Food limitation and growth in temperate epipelagic appendicularians (Tunicata)

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ABSTRACT: Through an extensive review of reports on appendicularian ecology, we have developed a set of equations on the feeding, metabolic and growth rates of temperate epipelagic appendicularian species. We have used these equations to study the conditions in which these species are likely to experience food-limited growth. As *Oikopleura dioica* is the most-studied appendicularian species, we have used equations developed for this one species to construct a metabolic budgetary model. Our results suggest that large *O. dioica* are less likely to experience food-limited growth than other mesozooplankton, and that growth during early development could be more limited by food concentration in the environment. The degree of food limitation strongly depends on the assimilation efficiency of non-autotrophic material, which comprises a great proportion of the appendicularian diet. However, examination of direct measurements of growth rate over a wide range of food concentrations showed no significant relationship between food concentration and weight-specific growth rates. Temperature alone explained more than 60% of the variance in appendicularian weight-specific growth rates. Since there were no clear differences in the growth rates of different appendicularian species, we have combined the available data to develop a temperature-dependent equation to predict their weight-specific growth rates. We have also modified the growth rate equation to take into consideration the expenditure in house secretion. Combination of this growth rate equation with biomass estimations allows us to evaluate their contribution to secondary production. In contrast with the traditional view of appendicularians as important members of oligotrophic ecosystems, our results show that in the study area their contribution to secondary production was higher during more productive conditions.

KEY WORDS: Appendicularian · Growth · Ingestion · Respiration · *Oikopleura* · *Fritillaria*

INTRODUCTION

The importance of food availability in limiting zooplankton growth has been a long-standing point of controversy (Ikeda et al. 2001). According to the approach followed by Huntley & Boyd (1984), the growth of zooplankton is limited when the food concentration (FC) is between the maintenance (C_m) and the critical (C_c) food concentrations ($C_m < FC < C_c$). When $FC = C_m$ the assimilated energy balances the minimum metabolic requirements and there is no energy left for growth. When FC are $>C_c$ growth rates

are maximal and are therefore unaffected by an increase in FC.

Most of the studies on food limitation of zooplankton growth have focused on copepods (Ikeda et al. 2001 and references therein). However, other groups with different feeding strategies, such as gelatinous organisms, may differ in their response to food limitation. Acuña (2001) combined filtration theory and physiological allometry, to conclude that C_m for the open-ocean salp *Pegea confoederata* is between 0.84 and 2.17 µg C l^{-1}, and suggested that the gelatinous body of pelagic tunicates enables them to survive in nutrition-

ally dilute environments. However, there is little information on the food concentrations under which pelagic tunicates reach their maximum growth rates. Harbison et al. (1986) found that some oceanic salps lack a mechanism to expel the food boluses that clog their pharyngeal filters when food concentrations are high, and suggested this as a cause for their absence from neritic waters. In contrast, appendicularians discard their filter house and secrete a new one every few hours, even when food is scarce (Fenaux 1985). This raises the question as to whether, under oligotrophic conditions, appendicularian ingestion rates are able to support their high metabolic (Gorsky et al. 1987) and growth (Hopcroft & Roff 1995) rates on top of the energy cost that results from discarding 15% of their body carbon every few hours in the form of filter houses (Sato et al. 2001).

In a study on appendicularian feeding physiology (López-Urrutia et al. 2003, this issue), we have developed equations to predict appendicularian ingestion rates. Here we use these equations to apply Huntley & Boyd's (1984) approach to determine the conditions under which appendicularians are likely to experience food limitation in nature. The appendicularian growth and metabolic parameters required by the Huntley & Boyd approach were not readily available. We have therefore compiled published data on appendicularian metabolism, development time and growth, and combined them with biometrical measurements to model appendicularian growth. Most of the available data is restricted to temperate epipelagic species, particularly *Oikopleura dioica*. Therefore, we have applied Huntley & Boyd's (1984) approach to this single species and we evaluated differences between species when data for other species were available. In addition to Huntley & Boyd's approach, we have compiled weight-specific growth rates to study their relationship with *FC*. We have modified the weight-specific growth rate equation to take into account the expenditure in house production and incorporated it into the temperature-dependent growth rate equation. Finally we have used this equation in combination with biomass measurements to evaluate the contribution of appendicularians to zooplankton secondary production.

MATERIALS AND METHODS

Huntley & Boyd (1984) based their study of food limitation in zooplankton on the calculation of the difference between the energy assimilated and respiration, i.e. the scope for growth:

$$SG = \frac{\alpha \times I(W_b, T, FC) - R(W_b, T)}{W_b} \quad (1)$$

where *SG* is the appendicularian weight-specific scope for growth, α is the assimilation coefficient (dimensionless), $I(W_b, T, FC)$ is the ingestion rate as a function of body weight (W_b), food concentration (*FC*) and temperature (*T*), and $R(W_b, T)$ is respiration as a function of body weight and temperature. Definitions of the symbols and units used are listed in Table 1.

There is a minimum or maintenance food concentration (C_m) at which assimilation balances respiration and there is no energy left for growth. C_m can be found by setting *SG* = 0 in Eq. (1) and solving for *FC*. Above a critical food concentration (C_c), growth rates are not limited by the availability of food and attain a maximum that is determined only by temperature. This maximum is the thermally defined upper limit of appendicularian growth (g_{Tmax}). C_c is the *FC* for which Eq. (1) satisfies $SG = g_{Tmax}$.

Therefore, determination of C_m and C_c requires knowledge of $I(W_b, T, FC)$, $R(W_b, T)$ and g_{Tmax}. We first determine how appendicularian ingestion, respiration and growth rates are related to temperature, body weight and food concentration. We formulate these relationships for *Oikopleura dioica*, for which most of the key parameters are known, and study the conditions under which this species is likely to be food limited using the approach followed by Huntley & Boyd (1984). However, we try to determine differences between appendicularian species-specific data when possible. Finally, we apply the growth rate equations obtained to *in situ* conditions to evaluate the contribution of appendicularians to secondary production.

Ingestion. The ingestion rate of a filter-feeder equals its clearance rate multiplied by the concentration of food (Huntley & Boyd 1984). In appendicularians, a proportion of the particles cleared remains attached to the filter house and is not ingested (up to 80%: Acuña & Kiefer 2000). Therefore, their ingestion rates cannot be estimated by the product of clearance rates by food concentration, and the approach of Huntley & Boyd (1984) needs to be modified. To obtain equations to estimate ingestion rates (*I*) from knowledge on body weight (W_b), food concentration (*FC*) and temperature (*T*) we have followed an approach based on the gut-content technique. The gut content of appendicularians can be estimated from body size according to equations in López-Urrutia et al. (2003). The gut-passage time can be estimated from temperature and food concentration using the data in López-Urrutia & Acuña (1999). If we divide the gut content by the gut-passage time, we obtain an estimate for the ingestion rate that depends on body size, temperature and food concentration.

López-Urrutia et al. (2003) have shown that for most appendicularian species >60% of the material ingested comes from non-autotrophic food. The degree

to which non-autotrophic material is assimilated has crucial implications for the calculation of the assimilated energy obtained from the ingested food, and consequently for the determination of food limitation in appendicularians. However, there is only information on the assimilation efficiency of phytoplankton food (Gorsky 1980). Therefore, in order to provide a first evaluation of the importance of non-autotrophic material in the metabolic balance of appendicularians, we have used both total and autotrophic gut contents (TGC and AGC, µg C ind.$^{-1}$; López-Urrutia et al. 2003) to develop 2 separate equations to estimate ingestion rates on total particulate material (IT) and on autotrophic prey (IA), respectively. IA multiplied by the assimilation constant for phytoplankton (α) represents an estimate of the lower limit for the total assimilated energy (i.e. if the non-autotrophic material were not assimilated at all), while IT multiplied by the assimilation constant for phytoplankton (α) would represent the total assimilated energy if the non-autotrophic material were assimilated with the same efficiency as the autotrophic material.

