoda, 1959). The animals were viewed and counted under a Zeiss stereomicroscope at ×40 and ×60 magnifications. The number of animals counted depended upon their seasonal abundance, ranging from 1–464 subsample^{-1}. The number counted in each subsample resulted in median 95% confidence intervals (i.e. analytical error) of 18% of the count (Alden, 1982). Population growth rate was calculated using the equation, $r = (\ln N_{ti+1} - \ln N_{ti})/(t_{i+1} - t_i)$ (Odum, 1971), where N represents mean abundance and 't' time in days at the i^{th} time point. In order to smooth the data to reduce stochastic variability a three-point moving average was applied to the abundance data prior to the calculation of population growth rate (Diggle, 1990). Throughout the study, it was assumed that the individuals sampled in Conception Bay all belonged to a single population, because the actual spatial scale of the entire population of *O. Vanhoeffeni* is not known.

Somatic growth rate and production

For the estimation of growth rate, trunk lengths of individual *O. vanhoeffeni* within each cohort were converted to carbon weight using the equation $C\ (\mu g) = 4.03\ TL\ (mm)^{3.45}$ (Deibel, 1988). Trunk lengths of individuals fixed in 95% ethanol were corrected for shrinkage by 18.0 ± 3.0% (N = 14) before conversion to weight. To test if the somatic growth pattern of the cohorts was exponential, the relationship between ln-transformed weight and time for each cohort was examined for linearity. If this linear relationship was statistically significant, instantaneous growth rate was estimated by fitting the exponential growth function $W_t = W_o\ e^{gt}$, where W_o represents the initial mean weight, W_t the mean weight of each cohort at time 't' and 'g' the instantaneous growth rate (d^{-1}). If the relationship between ln-weight and time was not linear, one-way ANOVA and *post-hoc* analysis (Tukey test) were used to determine the time periods when significant growth occurred, and the instantaneous growth rate within these time periods was estimated using the equation $W_t = W_o\ e^{gt}$. All statistical analyses were performed with SPSS 9.0.0 (SPSS Inc., Chicago, IL).

Daily somatic production was computed as $Pg = g \times B$, where g (d^{-1}) represents the instantaneous growth rate and B (mg C m^{-2}) the biomass in carbon weight at each sampling day. Biomass was estimated by converting the trunk length–frequency distribution into a carbon weight–frequency distribution and multiplying the distribution by the mean abundance data from triplicate samples. Production of *O. vanhoeffeni* from 2001 to 2002 and 2002 to 2003 was calculated using the instantaneous growth rates of cohort 2 and cohort 3 respectively (see Results). Daily production was integrated over each year to estimate annual production, assuming that each data point remained constant between the sampling intervals. Daily somatic production was integrated over each year using the midpoint rule:

$$Pg = \int_a^b f(x)dx \approx \sum_{k=1}^{n} [Y_k + (Y_{k+1} - Y_k)/2](X_{k+1} - X_k)$$

where the integration of production over time series (a to b) was approximated by summing the rectangular area under the time series curve where the area of the rectangle is centred at the midpoint between two successive sample points, k and k + 1. Y and X represent daily production in mg C m^{-2} and sampling time in days, respectively.

The daily house production (Pe) of *O. vanhoeffeni* ranged from <1 to 6 houses d^{-1} with a mean of 1.6 ± 1.0 houses d^{-1} at temperatures from −1 to 6°C (Riehl, 1992). Given that the carbon content of a clean house is about 23% of body carbon (Deibel, 1986), *O. vanhoeffeni* produces approximately 37% of its body weight in houses each day (Deibel, 1988). Thus, the daily house production rates of *O. vanhoeffeni* were estimated as 37% of the somatic weight. Annual house production was integrated between each collection interval and summed over each year of the study using the midpoint rule.

Size at maturity and potential fecundity

Mature individuals (with a well-developed gonad expanded and covering the area of the entire posterior trunk; Shiga, 1976, 1993a) were sorted from the samples preserved in Bouin's solution and their trunk lengths measured. Mean trunk length at maturity was calculated at each sampling time point whenever mature individuals were found. Replicate individuals at these mean trunk lengths (2–3 individuals) were removed from the samples between 20 February 2002 and 25 June 2003, dehydrated in a graded ethanol/water series and cleared in xylene. They were then embedded in paraffin and serially sectioned at 6 μm intervals. Sections were stained with haematoxylin and eosin to help visualize the oocytes and ovary. The sections of ovary often contained developing oocytes and accessory cells. The total area occupied by the oocytes and their mean diameter were measured at ×4 to ×20 magnifications using ImagePro software (Version 4.0). Potential fecundity was calculated as: potential fecundity = total volume of oocytes/mean volume of an oocyte; total volume of oocytes = volume of ovary × mean % of ovary area occupied by oocytes. Volume of ovary = Σ area of ovary in every consecutive N^{th} section × N × 6 μm, where N = 1/10 of total thin sections taken. Mean % of ovary area occupied by oocytes was calculated from all thin sections of ovary observed. Mean volume of oocytes = 4/3 π × (mean radius of oocyte)^3 and the mean volume of an oocyte was calculated from all the measured oocytes. The number of oocytes measured for *O. vanhoeffeni* ranged from 23 to 177 oocytes. Potential fecundity is likely an overestimate of actual fecundity because not all oocytes reach maturity and those that fail to mature are eventually reabsorbed (Last, 1972; Ganot *et al.*, 2008). True fecundity was not determined in this study because of the difficulty in obtaining individuals with fully mature but unruptured gonads using net tows. However, true fecundity could be approximately 50% of potential fecundity if oogenesis of *O. vanhoeffeni* is similar to that of *Oikopleura dioica*, in which nearly 50% of oocytes are reabsorbed at the end of maturation (Last, 1972).

