

# Ontogenetic changes in the feeding functional response of the marine copepod *Paracartia grani*

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**ABSTRACT:** The feeding activity of copepods is crucial for the structure and functioning of marine ecosystems. Quantification of feeding rates of different copepod life stages across a range of prey densities (functional response) is essential knowledge for improvement of plankton dynamic models. In this study, we conducted experiments to compare the feeding functional responses of nauplii, copepodites, and adults of the marine copepod *Paracartia grani* (formerly *Acartia grani*) when grazing on the flagellate *Rhodomonas salina*. We found that all copepod stages followed a sigmoid curve in their functional responses (Holling Type III model), indicating a metabolic threshold constraining foraging effort at low prey densities. Maximum clearance rates of nauplii and copepodites increased with body mass with a power scaling factor of 1, but maximum clearance rates of adults did not follow the pattern observed for juvenile stages, likely because of the relatively small prey size used in the experiments. Copepod maximum ingestion rates, however, showed allometric scaling along ontogeny that was closer to the typical 0.75 power law and seemed to not be so dependent on prey size. The insights obtained from our study highlight stage-specific differences in copepod feeding activity, and can help improve our capability to estimate the energy flow through copepods in marine food webs.

**KEY WORDS:** Zooplankton · *Acartia* · Nauplii · Development · Grazing · Ingestion · Clearance rate · Functional trait

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## 1. INTRODUCTION

Zooplankton constitute the main link between primary producers (phytoplankton) and higher trophic levels in marine food webs (Calbet 2001, Calbet & Saiz 2005). They are a key component of the biological pump and play a major role in nutrient recycling in the photic layer (Steinberg et al. 2000, Alcaraz et al. 2010, Turner 2015). Within marine mesozooplankton, copepods typically account for 35–70% of the biomass and represent more than 90% of the abundance (Longhurst 1985). Consequently, the resource exploitation conducted by copepods is crucial for the structure and functioning of marine ecosystems.

Functional responses of copepods are defined as the relationship between their vital rates (e.g. feeding rates, egg production rates) and prey availability (Solomon 1949, Holling 1966). Because of the major

role of copepods in the zooplankton, copepod functional responses have great implications for plankton population dynamics (Runge 1988, Gentleman & Neuheimer 2008, Kiørboe et al. 2018). The quantification of functional responses in both field and laboratory studies enables the development of mathematical models to forecast the response of plankton communities to changing species densities (Morozov 2010, Morozov et al. 2012). These predictive models are intrinsically very sensitive to the parameterization of functional responses (e.g. the shape of the functional response) and for this reason, the proper analysis of copepod functional responses becomes an imperative task to improve our capability to assess potential variations in the future composition of plankton communities and the biogeochemical fluxes that occur through them (Gentleman & Neuheimer 2008, Wollrab & Diehl 2015, Egilmez & Morozov 2016).

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Traditionally, the study of feeding activity patterns in copepods has been limited mostly to adults, particularly females. In this respect, feeding functional responses have been well documented for adults of key marine copepod species using a wide variety of prey types, and the records are much more numerous for females than for males (Støttrup & Jensen 1990, Isari & Saiz 2011, Gonçalves et al. 2014, Saiz et al. 2014). Females have been preferred over males in grazing experiments mainly because of their longer life span, higher abundances in natural populations, and fundamental role in recruitment (Kouwenberg 1993, Kiørboe 2006, Kiørboe et al. 2015). However, evidence of distinct feeding behaviours between the sexes (e.g. lower feeding rates in males) demonstrates that gender differences should be taken into account when analysing feeding activity patterns in marine copepods (Lampitt 1978, Uye & Kayano 1994, Saage et al. 2009, Chen et al. 2010, van Someren Gréve et al. 2017b).