Appendicularian trunk-length measurements (TL) in López-Urrutia et al. (2003) were converted to body weight (W_b) using body weight-trunk length relationships. Power relationships between gut carbon content and body weight were then obtained using geometric mean regression (GMR: Ricker 1984) on log$_{10}$-transformed gut-carbon content (AGC and TGC) and body weight (W_b) data. Direct body carbon-trunk length relationships are only available in the literature for *Oikopleura dioica*. For the remaining species, these relationships were obtained by compiling published, simultaneous trunk length and dry weight measurements (Table 2). In those cases where the ash-free dry weight was reported, it was back-transformed to dry weight assuming an ash content of 10% dry weight (Hopcroft et al. 1998). We then converted dry weight to carbon weight using the equation in Gorsky et al. (1988) and the relationships between trunk length and body carbon were obtained calculating the GMR on log$_{10}$-transformed data. We followed the same approach for *O. dioica* in order to compare the equation for this species with previously published regressions obtained by direct measurement of carbon content. The relationship that was obtained for *Fritillaria pellucida* was used for *F. borealis*, since no data were available for this species.

Respiration. To develop equations to predict the minimum carbon requirements for metabolism (R) as a function of temperature (T) and body weight (W_b), we used data from Gorsky et al. (1984, 1987) on the respiration rates of *Oikopleura dioica* and *O. longicauda*. After digitising their data, we transformed data on oxy-

Table 1. Abbreviations

Symbol	Parameter
W_T	Total appendicularian weight (body, tail and cumulative carbon of houses produced to that point, µg C)
W_H	Weight of all houses produced by an individual during its lifetime (µg C)
W_b	Appendicularian body weight (body and tail but not houses, µg C)
W_a	Adult appendicularian body weight (µg C)
W_e	Egg weight (µg C)
TL	Trunk length, from mouth to distal gonad end (µm)
ω	Exponent of weight-length relationship (dimensionless)
a	Coefficient of allometric relationship between appendicularian weight and trunk length (complex dimensions depending on weight-length allometric exponent (ω): µg C µg C$^{-\omega}$ ind.$^{-1}$ d^{-1})
g_T	Total appendicularian (body and house) growth rates (d^{-1})
g_{Tmax}	Thermally defined upper limit for total appendicularian growth rates (d^{-1})
g_b	Growth rates of appendicularian body (d^{-1})
b	Body growth allocation, ratio between g_b/g_T (dimensionless)
D	Development time (d)
SG	Scope for growth (d^{-1})
T	Habitat temperature (°C)
FC	Food concentration (µg C)
C_m	Maintenance food concentration (µg C)
C_c	Critical food concentration (µg C)
α	Assimilation constant (dimensionless)
I	Ingestion rate (IA, autotrophic prey, IT, total ingestion: µg C ind.$^{-1}$ d^{-1})
GC	Gut content (TGC: total carbon, AGC: autotrophic carbon, µg C ind.$^{-1}$)
GPT	Gut-passage time (min)
R	Respiration rate (µg C ind.$^{-1}$ d^{-1})
m	Respiratory allometric exponent (dimensionless)
k	Respiratory allometric coefficient (complex dimensions depending on respiratory allometric exponent [m]: µg C µg C^{-m} ind.$^{-1}$ d^{-1})

Table 2. Summary of appendicularian species, variables and publications. Symbols as in Table 1. W_bTL: data used for calculation of body weight versus length relationships

Species	Variables measured	Source
Oikopleura dioica	W_bTL, D	Paffenhöfer (1973)
O. dioica, Fritallaria borealis	W_bTL, D, g_b	Paffenhöfer (1976)
O. fusiformis, O. longicauda	W_bTL	Alldredge (1976b)
O. dioica	D, g_b[a]	Fenaux (1976a)
F. pellucida	W_bTL, g_b[a]	Fenaux (1976b)
O. dioica	D, g_b[a], α	Gorsky (1980)
O. dioica	g_b, W_e	King et al. (1980)
O. dioica	D, g_b[a]	King (1982)
O. longicauda	W_bTL, D, g_b[a]	Fenaux & Gorsky (1983)
O. longicauda	R[a]	Gorsky et al. (1984)
O. dioica	g_b[a]	Fenaux et al. (1986a)
O. dioica	W_bTL, R	Gorsky et al. (1987)
O. dioica, O. longicauda, F. pellucida	W_bTL	Gorsky et al. (1988)
O. dioica	D, g_b	Hopcroft & Roff (1995)
O. dioica	g_b	Nakamura et al. (1997)
F. borealis, O. longicauda, F. haplostoma, Appendicularia sicula, O. dioica	W_bTL, g_b	Hopcroft et al. (1998)
O. dioica	GPT	López-Urrutia & Acuña (1999)
O. dioica, O. longicauda, O. fusiformis, O. rufescens, Megalocercus huxleyi, Stegosoma magnum, A. sicula, F. formica	D	Sato et al. (1999)
O. dioica	D	Acuña & Kiefer (2000)
O. dioica	W_bTL, D, g_b[a], W_H	Sato et al. (2001)
O. dioica, O. longicauda, O. fusiformis, F. pellucida, F. borealis	GC	López-Urrutia et al. (2003)

[a]Growth rates not reported in original study, but estimated from data given therein

gen consumption (µl O_2 ind.$^{-1}$ h^{-1}) to carbon requirements for metabolism (R, µg C ind.$^{-1}$ d^{-1}) using a conversion factor of 0.536 µg C µl^{-1} O_2 and a respiratory quotient of 0.97 (Ikeda et al. 2000). Trunk lengths were transformed to body carbon using the relationships obtained as described above.

Growth rate. Calculation of C_c requires determination of the thermally defined upper limit for appendicularian growth ($g_{T\max}$). Huntley & Boyd (1984) used a compilation of studies in which the growth rates of copepods were measured under conditions of excess food to calculate a relationship between food-saturated or maximum growth rates and temperature. Unfortunately, this relationship is not available for appendicularians. We have therefore compiled all published data on direct measurements of weight-specific growth rates of the appendicularian body (g_b) and analysed them in 2 ways. First, the presence or absence of a relationship between growth rate and food concentration provides a straightforward indication as to whether appendicularian growth rates are related to food concentration, and therefore, on the existence of food-limited growth. Since this was not the case, and we found no evidence of food limitation (see 'Results'), we followed a similar method to that described by Eppley (1972) for phytoplankton to define the upper limit for growth at a given temperature ($g_{T\max}$). According to this method, $g_{T\max}$ was defined as the upper 95% confidence limit for individual measurements of the

exponential relationship between growth rate and temperature. House production can represent a high percentage of the biomass produced by appendicularians; we will therefore modify these growth rate estimates to take into account the expenditure in house production.

Body growth: The growth of the appendicularian body (trunk, gonads and tail, but not houses) can be described by an exponential equation (Paffenhöfer 1976; Fenaux et al. 1998) of the form:

$$W_b = W_0 \, e^{g_b t} \qquad (2)$$

where W_b (µg C ind.$^{-1}$) is the animal body weight (trunk, tail and gonads) at Time t_i, W_0 is the body weight at time t_0, t (d) is the time interval (i.e. the difference $t_i - t_0$) and g_b (d^{-1}) is the weight-specific instantaneous growth rate of the appendicularian body.

To generate a database on weight-specific growth rates, we have compiled all published laboratory or field measurements of g_b (references in Table 2). These direct measures of g_b have been obtained by 2 different methods based on the measurement of the increase in appendicularian body weight with time: (1) The measurements of Hopcroft & Roff (1995), Nakamura et al. (1997) and Hopcroft et al. (1998) are based on the creation of artificial cohorts from field-collected individuals that were then maintained in microcosm incubations with natural seawater. The growth rate was then calculated from the increase in the size-frequency

distribution of the appendicularian population with time. (2) The second method is based on the measurement of the increase in body weight with time at different intervals throughout the life cycle of individuals from the same laboratory cohort (references in Table 2). When trunk length and time measurements were reported in the original publication instead of g_b, we transformed trunk length to body weight using the relationships obtained as described above, and calculated g_b as the slope of the relationship between $\log_e$ body weight and time (Eq. 2). Temperature and food concentration were also compiled when available. When food concentration was not reported in total carbon units, it was transformed from food volume assuming that 1 mm^3 of phytoplankton contains 200 µg C (Mullin et al. 1966) or from the chlorophyll concentration using the equation of Legendre & Michaud (1999).