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RESULTS

Temperature and chlorophyll-*a* concentration

Temperature fluctuated seasonally in the upper mixed layer with an increase to a maximum of 15.4–16.6°C in late August and a decrease to a minimum of 1.0 to −0.8°C in late March to early April (Figure 2A). A thermocline was present within the upper 60 m from June to December which eroded as winter mixing occurred to a depth of 100 to 150 m. The temperature below 150 m remained <0°C throughout the time series. Seasonal variation in chlorophyll-*a* concentration occurred mostly within the upper 100 m (Figure 2B). The spring bloom began in March and peaked in May with a maximum chlorophyll-*a* concentration of 5.8 μg l^{-1} in 2002 and 3.5 μg l^{-1} in 2003. A minor bloom occurred in August 2001 (2.4 μg l^{-1}). The minimum concentration of chlorophyll-*a* was found in July 2001 (0.9 μg l^{-1}) and in October 2002 (1.0 μg l^{-1}). Given that most larvaceans live in the upper 100 m of the water column year around (Choe & Deibel, 2008), habitat temperature and chlorophyll-*a* used for statistical analyses are represented by the mean values of 100, 1-m depth bins within the upper 100 m of the water column.

Generation time and population growth rate

Four cohorts of *Oikopleura vanhoeffeni* were identified between June 2001 and June 2003 (Figures 3 & 4A). Based upon the first appearance of cohort 3 (2002) and cohort 4 (2003), the primary annual spawning event appears to have begun between mid-February and mid-April. Because larvaceans are semelparous, the final appearance of cohorts 1 (2001), 2 (2002) and 3 (2003) suggests that the annual spawning events ended between mid-April and mid-June. Some individuals in cohorts 2 and 3 became sexually mature early, in the autumn of their first year at a small statolith diameter (shaded ranges of statolith diameter-at-maturity in Figure 4A). However, there is no evidence in the cohort analysis or in the time series of population growth rate (Figure 4A, B) that successful recruitment occurred in autumn. In autumn (October and November) the scarcity of animals precluded frequency analysis of the age distribution. Based upon all of the evidences above, the generation time of *O. vanhoeffeni* was essentially one year.

As the new cohorts recruited in spring (cohorts 2 and 3; Figure 4A), population growth rates reached a maximum of 0.08 d^{-1} at the end of April 2002 and 0.18 d^{-1} in May 2003 (Figure 4B). *Oikopleura vanhoeffeni* suffered high mortality during late summer with negative growth rates of −0.15 d^{-1} in August of both years (Figure 4B). There was little or no evidence of overwintering mortality.

Somatic growth, population biomass and production

Animals from cohort 2 grew exponentially over an entire year (Figure 5A, B) with an instantaneous rate of 0.017 d^{-1}.