Similar to males, juvenile copepods (i.e. nauplii and copepodites) have been greatly neglected in previous research addressing copepod feeding patterns. Juvenile copepods outnumber adults throughout the year in plankton communities (Webber & Roff 1995, Calbet et al. 2001, Turner 2004). They play a key ecological role as major grazers of phytoplankton and small heterotrophs. Therefore, studying their feeding activity is fundamental to evaluating the grazing pressure on the smaller plankton fraction in marine ecosystems (Lučić et al. 2003, Turner 2004, Almeda et al. 2011). The first investigations that focused attention on the feeding patterns of the early stages of copepods focused on their rates of grazing on phytoplankton (Mullin & Brooks 1967, Paffenhöfer 1971, Fernández 1979). In response to increasing interest in this topic, further investigations were carried out on other aspects, such as their foraging behaviour, prey size spectrum, and prey selection (Berggreen et al. 1988, Paffenhöfer 1998, Henriksen et al. 2007, Helenius & Saiz 2017). In terms of feeding functional responses, Fernández (1979) was the first author to provide empirical data on naupliar grazing rates of *Calanus pacificus* across a wide range of prey types and food concentrations. Since then, feeding functional responses have been described for juvenile copepod stages of other genera, such as *Acartia/Paracartia* (Henriksen et al. 2007, Ismar et al. 2008, Helenius & Saiz 2017), *Oithona* (Henriksen et al. 2007, Almeda et al. 2010, Saiz et al. 2014), and *Centropages* (López et al. 2007).

Despite this valuable information, we think that the current literature on marine copepods has not com-

pletely addressed the changes in feeding functional response through the entire copepod life cycle. For instance, Almeda et al. (2010) analysed feeding functional responses up to early copepodites, and Saiz et al. (2014) worked with nauplii and adults but not with copepodites. Berggreen et al. (1988) reported changes in the prey size spectrum of *Acartia tonsa* from nauplii to adults, but in their study, the feeding functional responses were not analysed. Thus, it appears that we still lack a complete record regarding how feeding functional patterns change through ontogeny in marine copepods. To the best of our knowledge, only Santer & van den Bosch (1994) have studied this issue, with the freshwater species *Cyclops vicinus*.

Thus, the main goal of this study was to assess ontogenetic changes in the feeding functional response of marine copepods. To accomplish our objective, we conducted grazing experiments in the laboratory with different development stages of the calanoid copepod *Paracartia grani* (formerly *Acartia grani*) and a broad range of prey concentrations of the flagellate *Rhodomonas salina*. *P. grani* is a common neritic species that has been observed from high to middle latitudes in the eastern Atlantic and across the Mediterranean Sea (Boyer et al. 2012). In our study, we compared feeding functional patterns among different *P. grani* life stages (nauplii, copepodites, adults) and sexes (males and females). We expected that the values of the fundamental parameters defining the feeding functional response (maximum clearance and ingestion rates, half-saturation constants) would be influenced by changes along ontogeny in the allometric scaling of metabolic requirements (Ikeda et al. 2001, Saiz & Calbet 2007) and variations in morphological and behavioural traits (Paffenhöfer 1998).

## 2. MATERIALS AND METHODS

### 2.1. Experimental cultures

For the experiments, the cryptophyte *Rhodomonas salina* was used as prey (equivalent spherical diameter [ESD]: 6.9  $\mu\text{m}$ , carbon [C] content: 38  $\text{pg cell}^{-1}$ , nitrogen [N] content: 7.2  $\text{pg cell}^{-1}$ ; Helenius & Saiz 2017). A culture of *R. salina* was grown in f/2 medium (Guillard 1983) and kept in the exponential growth phase by diluting 1/3 of the culture daily. For the copepods, a cohort of *Paracartia grani* was obtained from a stock culture maintained at the Instituto de Ciencias del Mar (ICM, CSIC) for more than 10 yr

(Saiz et al. 2015). To produce the cohort, eggs were siphoned out from the bottom of the copepod stock culture and inoculated into 20 l polycarbonate tanks filled with 0.1  $\mu\text{m}$  filtered seawater. Approximately 24 h after the egg addition, unhatched eggs were removed from the bottom with a siphon to ensure the uniformity of the cohort. The abundance of copepods in the cohort tank started with ca. 15 000 nauplii, and decreased as copepods were taken out for experiments (ca. 1000 adults by the end). The cohort was fed ad libitum at concentrations ranging from 7 (nauplii) to 20 (adults) ppm of *R. salina*. *R. salina* is a nutritionally sufficient prey that has been commonly used in the maintenance of *Acartia* cultures (Støttrup & Jensen 1990, Broglio et al. 2003, Saiz et al. 2015). Both the phytoplankton and the copepod cultures used for the experiments were kept in the laboratory in a cold room at  $19 \pm 1^\circ\text{C}$  and under a 10 h light:14 h dark photoperiod.