We have also compiled literature data on appendicularian generation or development time, D (both terms are similar in appendicularians since they are semelparous, and fertilization and hatching occurs within a few hours after spawning: Nishino & Morisawa 1998). Generation time is the most important determinant of the rate of population growth (e.g. Gillooly 2000). Therefore, we studied the relationship between development time and temperature and food concentration. Most of the data on development time are from the same experiments used above for the estimation of growth rates; when they were independent experiments, then an estimation of g_b was obtained from the relationship:

$$g_b \quad = \quad \frac{\log_e\left(\dfrac{W_a}{W_e}\right)}{D} \qquad (3)$$

where W_a (µg C) is the body weight of mature individuals and W_e (µg C) is the egg weight. Eq. (3) is derived from Eq. (2), setting t_0 equal to time at egg stage, and t equal to development time. When data on development time were not accompanied by data on adult weight in a publication, we used the maximum weight reported by Alldredge (1976b) for that species. Egg weight was assumed to be constant for all appendicularian species and equal to the values reported by King et al. (1980) for *Oikopleura dioica* (0.0155 µg C). The logarithmic transformation of W_a and W_e in Eq. (3) implies that the choice of adult body weights and egg weights has less effect on the growth rate estimates than differences in development time (Huntley & Lopez 1992). These estimates represent the only approximation available for the weight-specific growth rate of some species (*Megalocercus huxleyi*, *Oikopleura fusiformis* and *Stegosoma magnum*). However, due to the assumptions involved in our estimation of the numerator in Eq. (3) and to pos-

sible biases in the growth rates estimated by this equation (see Kleppel et al. 1996 for a detailed discussion), these data were maintained as independent estimates, separate from the dataset based on direct measurements of growth rate.

Incorporation of house production in appendicularian growth equations: During house production, a proportion of the total appendicularian weight (trunk, gonads, tail and house) is discarded periodically. This discarded carbon is not taken into account in the growth rate equations based on the measurement of the increase in body weight with time (Eqs. 2 & 3). However, house production can represent a high percentage of the biomass (Sato et al. 2001) and should therefore be included in growth rate estimates. While house production (discarding an old house and expanding a new one) is an episodic event, house secretion (secretion of the mucous sleeve that covers the oikoblastic epithelium) is a continuous process (Fenaux 1985, Flood & Deibel 1998, Spada et al. 2001). Thus, house secretion represents an energy compartment into which a proportion of the total growth is continuously devoted. According to this, Eq. (3) can be rewritten for both body and house in the form:

$$g_T \quad = \quad \frac{\log_e\left(\dfrac{W_T}{W_e}\right)}{D} \qquad (4)$$

where W_T is the sum of the mature individual body carbon (W_a) and the cumulative weight of all the houses produced by an individual during its lifetime (W_H, µg C), g_T is the total weight-specific growth rate, and the remaining terms are as described above. Unfortunately, data on the carbon weight of appendicularian houses is still too scarce to calculate any direct relationships between g_T and temperature or food concentration. Nevertheless, Sato et al. (2001) estimated values of W_H for *Oikopleura dioica* as well as the development time and weight of adult individuals. We use their data to calculate g_b and g_T using Eqs. (3) & (4), which can then be used to estimate the proportion of the total growth (house plus body) which is allocated to body growth ($b = g_b/g_T$). Here we have assumed that b, which represents an integrated proportion over the period from hatching to spawning, is constant during development. Expressing house production as a proportion of the total growth also allows for zero house production rates before the first house has been produced and during spawning when the appendicularians are not secreting houses, since during these periods growth is zero.

Contribution of appendicularians to secondary production. To investigate the contribution of appendicularians to total secondary production, we calcu-
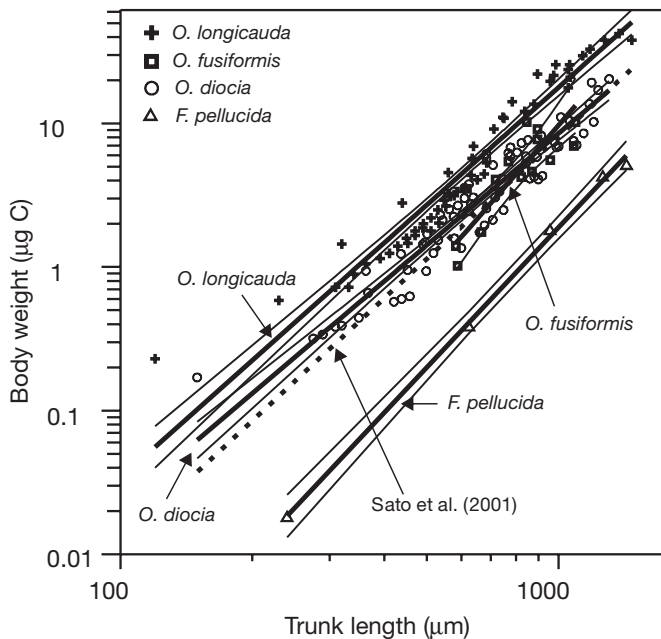
Fig. 1. *Oikopleura* spp. and *Fritillaria* spp. Relationships between appendicularian body weight and trunk length, using data from the literature; see Table 2 for sources and 'Materials and methods' for transformations of dry weight to carbon. Relationships were obtained by calculating geometric mean regression on $\log_{10}$-transformed data. Thick lines = regression lines, thin lines = 95% confidence limits for parameter estimates. Equations are summarized in Table 3. For comparison with relationships obtained by direct measurement of carbon content, regression line from data in Sato et al. (2001) for *Oikopleura dioica* is shown (dashed thick line)

lated the production of appendicularians and copepods using data in López-Urrutia et al. (2003). Appendicularian production was obtained from measurements of body weights and *in situ* abundance, in combination with the temperature-dependent growth-rate equation developed in this study. We estimated the production of copepods using the Huntley & Lopez (1992) temperature-dependent model in combination with copepod biomass estimated as the difference between total mesozooplankton biomass and appendicularian biomass. Total mesozooplankton dry mass is not reported by López-Urrutia et al. (2003), but it was available from the long-term zooplankton monitoring programme in the Cantabrian Sea (their Stns E1, E2, E3). Total mesozooplankton (retained by a 200 µm net) dry mass was measured following methods in Postel et al. (2000), and was converted to carbon units using a factor of 0.4 (Postel et al. 2000). The secondary production values obtained were compared with primary production measurements in López-Urrutia et al. (2003) to determine the relationship between the production of appendicularians and primary production.

RESULTS

Conversion factors

The body weight versus trunk length relationship obtained for *Oikopleura dioica* using the transformation of dry-weight data to body carbon is similar to those obtained by King et al. (1980), Gorsky et al. (1988) and Sato et al. (2001) from direct measurement of body carbon. For comparison, the equation obtained by Sato et al. (2001) is included in Fig. 1. The equations obtained (Fig. 1, Table 3) for the remaining species were therefore considered valid approximations and used to estimate body carbon from trunk length.