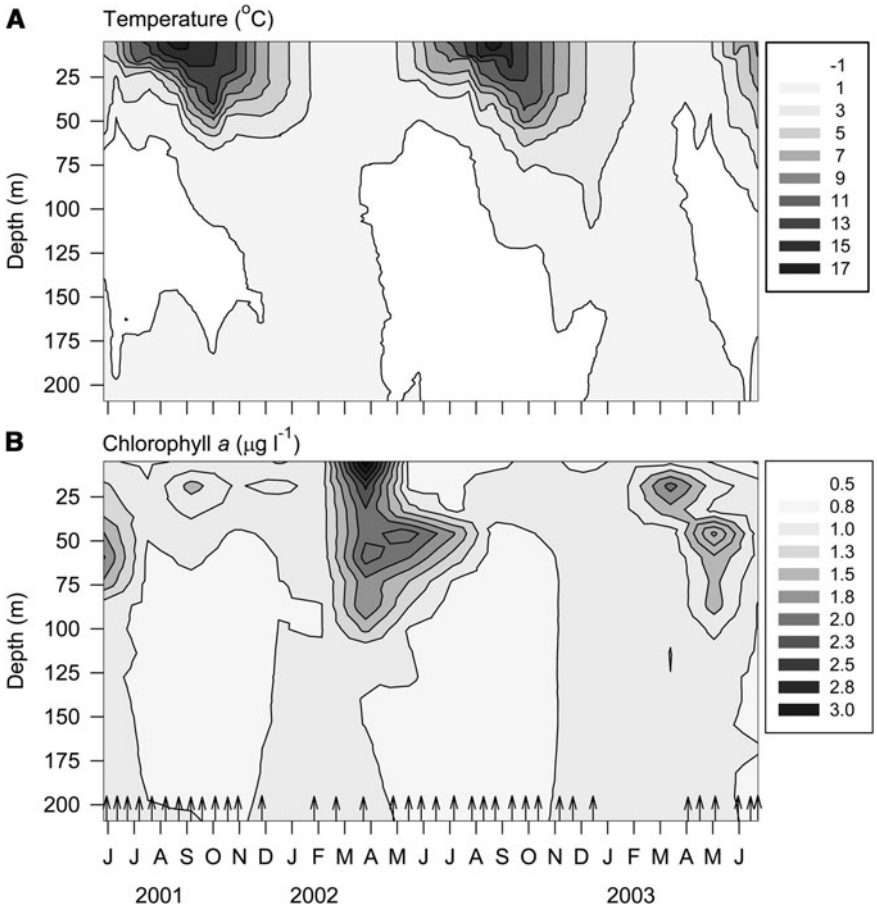

Fig. 2. Time–depth profiles of (A) temperature, and (B) concentration of chlorophyll-*a* in Conception Bay from June 2001 to June 2003 (Choe & Deibel, 2009). The arrows above the X axis indicate when conductivity–temperature–depth casts were made.

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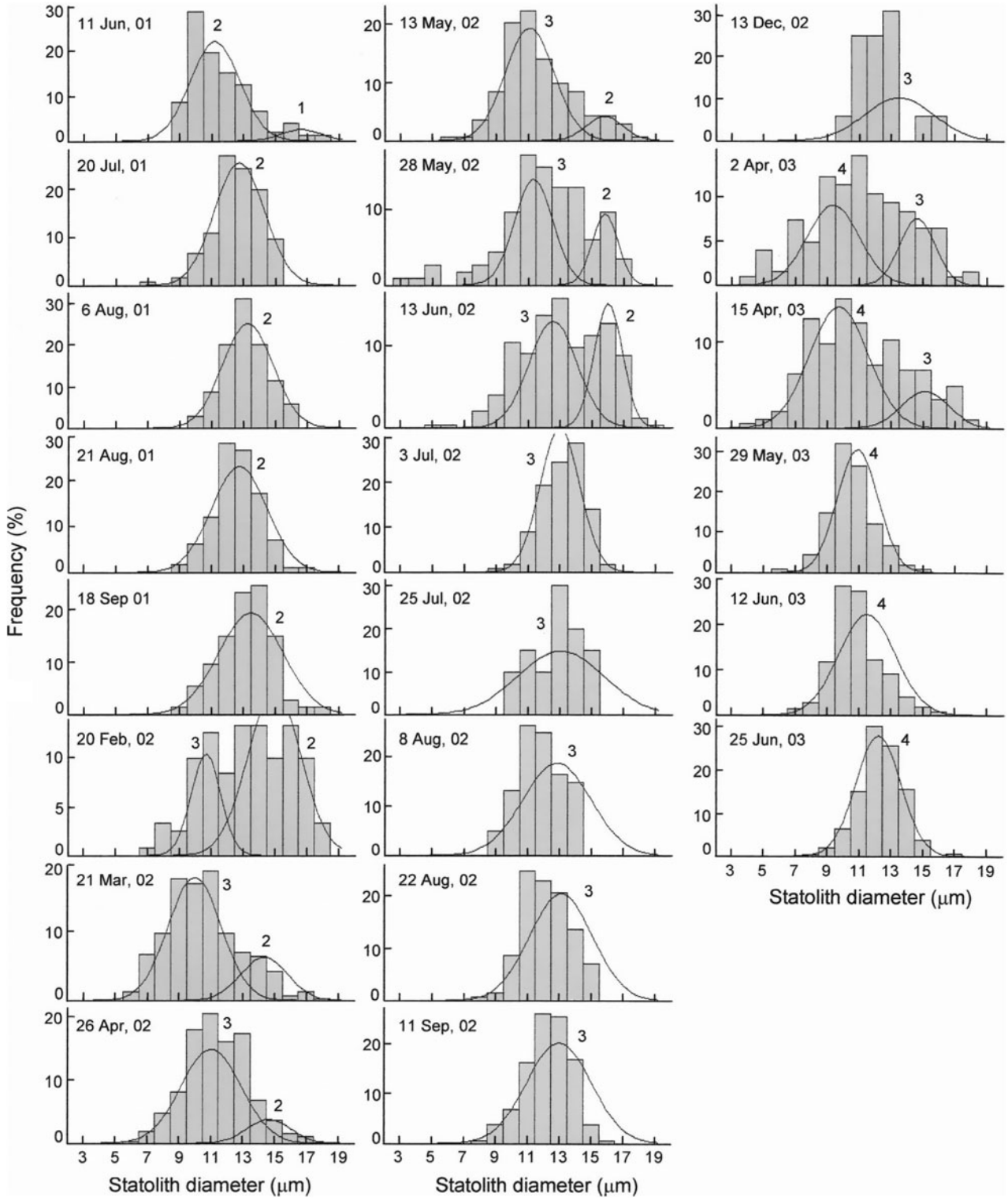