Table 3. *Oikopleura* spp. and *Fritillaria* spp. Summary of body weight (W_b, µg C ind.$^{-1}$) versus trunk length (TL from mouth to distal gonad end, µm) and of individual gut contents versus body weight equations developed (Figs. 1 & 2, respectively). Equations show parameter estimates ± SE; numbers in parentheses: sample size; r^2 values

Species	Body weight (W_b, µg C)	Gut content (µg C ind.$^{-1}$)	
		Total carbon	Autotrophic carbon
Oikopleura longicauda	$10^{-6.91 \pm 0.10}$ TL$^{2.72 \pm 0.28}$ (54; 0.93)	$10^{-1.326 \pm 0.032}$ $W_b^{1.283 \pm 0.042}$ (392; 0.58)	$10^{-2.058 \pm 0.032}$ $W_b^{0.941 \pm 0.040}$ (372; 0.32)
O. fusiformis	$10^{-9.5 \pm 1.6}$ TL$^{3.51 \pm 0.54}$ (14; 0.72)	$10^{-1.17 \pm 0.041}$ $W_b^{1.291 \pm 0.069}$ (233; 0.34)	$10^{-2.01 \pm 0.039}$ $W_b^{1.075 \pm 0.067}$ (212; 0.17)
O. dioica	$10^{-6.84 \pm 0.27}$ TL$^{2.59 \pm 0.10}$ (72; 0.90)	$10^{-1.114 \pm 0.025}$ $W_b^{1.358 \pm 0.056}$ (391; 0.58)	$10^{-2.029 \pm 0.025}$ $W_b^{1.174 \pm 0.053}$ (391; 0.20)
Fritillaria pellucida	$10^{-9.45 \pm 0.23}$ TL$^{3.241 \pm 0.081}$ (5; 0.99)	$10^{-0.803 \pm 0.052}$ $W_b^{1.52 \pm 0.098}$ (71; 0.71)	$10^{-1.992 \pm 0.054}$ $W_b^{0.91 \pm 0.10}$ (71; 0.13)
F. borealis	–[a]	$10^{-1.16 \pm 0.052}$ $W_b^{1.222 \pm 0.010}$ (71; 0.71)	$10^{-1.52 \pm 0.056}$ $W_b^{1.011 \pm 0.010}$ (85; 0.08)

[a]No body weight data available for *F. borealis*, equation for *F. pellucida* used as an approximation

Fig. 2. *Oikopleura* spp. and *Fritillaria* spp. Relationships between gut content and body weight (W_b, µg C) based on data in López-Urrutia et al. (2003). Gut contents in A and B represent autotrophic material ingested (*AGC*, µg C ind.$^{-1}$), gut contents in C and D represent estimates of total particulate carbon ingested (*TGC*, µg C ind.$^{-1}$). (A) (C) Comparison of equations obtained for the different appendicularian species; lines represent geometric mean regression (GMR) of $\log_{10}$-transformed data (thick lines) and 95% confidence limits for parameter estimates (thin lines); regression equations for each species are presented in Table 3. (B) (D) Relationships between gut content and body weight obtained by pooling data for the different species; equations show parameter estimates ± 95% confidence limits (thin lines) of the GMR regression on the $\log_{10}$-transformed values (thick line)
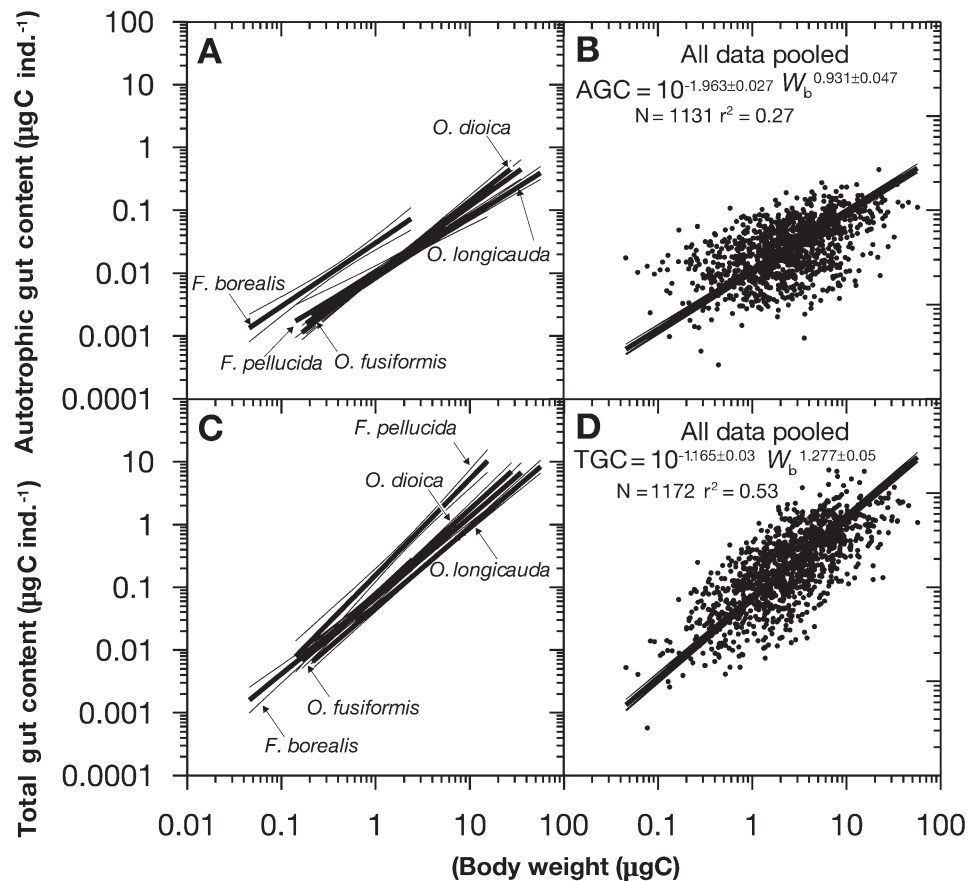
Ingestion rates

After transforming data on appendicularian trunk length from López-Urrutia et al. (2003) to carbon units, we calculated GMR for each species using $\log_{10}$-transformed total (*TGC*) and autotrophic (*AGC*) gut-carbon contents and body weights (W_b, µg C) (Fig. 2A,C). There were significant differences between species in the gut carbon contents versus body weight power regressions (Table 3), as indicated by both the 95% confidence limits and by an ANCOVA of the least-squares regression models (test of parallelism: $F_{4,1162} = 5.91$, p < 0.001 for *TGC*, and $F_{4,1121} = 1.89$, p = 0.11 for *AGC*; ANCOVA, $F_{4,1162} = 17.29$, p < 0.001 for *TGC* and $F_{4,1121} = 2.72$, p = 0.028 for *AGC*). The high degrees of freedom in the ANCOVA mean that, although significant, some effects may not explain large proportions of variance (Graham 2001). Differences between species accounted for less than 9%, while body weight accounted for over 40% of the total variance. Therefore, data for the different species were pooled and a general equation was calculated (Fig. 2B,D). The total variance explained (approx. 50%) is not very high, probably because there is a systematic variability in

the gut contents of appendicularians due to their continuous ingestion and discrete defecation. The true explanatory power, once this irreducible variability is taken into account, should be much higher (López-Urrutia & Acuña 1999).

Although López-Urrutia & Acuña (1999) obtained a power equation to predict gut-passage time from temperature and food concentration ($GPT = 51.67\,e^{-0.0376\,T}\,FC^{-0.245}$), we have instead fitted their data to an inverse Michaelis-Menten equation by iterative non-linear regression using a Marquardt algorithm, and applied that equation in our calculations:

$$GPT = e^{0.0376T}\,\frac{37.6 + FC}{0.084FC}, r^2 = 0.39$$

The reason for doing so is that ingestion rate versus food concentration curves follow a saturating pattern in appendicularians (see for example Acuña & Kiefer 2000). Since gut contents are not related to food concentration (López-Urrutia et al. 2003), it made sense to model *GPT* versus food concentration data according to an inverse hyperbolic equation in order to make the equations in this work structurally consistent with a saturating pattern. In any case, use of either a power or

Table 4. Summary of equations developed to estimate physiological and growth rates based on data for *Oikopleura dioica* and on all data available (i.e. all species included). Equations show parameter estimates ± SE; numbers in parentheses: sample size; r^2 values

Parameter	*Oikopleura dioica*	All data
Total ingestion[a] (IT, total carbon, µg C ind.$^{-1}$ d^{-1}) =	$\dfrac{9.3 \times FC \times e^{0.0376\,T} \times W^{1.358}}{37.6 + FC}$	$\dfrac{8.27 \times FC \times e^{0.0376\,T} \times W^{1.277}}{37.6 + FC}$
Autotrophic ingestion[a] (IA, autotrophic carbon, µg C ind.$^{-1}$ d^{-1}) =	$\dfrac{1.132 \times FC \times e^{0.0376\,T} \times W^{1.174}}{37.6 + FC}$	$\dfrac{1.32 \times FC \times e^{0.0376\,T} \times W^{0.931}}{37.6 + FC}$
Assimilation constant (α) =	0.61 ± 0.22 (3)	–
Respiration (R, µg C ind.$^{-1}$ d^{-1}) =	$e^{-1.33 \pm 0.34} \times e^{0.067\,(\pm 0.018)\,T} \times W^{0.5984 \pm 0.064}$	$e^{-1.30 \pm 0.36} \times e^{0.066\,(\pm 0.018)\,T} \times W^{0.665 \pm 0.069}$
Development time (D, d) =	$e^{3.29 \pm 0.13} \times e^{-0.085\,(\pm 0.007)\,T}$ (60; 0.70)	$e^{3.25 \pm 0.27} \times e^{-0.08\,(\pm 0.01)\,T}$ (72; 0.64)
Body growth rate (g_b, d^{-1}) =	$e^{-1.47 \pm 0.15} \times e^{0.0807\,(\pm 0.0072)\,T}$ (60; 0.68)	$e^{-1.546 \pm 0.093} \times e^{0.0815\,(\pm 0.0039)\,T}$ (131; 0.77)
Body growth allocation ($b = g_b/g_T$) =	0.8196 ± 0.0089 (6)	
Total growth rate (g_T, d^{-1}) =	$0.28 \times e^{0.0807\,T}$	$0.25 \times e^{0.0815\,T}$
Total growth rate upper limit (g_{Tmax}, d^{-1}) =	$0.52 \times e^{0.0842\,T}$	$0.49 \times e^{0.079\,T}$

[a]All equations calculated by dividing different gut content versus body weight relationships by the same gut-passage time equation based on data for *O. dioica*

a Michaelis-Menten relationship has little influence on the results (data not shown). The relationship between gut content and body weight was divided by this equation to obtain the ingestion rate of appendicularians as a function of temperature, body weight and food concentrations (Table 4). The average food-assimilation constant for *Oikopleura dioica* obtained by Gorsky

(1980) was 0.61 (Table 4), close to the value reported for the cold-water appendicularian *O. vanhoeffeni* (0.67: Bochdansky et al. 1999) and for planktonic herbivores in general (0.7: Conover 1978).

Respiration rates

Following Huntley & Boyd (1984), respiration was assumed to vary as a power function of body weight in the form:

$$R = kW_b^m \qquad (5)$$

where k and m are the respiratory allometric coefficient and exponent, respectively, and W_b is the appendicularian body weight. We have assumed respiration to be independent of FC (see 'Discussion'). Eq. (5) was fitted, using GMR, to data for each species and temperature. The 95% confidence intervals of the respiration versus body weight GMR parameters obtained for *Oikopleura dioica* and *O. longicauda* at 20°C overlap (Fig. 3A), indicating no significant differences between the regression equations. In addition, an ANCOVA on the linear regression models showed no significant differences between the slopes (test of parallelism, $F_{1,26} = 2.47$, p = 0.13) or intercepts ($F_{1,27} = 2.63$, p = 0.12). While the allometric exponent (m) did not vary with tempera-
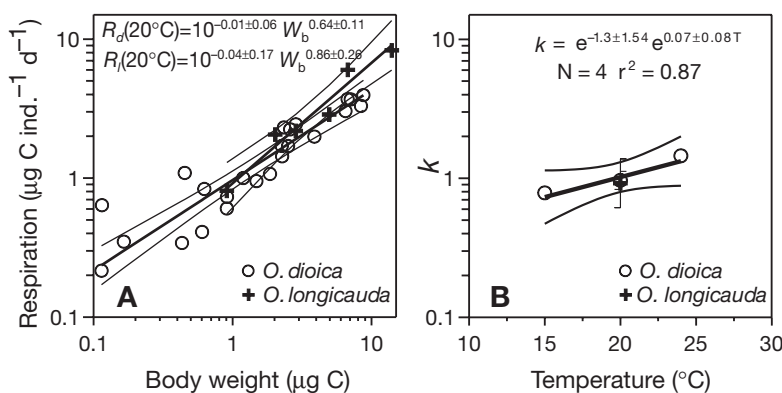

Fig. 3. *Oikopleura* spp. (A) Relationship between respiration and body weight at 20°C for *O. longicauda* (R_l; data from Gorsky et al. 1984) and *O. dioica* (R_d; data from Gorsky et al. 1987); relationships were obtained by calculating geometric mean regression on log$_{10}$-transformed data; equations show parameter estimates ±95% confidence limits. (B) Respiratory coefficient (k) as a function of temperature, vertical error bars represent 95% confidence intervals for k estimates at each temperature and species; thick lines: regression lines; thin lines: 95% confidence limits for parameter estimates
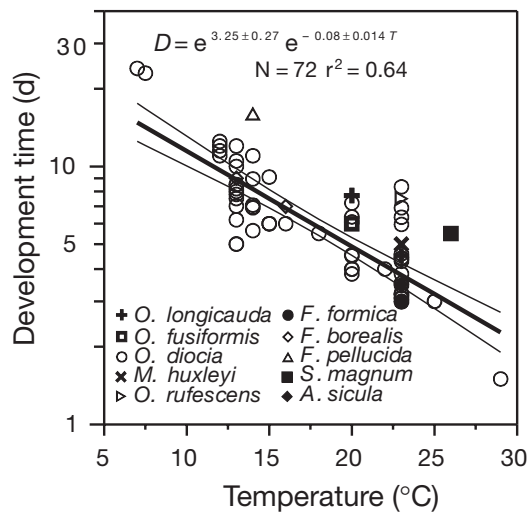
Fig. 4. *Oikopleura* spp., *Fritillaria* spp., *Megalocercus huxleyi*, *Stegosoma magnum* and *Appendicularia sicula*. Appendicularian development time (D) versus temperature (T) (see Table 2 for sources). Thick line: linear regression with $\log_e$-development time as dependent and temperature as independent variables, based on data for all species (see Table 3 for equation based on *O. dioica* data only); thin lines: 95% confidence limits for parameter estimates

nation of the development times (those independent of the laboratory experiments used in the calculation of growth rates, see 'Materials and methods') with adult body and egg weights resulted in 21 estimates of weight-specific growth rate using Eq. (3).

Our literature search resulted in 131 direct measurements of weight-specific growth rate; temperature was available for all estimates, while food concentration was reported in 89 cases. Of these 131 growth rates, 88 were obtained using the microcosm cohort methodology and 43 using laboratory-cultured individuals (see 'Materials and methods' for detailed explanation). The lack of overlap in the temperature ranges for which these values were obtained (Fig. 5A) did not allow evaluation of the effect of different methodologies, and both types of data were pooled and analysed together. Temperature explained most of the variance in weight-specific growth rates ($r^2 = 0.77$, Table 4). Food concentration was rejected as an explanatory variable by a forward stepwise multiple-regression model with $\log_e$-transformed growth rates as dependent and temperature and $\log_e$-transformed food concentrations as independent variables ($t_{1,88} = 0.57$, p = 0.57). Examination

ture, the allometric constant k increased exponentially with temperature (Fig. 3B). If we replace k in Eq. (5) by the exponential relationship between k and temperature (Fig. 3B) and m by the exponent of the power relationships between respiration and body weight (Fig. 3A) we obtain the weight and temperature-dependent equations to predict respiration presented in Table 4. The equation for *O. dioica* was used to estimate the minimum metabolic requirement for each individual as a function of its body weight and habitat temperature.