Fig. 3. *Oikopleura vanhoeffeni*. Frequency distributions of statolith diameter from samples collected between 11 June 2001 and 25 June 2003. Individual cohorts were defined as normally distributed components of the sample distributions (see Materials and Methods).

However, animals from cohort 3 did not grow exponentially (Figure 5C), confirmed by a non-linear relationship between ln-transformed weight and time (Figure 5D). Cohort 3 animals did not grow significantly until April 2003 ($P < 0.001$). If we assume their growth rate until December 2002 was zero, their instantaneous growth rate from December 2002 to April 2003 was 0.043 d^{-1}.

The population biomass ranged from 0.01 to 483 mg C m^{-2} and increased during April and May with an annual mean and standard deviation of 66.5 $\pm$ 128 mg C m^{-2} from June 2001 to June 2002 and 25.0 $\pm$ 48.5 mg C m^{-2} from July 2002 to June 2003 (Figure 6; Table 1). Daily somatic production of the population ranged from <0.01 to 8.12 mg C m^{-2}, with maximum production occurring

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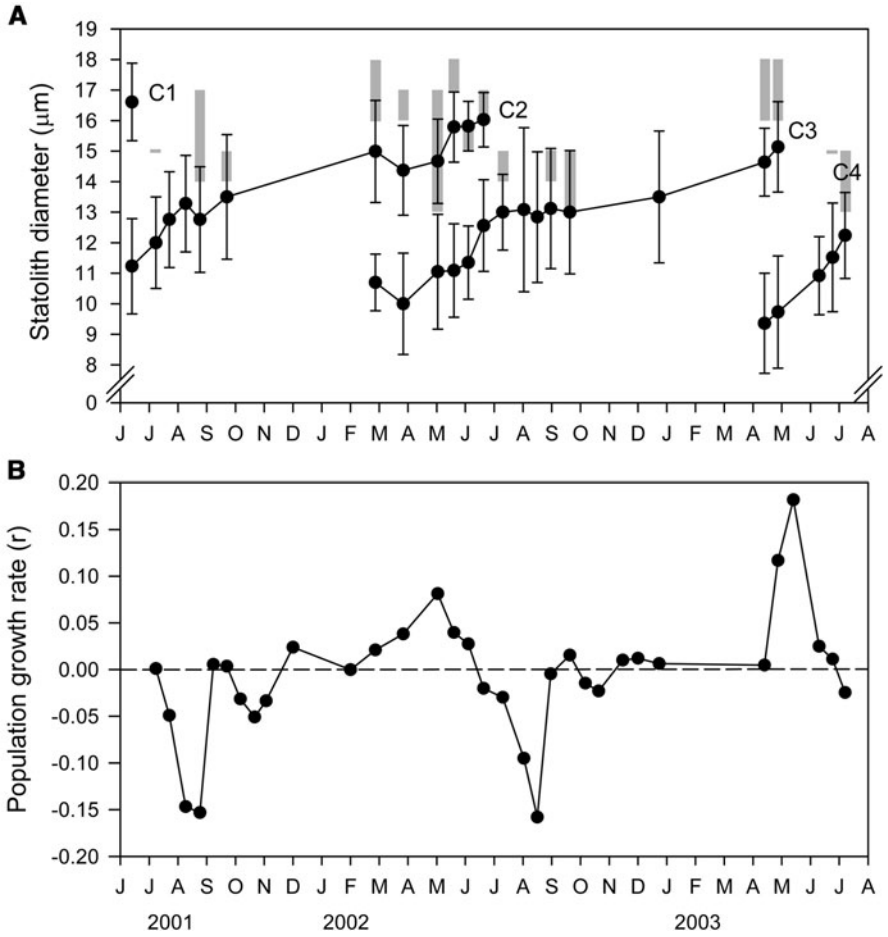

Fig. 4. *Oikopleura vanhoeffeni*. (A) Time series of statolith diameter for cohorts 2, 3, and 4. Cohorts were defined as in Figure 3. Shaded areas represent the range of statolith diameter at maturity; (B) time series of population growth rates.

during spring (Figure 6); annual production was 343 mg C m^{-2} y^{-1} in 2001/2 and 359 mg C m^{-2} y^{-1} in 2002/03 (Table 1). The annual $P_{somatic}/B$ ratio was 5.2 in 2001/2 and 14.3 in 2002/3 (Table 1). Daily house production of the population ranged from < 0.01 to 179 mg C m^{-2}, with a prominent increase in spring (Figure 6). The annual house production rate was 8.4 g C m^{-2} y^{-1} in 2001/2 and 3.4 g C m^{-2} y^{-1} in 2002/3 (Table 1), giving a P_{total}/B ratio (where $P_{total} = P_{somatic} + P_{house}$) of 131 in 2001/2 and 150 in 2002/3.