Body growth rates

We compiled 71 measurements of development time; temperature data were available for all measurements, while food concentration was only reported in 52 cases. Development time was strongly dependent on temperature (Fig. 4), while food concentration was rejected by forward stepwise regression models and by analyses of temperature-corrected development times (data not shown, see results below for growth rate for a description of the type of analyses performed). Combi-
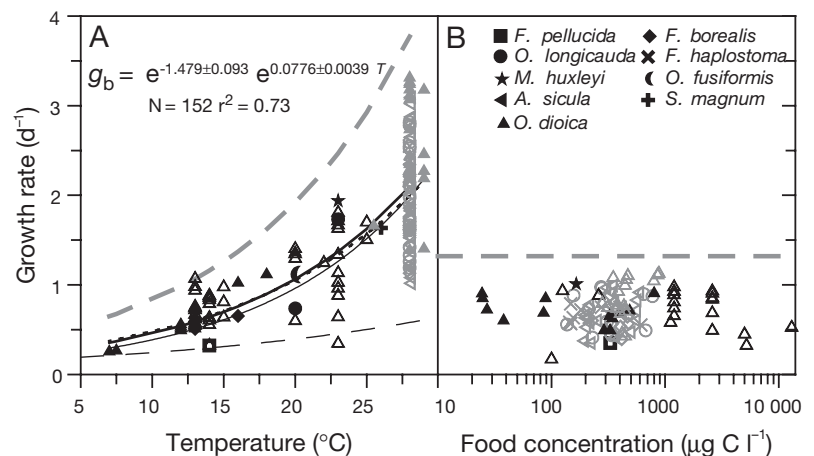

Fig. 5. *Oikopleura* spp., *Fritillaria* spp., *Megalocercus huxleyi*, *Stegosoma magnum* and *Appendicularia sicula*. (A) Instantaneous weight-specific body growth rate (g_b, d^{-1}) as a function of temperature (T). Grey symbols: data from microcosm incubations of natural populations; open symbols: growth-rate estimates from laboratory experiments; black symbols: growth-rate estimates based on development time in combination with adult and egg weight estimates (see 'Materials and methods'). Equation corresponds to least-squares regression (thick continuous line) between $\log_e$ growth rate and temperature (±95% confidence limits) using all data from different methods and species; thick grey dashed lines: upper 95% confidence limit of individual estimates, used as an estimate of the thermally defined upper limit for body growth; thick dotted line: relationship obtained using all data except those derived from development time (see Table 4 for regression equation); thin line: relationship obtained using data for all species except *O. dioica*. For comparison, the relationship obtained by Hirst & Lampitt (1998) for marine copepods is also included (thin dashed bottom line). (B) Weight-specific body growth rates (g_b, d^{-1}, adjusted to 15°C using equation obtained in (A) versus food concentration)
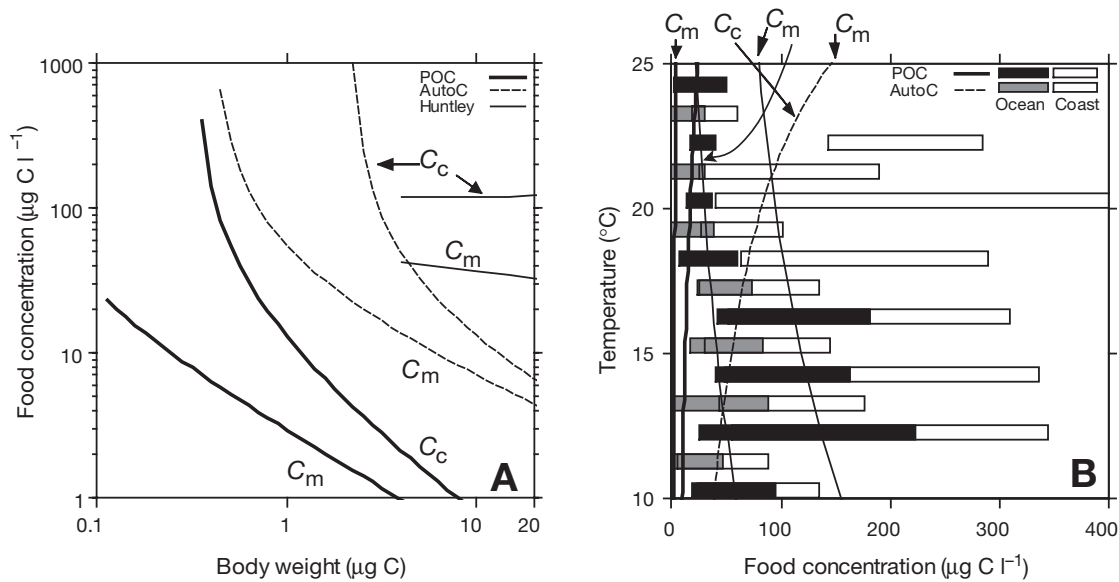
Fig. 6. *Oikopleura dioica*. (A) Maintenance food concentration C_m (where assimilation balances respiration) and critical food concentration C_c (above which growth is not food-limited) as a function of body weight at 15°C. Dashed lines: estimates based on ingestion rates with autrophic carbon; thick continuous lines: values based on ingestion rates with total particulate carbon, assuming that all particulate material is assimilated with the same efficiency (0.61); thin continuous lines: calculated from Huntley & Boyd (1984) equations for marine zooplankton assuming 0.4 µg C µg^{-1} dry weight. (B) Typical food concentrations in oceanic areas (>300 m bottom depth, filled bars) and in coastal regions (<300 m bottom depth, open bars) obtained using particulate organic carbon and chlorophyll data (from US National Oceanographic Data Center, Silver Spring, Maryland, USA); data were binned into 2°C intervals and the first and third quartiles of the food concentrations within each bin were used as the ranges for the bars displayed. Horizontal bars beginning with black segments represent data on total particulate organic carbon concentration (POC); horizontal bars beginning with grey segments represent autotrophic carbon concentration (AutoC) estimated from chlorophyll using chlorophyll to autotrophic carbon relationship in Hewes et al. (1990). Lines represent maintenance food concentration (C_m), and critical concentration (C_c) as a function of habitat temperature for an individual of 1 µg C body weight; dashed line: estimates based on ingestion rates of autrophic carbon; thick continuous lines: values based on ingestion rates of autrophic carbon; thin continuous lines: values for marine zooplankton calculated using equations in Huntley & Boyd (1984) for an individual of 4 µg C (assuming 0.4 µg C µg^{-1} dry weight)

of the weight-specific growth rates adjusted to 15°C (using the body growth rate vs temperature relationship in Table 4) did not reveal any changes in growth rate with food concentration despite the wide range of concentrations considered (21 to 13 000 µg C l^{-1}, $F_{1,87}$ = 1.26, p = 0.26, Fig. 5B), suggesting that all the growth rate measurements compiled were under saturating food concentrations. Weight-specific growth rates were also independent of adult appendicularian body weight (power regression on growth rates adjusted to 15°C vs adult body weight, $F_{1,123}$ = 0.622, p = 0.43, data not shown). Therefore, a temperature-dependent growth-rate equation for the appendicularian body was calculated using all available data (g_b: Table 4, Fig. 5A). For comparison, the temperature- and body weight-dependent model of growth rate in copepods (Hirst & Lampitt 1998) is included in Fig. 5A, after substituting body weight in their multiple-regression equation by 0.075 µg C (the minimum body weight in their data and therefore the higher weight dependent growth rate). Although most of the compiled weight-specific growth rates were for *Oikopleura dioica* (60 out of 131) and

measurements for other species are still too scarce to make any conclusive distinctions, visual comparison did not reveal significant differences between species. In addition, the variability in the measured growth rates for different species was not markedly different from the variability observed within different measurements for *O. dioica* (Fig. 5). Temperature-dependent growth rate equations obtained using the data for *O. dioica* and the data for the remaining species separately were not significantly different (test of parallelism, $F_{1,127}$ = 0.2, p = 0.65, ANCOVA, $F_{1,127}$ = 0.58, p = 0.44).

The temperature-dependent equation obtained using growth rate estimates derived from development times using Eq. 3 was not significantly different from the relationship obtained from data of direct measurements of growth rate (test of parallelism, $F_{1,148}$ = 0.081, p = 0.77, ANCOVA, $F_{1,148}$ = 0.139, p = 0.71), suggesting that when direct measurements of weight-specific growth rates cannot be obtained, estimates using Eq. (3) should provide a valid approximation. Combination of both datasets (direct measurements and indirect esti-

mates through development time) resulted in the temperature-dependent equation presented in Fig. 5A.

House production and growth rates

Body growth allocation (b) depends on the house production rate, the carbon content of the houses and the body weight-specific growth rates. However, studies in which all these 3 parameters were measured simultaneously are still too scarce to analyze the relationship of b with temperature, salinity or food concentration. We therefore assumed that b is constant. Recalculation of data in Sato et al. (2001) using Eqs. (3) & (4) resulted in a body growth allocation (b) of 0.82 (Table 4). Therefore, the total growth rate of appendicularians (g_T) was estimated by multiplying equations to estimate the body growth (g_b: Table 4) by a factor of 1.22 ($1/b$). Accordingly, the thermally defined upper limit for the growth rate of *Oikopleura dioica* (g_{Tmax}) was obtained by multiplying the upper 95% confidence interval for individual estimates of the exponential relationship between g_b and temperature (Table 4) by 1.22. This equation defines the maximum growth rates (g_{Tmax}) of *O. dioica* as a function of temperature, and was used in the Huntley & Boyd (1984) approach. Since the information available on house production rates and carbon content of the houses of other appendicularian species is still limited, we have assumed that the estimate of b obtained for *O. dioica* was adequate for the other species. Alldredge (1976a) showed that the carbon content of discarded houses varies between species, but b depends also on the house production rate and the body growth rate; thus, we could not transform the data in Alldredge (1976a) to species-specific body-growth allocation estimates.

Food limitation and the Huntley & Boyd approach

C_m and C_c estimates for *Oikopleura dioica* based on ingestion of autotrophic and total carbon suggest that the degree of food limitation depends strongly on the extent to which the ingested non-autotrophic material is assimilated (Fig. 6). Our lack of knowledge on these assimilation rates prevents us from reaching a firm conclusion on the concentrations at which *O. dioica* would be likely to experience food-limited growth. Also, the gut-content values for autotrophic and total food are likely to be underestimates, since they do not take into consideration the chlorophyll degradation or compression of food particles in the gut (although this underestimation is probably small or absent: see López-Urrutia et al. 2003). Therefore, use of these ingestion rates would lead to overestimation of C_m and C_c.

Our results suggest that, even under the assumption that C_m and C_c are overestimated and that *Oikopleura dioica* only depends on autotrophic prey, large individuals are less likely to experience food-limited growth than other similarly sized groups of marine zooplankton (Fig. 6), since their C_m and C_c values lie below those estimated by Huntley & Boyd (1984) (Fig. 6A). However, appendicularian growth during early development is likely to be more limited by the concentration of food in the environment (Fig. 6A). Comparison
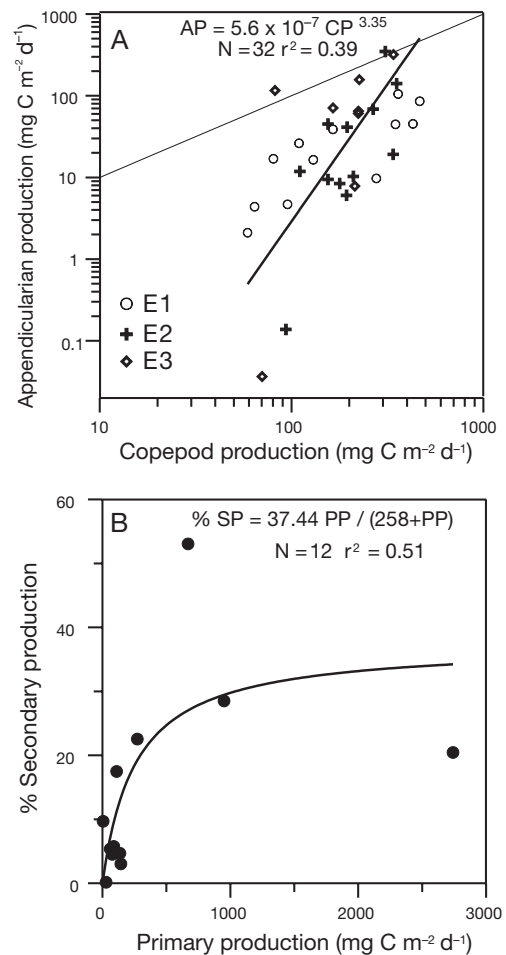

Fig. 7. (A) Relationship between appendicularian community production (AP) and copepod production (CP). Appendicularian production estimated from López-Urrutia et al. (2003) in combination with the temperature-dependent growth-rate equation in this study (see Table 4). Copepod production calculated using the Huntley & Lopez (1992) model for temperature-dependent growth of copepods; copepod biomass estimated as difference between total mesozooplankton biomass and appendicularian biomass; thin line: Level at which appendicularian production equals copepod production. (B) Estimated percentage of total secondary production attributable to appendicularians (% SP) as a function of primary production at Stn E2 in López-Urrutia et al. (2003); line represents Michaelis-Menten model fitted by iterative nonlinear regression using a Marquardt algorithm

of C_m and C_c for both autotrophic and total ingestion with carbon concentrations in the field (Fig. 6A) suggests that *O. dioica* would obtain enough energy to survive from phytoplankton in coastal, but not in oceanic environments, where the assimilation of non-autotrophic material would be a key requirement.

Contribution of appendicularians to secondary production

The appendicularian and copepod production rates obtained through combination of biomass estimates with temperature-dependent growth-rate models (equation in Table 4 for appendicularians and Huntley & Lopez's [1992] equation for copepods) indicate a possible relationship between appendicularian and copepod production (Fig. 7A). The percentage contribution of appendicularians to total mesozooplankton production (appendicularians plus copepods) increased with increasing primary productivity up to ca. 32.7% (Fig. 7B). These values should be viewed with caution, since they are probably underestimates of the contribution of appendicularians to total secondary production. Likewise, the contribution of copepods to secondary production may be overestimated in oligotrophic regions because the Huntley & Lopez (1992) model is probably biased towards higher, food-satiated growth rates (Hirst & Lampitt 1998).

DISCUSSION

We are far from understanding the factors that control appendicularian populations and their importance as secondary producers. Some of the key parameters in appendicularian physiology are only known for a few species, and many data are restricted to experimental information from laboratory cultures of *Oikopleura dioica*. The lack of knowledge on the metabolic and growth rates and on the developmental times of many species, particularly the cold-water and deep-oceanic appendicularians, does not currently allow evaluation of species-specific differences or the degree to which generalizations on appendicularian physiology are valid. However, our compilation seems to confirm that appendicularians as a group display high metabolic and growth rates, which implies that their contribution to secondary production is potentially important.

Do appendicularians experience food limitation?

Because of the scarcity of data, our investigation of food limitation using the Huntley & Boyd (1984) approach has been restricted to *Oikopleura dioica*. Our results suggest that *O. dioica* would only experience food-limited growth under oligotrophic conditions and during early development. Although determination of food limitation in copepods is still a matter of discussion (Hirst & Lampitt 1998), our results suggest that appendicularians are generally less likely to experience food limitation than copepods (Fig. 6). The low maintenance food concentrations are in agreement with theoretical studies (Acuña 2001), which indicate that the watery body of gelatinous organisms may represent an adaptation for survival in oligotrophic environments.