Size at maturity and potential fecundity

Mean trunk length at maturity increased during winter and peaked during spring (Figure 7A) with a range from 0.5 to 3.4 mm (680% variation) over the entire sampling period and the variation was negatively related to temperature ($r^2 = 0.57$, $N = 24$, $P < 0.001$) and positively related to chlorophyll-*a* concentration ($r^2 = 0.48$, $N = 24$, $P < 0.001$). Seasonal variation in potential fecundity was similar to trunk length at maturity (range 79–4976 oocytes ind^{-1}) because fecundity was a function of body size (Figure 7B).

DISCUSSION

The boreal larvacean *Oikopleura vanhoeffeni*, which experiences subzero temperature for about six months of the year in Conception Bay, has a generation time of approximately one year. This generation time is similar to previous estimates of an annual life span for *O. vanhoeffeni* in the Foxe Basin, Canadian Arctic archipelago (Grainger, 1959), based on the observation of seasonal variation in the abundance and annual appearance of small juveniles. Generation times of larvaceans living in cold environments are much greater than those of species that live in temperate and tropical regions, which decreases from 27 days to 1 day at temperatures from 7°C to 29°C (Lopéz-Urrutia *et al.*, 2003 and references therein). Thus, the generation time of larvaceans on a global scale shows a negative relationship with temperature from −1 to 29°C, as is generally the case in poikilotherms (Shaw & Bercaw, 1962; Gillooly, 2000).

The exponential somatic growth pattern of cohort 2 demonstrates that individuals obtained sufficient energy to maintain growth throughout the year 2001–2002. The omnivorous and efficient feeding behaviour of this species may explain continuous growth, given that larvaceans in Conception Bay are able to ingest most of the seasonally variable prey species, ranging from a large proportion of bacteria and flagellates in summer and autumn, supplemented by diatoms in spring (Urban *et al.*, 1992). However, cohort 3 did not display significant growth from spring to winter in 2002, but accelerated in growth in spring of 2003. The reason behind the discontinuous growth in cohort 3 is not clear. In addition, the spring diatom bloom was not

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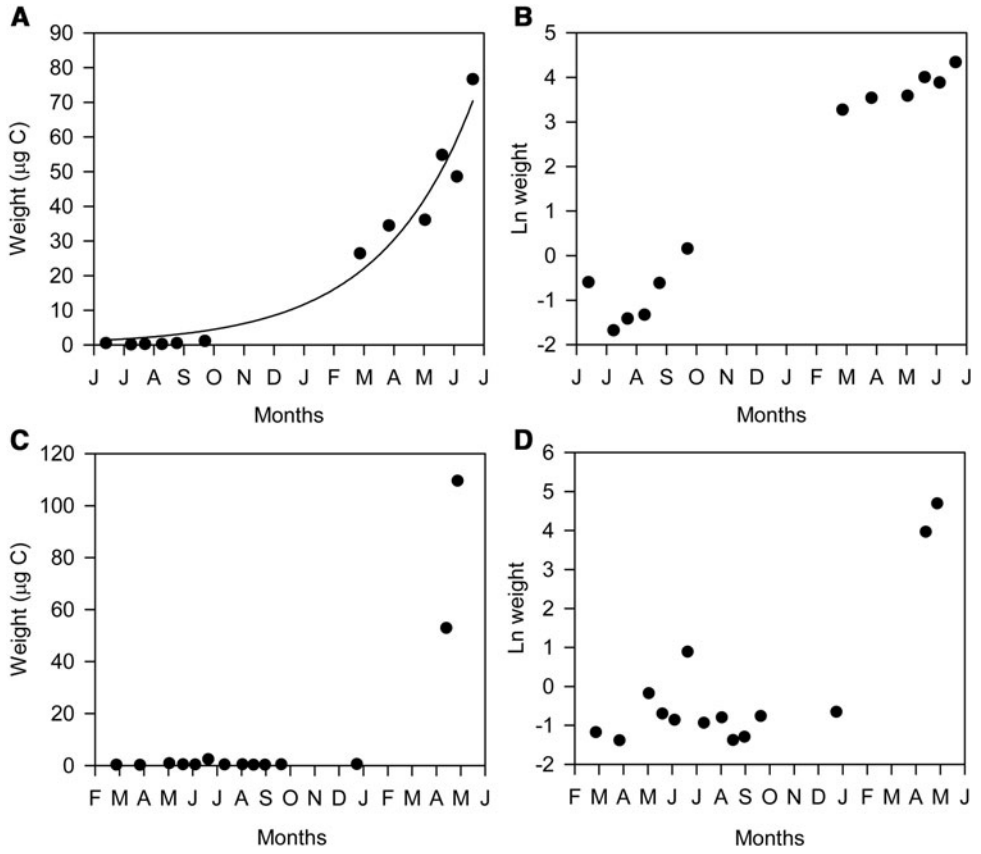

Fig. 5. *Oikopleura vanhoeffeni*. (A) Weight of animals in cohort 2 versus time; (B) ln-transformed weight of cohort 2 versus time; (C) weight of animals in cohort 3 versus time; (D) ln-transformed weight of cohort 3 versus time.

advantageous to the growth of young individuals in 2002 but was for the growth of older individuals in 2002 and 2003. Perhaps, large diatom cells decreased the efficiency of feeding in young individuals by clogging the inlet filters of the houses, implying that food size is an important determinant of intraspecific variation in growth of larvaceans. The accelerated growth during the spring diatom bloom, despite the coldest water temperatures, suggests that abundant food can overcome temperature limitation of somatic production by this cryophilic larvacean species.

The weight-specific growth rates of *O. vanhoeffeni* in Conception Bay are lower than those of other species from temperate and tropical regions (Table 1), and also lower than the range of 0.26 to 3.31 d^{-1} obtained from laboratory and field measurements at temperatures from 7 to 29°C (Lopéz-Urrutia *et al.*, 2003). The somatic production and P/B ratio of larvaceans in Conception Bay are also lower than values for species in temperate and tropical regions (Table 1), in part because growth rate is lower and biomass is higher in Conception Bay than in warm-water systems.

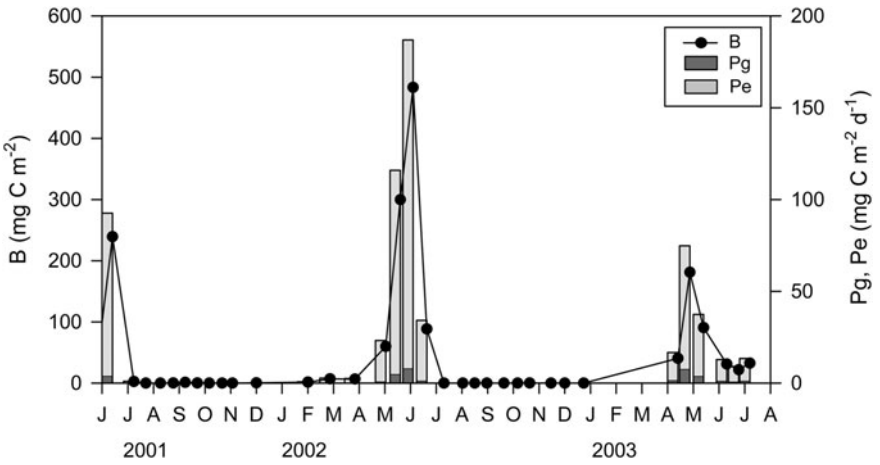

Fig. 6. Biomass (B), somatic production (Pg) and house production (Pe) of *Oikopleura vanhoeffeni*.

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Table 1. Mean biomass (B), instantaneous growth rate (g), annual somatic production (Pg), annual house production (Pe), and P/B ratio of larvacean species. Pt, total production (somatic + house production).

	Location	T (°C)	B (mg C m^{-2})	G (d^{-1})	Pg (g C m^{-2} yr^{-1})	Pe (g C m^{-2} yr^{-1})	Pg/B	Pt/B	Reference
Oikopleura dioica	Seto Inland Sea	8.9–28.2	12	0.26–3.0	7.15	–	596		Uye & Ichino (1995)
Larvaceans	Off Lime Cay	27–29	5.5	0.97–1.56	1.9–4.6	1.2–2.4	346–836	564–1273	Clarke & Roff (1990)
Larvaceans	Kingston Harbour	27–30	15.5	2.03–2.49	14	7.1–14.3	903	1361–1826	Hopcroft & Roff (1998)
Oikopleura longicauda	Toyama Bay	11.1–23.5	25.6	0.592	4.5	11.3	176	617	Tomita *et al.* (1999)
Oikopleura vanhoeffeni	Conception Bay	−1–6*	25–66	0.017–0.043	0.343–0.359	3.4–8.4	5.2–14.3	131–150	This study

*, mean temperature was taken above 100 m where most of the larvaceans were found. Surface temperature ranged from −1 to 17°C. Biomass and production expressed in kJ was converted to carbon using 1g C = 42 kJ (Lalli & Parsons, 1993).