As appendicularians lack any selection mechanism by which they could favour ingestion of high-quality food, they will be more affected by changes in the composition of the available food than zooplankton that have evolved selective feeding strategies. The fact that the total food concentrations in nature are usually above the theoretical maintenance minimum of appendicularians does not rule out the possibility of resource limitation through differences in the assimilation efficiency of different types of food. Although we have attempted a first quantification of the importance of non-autotrophic versus phytoplankton food (Fig. 6), differences in the composition of the phytoplankton or heterotrophic communities and in the assimilation efficiencies of different food sources could have important implications for appendicularian growth rates and population dynamics. For example, Andersen (1986) found that assimilation in the salp *Salpa fusiformis* did not depend on algal concentration, but was greater with a flagellate than with a diatom diet. The high protein absorption efficiencies in *Oikopleura vanhoeffeni* (Bochdansky et al. 1999) and the high levels of protease activity (A. Bedo & R. Harris unpubl.) and O:P and N:P metabolic quotients (Gorsky et al. 1987) in *O. dioica* indicate that appendicularians do not differ from other zooplankton in having their production limited by the availability of nitrogen (i.e. proteins; Checkley 1980).

Another important physiological variable that was not considered by Huntley & Boyd (1984) and that we could not account for is the specific dynamic action or modification of the metabolic rates associated with changes in the feeding rates. Respiration varies with ingestion rate, and is therefore a function not only of the body weight but also of the food concentration. The measurements of respiration rate that we use for application of the Huntley & Boyd (1984) approach were conducted on individuals that were feeding (Gorsky et al. 1987). Therefore, these rates do not represent a minimum respiration or basal metabolism but an active metabolism. Accordingly, our assumption that there is no relationship between respiration and growth implies that our estimates of C_m are conservative, since the real basal metabolism should be lower, and therefore the real C_m should also be

lower. To summarize, if we had used basal instead of Gorsky et al.'s (1987) respiration rates, we would have arrived at the conclusion that appendicularians would be able to survive at even lower food concentrations. However, our estimates of C_c could be biased, since we do not know how much the respiration rate would vary at these higher food concentrations.

The number of parameters in the physiological or budgetary method developed by Huntley & Boyd (1984) and the compounding error associated with the difference between assimilation and respiration in Eq. (1) (Lehman 1988) clearly show that a better understanding of food limitation can be obtained through the study of the relationship between direct measurements of growth rate and food concentration (Huntley 1996). Both approaches (physiological or budgetary and direct measurement of growth) have their own pros and contras. We have used these 2 approaches in parallel since both address the same issue in a complementary manner and responds to different ecological questions. The budgetary physiological model allows an understanding of the mechanisms acting at the individual level (and by necessity requires simplifications: Levins 1966), while the empirical approach permits the development of predictive equations that can be used in combination with biomass measurements to estimate the contribution of appendicularian populations to total mesozooplanktonic secondary production. The fact that there was no significant relationship between food concentration and the directly measured weight-specific growth rates suggests that growth rates in appendicularians are not controlled by food concentration. However, this does not rule out the possibility of resource limitation due to changes in food quality, or the possibility that we may not be sampling the whole range of food available to appendicularians. Most studies from which we derived our growth rate estimates were performed under controlled laboratory conditions, in which all the available food was phytoplankton. Although some of the food concentrations used in our study, particularly those derived from chlorophyll estimates, did not include bacteria, exclusion of those food concentrations derived from chlorophyll data from the analysis renders the same lack of relationship between growth rates and food concentration (data not shown).

Our study suggests that young *Oikopleura dioica* are more prone to food limitation than older individuals (Fig. 6A). This conclusion is supported by observations on laboratory cultures of *O. dioica*, in which juveniles did not survive below 60 µg C l^{-1} while older and larger individuals grew at food concentrations of 40 µg C l^{-1} (K. King unpubl., cited in King 1982). Our study suggests that this pattern is due to differences between the exponents of the power functions relating body weight to ingestion (1.358 and 1.174; Table 4) and respiration

(0.5984) rates. In a comparison of faecal pellet volume and body weight of different zooplankton groups (Uye & Kaname 1994), appendicularians were the only group that had an allometric exponent greater than 1 (1.14). Paffenhöfer (1976) also measured allometric exponents of 1.19 and 1.24 for the ingestion rate of *O. dioica*. These values are higher than those for calanoid copepods and cladocerans (Peters & Downing 1984), which are closer to the general allometric exponent of 0.75 (Peters 1983). Whether this high allometric exponent of appendicularian ingestion rates is due to experimental error, or whether the gelatinous strategy of appendicularians distorts their allometry requires further investigation.

When food concentrations are below C_m, appendicularian populations are doomed to extinction because of their limited lipid-storage ability (Deibel et al. 1992) and because no dormant stages have been reported to date. This limited storage capacity and the high metabolic activity of appendicularians even during starvation (Gorsky et al. 1987) suggest that appendicularian populations are in a quasi-steady state with their environment, as is the case for small tropical and neritic zooplankton (i.e. they grow quickly and die quickly and the ratio of production to biomass is higher than for large copepods: Conover 1968).

Our results indicate that factors other than food quantity or quality play a significant role in controlling appendicularian communities (e.g. predation: Hopcroft & Roff 1998). The average number of eggs produced by *Oikopleura dioica* at 13°C is 200 (Paffenhöfer 1976). For a population of *O. dioica* to be maintained in steady state, the number of eggs that reach maturity and produce offspring should be 2 (assuming a 1:1 sex ratio; Fenaux et al. 1986b). Therefore, an average 99% mortality from egg to spawning is needed for a steady state population at this temperature. Paffenhöfer (1973) measured an approximate 45% mortality from hatching to spawning in isolated culture conditions. Much of this natural mortality occurs during the period from hatching to the start of feeding. Paffenhöfer (1976) attributes this mortality mainly to failure in unfolding the first filter house. However, other factors as egg sinking, fertilization and hatching success or predation have been rarely taken into account, although they could be limiting appendicularian populations.

Contribution of appendicularians to secondary production

Our compilation on appendicularian growth rates has allowed us to develop a temperature-dependent equation to estimate the production rate of temperate epipelagic species when data on appendicularian bio-

mass and temperature are available (Table 4, Fig. 7). The high individual growth rates of appendicularians compared to those of copepods (Fig. 5A and Hopcroft & Roff 1998) suggest that both the relative composition of mesozooplankton and the contribution of different groups to the total biomass should be taken into account if reliable estimates of secondary production are to be obtained. Comparison of the individual growth rates and development times obtained in this study with those of other groups of zooplankton (Hirst & Sheader 1997, Gillooly 2000) suggests that appendicularians significantly depart from the models developed for crustacean zooplankton. For example, at 15°C the development time of an appendicularian is 7.77 d, the weight-specific growth rate is 0.85 d^{-1} (using equations in Table 4), and the adult body weight is 4.14 µg C (Eq. 3 with an egg weight of 0.015 µg C). The development time for crustacean zooplankton of similar adult body weight is 20 d (Gillooly 2000), while the weight-specific growth rate for copepods is 0.09 d^{-1} (Hirst & Lampitt 1998). Therefore, appendicularian growth rates are close to one order of magnitude higher than those of copepods of similar body weight. The fact that copepods generally dominate mesozooplankton samples numerically and in biomass do not have to translate directly into a dominance of the secondary production, and our results suggest that groups other than copepods (appendicularians in this particular study) should not be disregarded when estimating mesozooplankton production (Fig. 7A).

Huntley & Lopez (1992) have suggested that in order to increase the precision of our estimates of production we should improve our knowledge on the sources of variability in biomass. Our results suggest that appendicularians could represent an average of 10% of the total mesozooplankton production, and that their relative contribution is not constant (Fig. 7B), reaching values close to 40% in productive environments. The fact that the appendicularian contribution to secondary production during our study increased with increased productivity suggests that their role in oligotrophic environments needs re-evaluation.

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