This pattern is a typical example of the low turnover rate of energy in cold-water ecosystems that results from lower growth rate, higher biomass and longer generation time (Waters, 1977; Brey & Gerdes, 1998). However, because of the high biomass, the annual population house production rate is high and comparable to warmer systems, even though the daily house production rate of individual *O. vanhoeffeni* (i.e. 37% of body weight; Deibel, 1988) is lower than that of warm water species (40 to 300% of body weight; Clarke & Roff, 1990; Hopcroft & Roff, 1998; Tomita

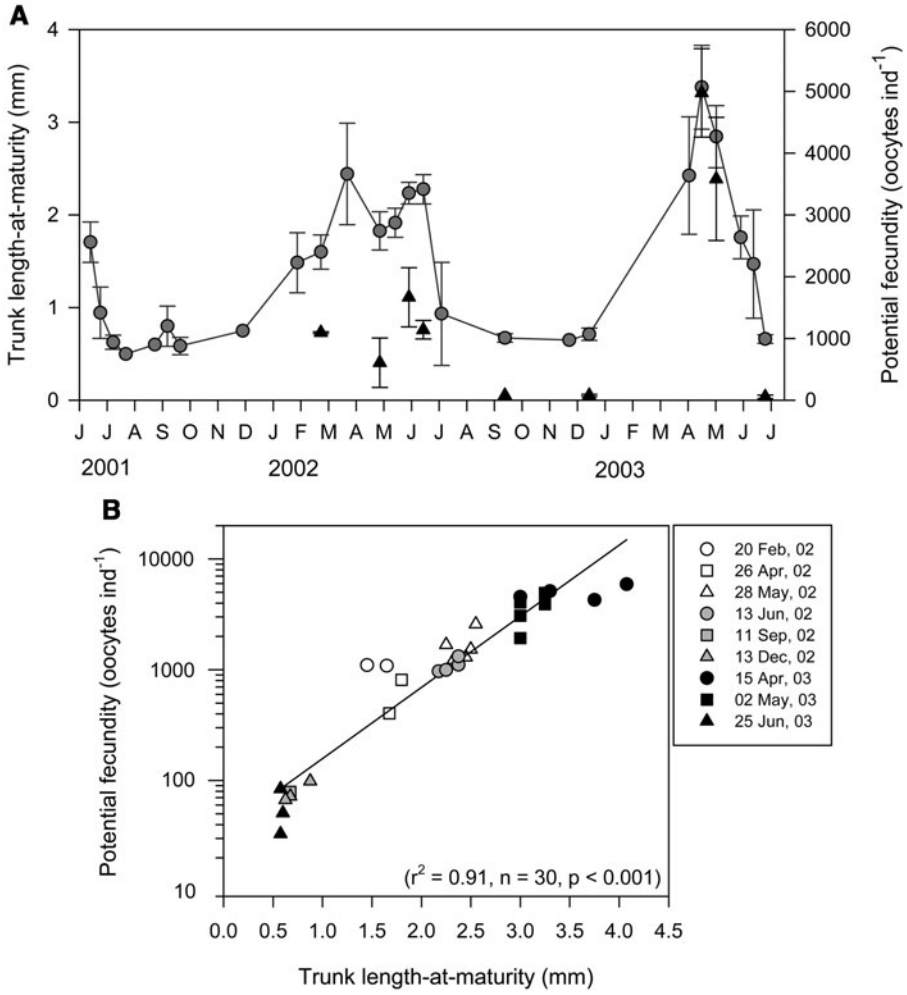

Fig. 7. *Oikopleura vanhoeffeni*. (A) Time series of trunk length-at-maturity (grey circle) and potential fecundity (black triangle). Error bars represent ± 1.96 SE of the means. Data points without error bars were obtained from a single measurement; (B) relationship between potential fecundity and trunk length-at-maturity. Different symbols indicate potential fecundity obtained at different dates. Assuming similar oocyte resorption to that of *Oikopleura dioica* (see text), egg production rate may be equal to ~50% of potential fecundity.

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et al., 1999; Sato *et al.*, 2001). Population house production rates far exceed somatic production rates in *O. vanhoeffeni*, whereas population house production by warm-water species is similar to somatic production (Table 1). Thus, it is essential to include house production in estimates of total carbon production by larvaceans, especially in cold-water systems.

Assuming a mean annual primary production for Conception Bay of 131 ± 5 g C m^{-2} yr^{-1} (Tian *et al.*, 2003), the total annual carbon production of *O. vanhoeffeni* (somatic + house production) was 6.7% of primary production in 2001/2002 and 2.9% in 2002/2003. These are remarkably high figures, considering that the transfer efficiency between primary and all secondary producers in marine ecosystems is approximately 10 to 13% (Pauly & Christensen, 1995; Ware, 2000). Based on an estimate of mean mesozooplankton production (primarily copepods) of 10.1 g C m^{-2} yr^{-1} in Conception Bay (Tian *et al.*, 2003), production of *O. vanhoeffeni* represented 87% of mesozooplankton production in 2001/2002 and 37% in 2002/2003. This range is similar to estimates from studies in other locations. Larvacean production in Kingston Harbour, Jamaica, is at least 50% of copepod production (Hopcroft & Roff, 1998) and may exceed copepod production (Hopcroft & Roff, 1995). Furthermore, temperate epipelagic larvaceans can represent an average of 10% and up to 40% of total mesozooplankton production in productive environments (López-Urrutia *et al.*, 2003, Sato *et al.*, 2008).

Mature individuals were present almost all year in Conception Bay (Figure 7A) and many of these individuals were in the middle of oogenesis with developing oocytes surrounded by accessory cells. A laboratory observation (Choe, unpublished) indicated that the period of oocyte growth, maturation and spawning in *O. vanhoeffeni* is over one to two days at 0–1°C. Rapid oogenesis is also noted in other larvacean species. Oocyte formation and maturation in *Oikopleura dioica* at 15°C are completed within 6 hours (Ganot *et al.*, 2007a) and spawning ensues immediately after maturation of oocytes is complete (Ganot *et al.*, 2007b). Because oocyte growth, maturation and spawning occur rapidly after the larvaceans enter oogenesis, mature *O. vanhoeffeni* which were found throughout the years in Conception Bay most likely spawned. However, it is not clear if fertilization, hatching and survival of juveniles were successful whenever the mature individuals were present since the major recruitment of juveniles occurred only once a year, during spring (Figure 4A).

Trunk length at maturity of *O. vanhoeffeni* increased over winter and spring as temperature decreased and food concentration increased. This is similar to *Oikopleura dioica* living at warmer water temperatures in the Inland Sea of Japan, which also showed seasonal variation in trunk length at maturity that was inversely related with temperature (Uye & Ichino, 1995). Thus, the inverse relationship of size at maturity with temperature of larvaceans in Conception Bay, and the Sea of Japan, seems to fit the conventional temperature–size rule, in which poikilotherms mature at a larger size at lower rearing temperatures (Ray, 1960; Atkinson, 1994). However, it is also possible that high food concentration in spring contributed further to the increase in trunk length at maturity in Conception Bay. Because temperature and food concentration covaried in Conception Bay, the relative effect of each on the size at maturity is uncertain. The results from laboratory studies on the effect of temperature and food availability on the size at maturity of other larvacean species are inconsistent. Trunk length at maturity of *O. dioica* remained the same at different temperatures (Fenaux, 1976) and food concentrations (Troedsson *et al.*, 2002), although Lombard *et al.* (2009) found a significant effect of food concentration. All these observations suggest that size at maturity is generally a plastic trait in larvacean species.

Potential fecundity of *O. vanhoeffeni* increased with body size (Figure 7B) as temperature decreased and food concentration increased over the winter and spring, indicating resource partitioning between somatic growth and reproductive output. However, the relationship between body size and fecundity differs in another larvacean species. The trunk length at maturity of *O. dioica* remained constant but fecundity increased with invariable egg size as food concentration increased (Troedsson *et al.*, 2002). Such trade-off between somatic growth and reproduction was not observed in another study. Fecundity and trunk length at maturity of *O. dioica* increased as the rearing temperature decreased and there was a positive relationship between trunk length and fecundity while egg size remained constant (Fenaux & Gorsky, 1981). Thus, there are inter- and intraspecific variations in allocation of energy in somatic growth and reproduction in larvaceans.

Oikopleura vanhoeffeni experienced negative population growth in July and August (Figure 4B). This may have resulted from high mortality due to intense competition for food during summer when the plankton food web is most active. The abundance of zooplankton in Conception Bay, e.g. the copepods *Calanus finmarchicus*, *Pseudocalanus* spp. and *Oithona similis*, and the larvacean *Fritillaria borealis*, increases between June and September (Davis, 1982). Predation may also contribute to high mortality in larvaceans during summer. Recruitment of the chaetognath *Parasagitta elegans*, a major predator of larvaceans (Feigenbaum, 1982; Alvarez-Cadena, 1992; Purcell *et al.*, 2005), also occurs in the upper water column of Conception Bay during July and August (Davis, 1982; Choe & Deibel, 2000). Furthermore, the larvae of many fish species increase in Conception Bay and in other Newfoundland coastal regions in July and August (Davis, 1986; Frank & Leggett, 1983; Laprise & Pepin, 1995).

In coastal Newfoundland waters, *O. vanhoeffeni* does not store lipid as an energy reserve (Deibel *et al.*, 1992) and does not enter dormancy over winter because it feeds on available pico- and nanoplankton (Urban *et al.*, 1992). As a result, we have shown in this study that it is capable of exponential somatic growth throughout the winter. Also, instead of storing energy obtained from the spring diatom bloom, it apparently invests the energy into growth and reproduction by becoming sexually mature at the largest body size with highest fecundity, resulting in maximum population growth. The secondary production of *O. vanhoeffeni* during spring represents a large proportion of primary and mesozooplankton production in Conception Bay. Thus, *O. vanhoeffeni* is well adapted to seasonally driven cold-water systems with its growth and reproductive cycle coupled to the annual periodicity of primary production.

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