## 2.2. Functional response experiments

In total, 6 feeding functional response experiments were carried out successively using different copepod life stages from the same *P. grani* cohort, encompassing 2 experiments conducted with nauplii, 2 experiments with copepodites, and 2 experiments with adults (one with males and one with females). Prior to each experiment, copepods were collected from the cohort using a 60  $\mu\text{m}$  (nauplii and copepodites) or a 200  $\mu\text{m}$  (adults) mesh and placed in filtered seawater for 2.5–3 h while setting up the experiment. For each functional response experiment, 6 prey concentrations of exponentially growing *R. salina* were prepared. The range of prey concentrations was based on previous knowledge (Calbet & Alcaraz 1997, Helenius & Saiz 2017) to cover limiting to satiating food conditions (500–12 000 cells  $\text{ml}^{-1}$  for NII–III, 500–14 000 cells  $\text{ml}^{-1}$  for NV–VI, 500–16 000 cells  $\text{ml}^{-1}$  for CI–II, 1000–20 000 cells  $\text{ml}^{-1}$  for CIII–IV, and 1000–24 000 cells  $\text{ml}^{-1}$  for adults). Prey concentrations were measured with a Beckman Coulter Multisizer III particle counter. A total of 8 bottles were filled with each prey concentration: 2 served as initial bottles (only prey), 3 as control bottles (only prey), and 3 as experimental bottles (prey and copepods). Bottle volumes ranged from 72 ml for early nauplii to 620 ml for adults. All bottles were filled following a 3-step procedure (one-third of the bottle was sequentially filled each time) to ensure homogeneity of prey densities among bottles. Inorganic nutrients (5 ml  $\text{l}^{-1}$  of f/2 solution, i.e. a final

concentration equivalent to f/400) were also added to each bottle to compensate for any differential effect of copepod nutrient excretion on algal growth. Once the bottles were filled with the prey suspensions, the copepods were added to the bottles either as aliquots (nauplii and copepodites) or individually with a pipette (adults). For the aliquots, the concentration of nauplii/copepodites in the filtered seawater was estimated on the basis of replicated counts of subsamples drawn with an automatic pipette, and then the aliquot volume of the copepod suspension required to reach the desired copepod concentration was added to each experimental bottle. To compensate for dilution in the experimental bottles, the same volume of filtered seawater was added to the initial and control bottles. Copepod adults were transferred to suspensions of the respective prey concentration to avoid any dilution effects, and then they were individually removed and transferred to the experimental bottles. Given that different copepod stages (sizes) and different prey concentrations were tested, the number of copepods added to each bottle was adjusted based on unpublished previous data to result in a reduction of ca. 30% of the prey concentration during incubation. Thus, the number of individuals incubated in the bottles ranged from low to high copepod abundance across the different prey concentrations (80–240 NII–III, 40–160 NV–VI, 40–220 CI–II, 25–90 CIII–IV, 10–35 adult males, and 10–30 adult females). All bottles were sealed with plastic film to avoid air bubbles and capped. The initial bottles were sacrificed at the very beginning of the incubation periods to assess actual initial prey concentrations using the Coulter counter. Some extra copepods were preserved in 4% formaldehyde for measurement of initial copepod size. Control and experimental bottles were mounted on a rotating plankton wheel (0.2 rpm) and incubated for 20–24 h at  $19 \pm 1^\circ\text{C}$  and under a 10 h light:14 h dark cycle (photosynthetically active radiation [PAR] 15–34  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). After the incubations, suspensions from control and experimental bottles were filtered through a submerged sieve with a 60  $\mu\text{m}$  (nauplii and copepodites) or a 200  $\mu\text{m}$  (adults) mesh to separate copepods from prey. The final prey concentrations in each bottle were measured, as they were for the initial bottles, with the Coulter counter. The experimental copepods were checked for activity under a stereomicroscope and then fixed with formaldehyde (4% final concentration) for quantification, stage determination, and final body size measurements. Prey sizes were calculated as the geometric mean between initial and final prey volumes measured with the par-

Table 1. Parameters of the feeding functional responses of *Paracartia grani* on *Rhodomonas salina*. Maximum clearance rates ( $F_{\max}$ ), maximum ingestion rates ( $I_{\max}$ ), half-saturation constants ( $K_m$ ), and prey concentrations at which 90% of the maximum ingestion rates were reached ( $C_{90}$ ) are shown for the different copepod stages and sizes (N: nauplii; C: copepodites; Ad: adults). Means  $\pm$  SE are provided

Copepod stage	Copepod size ( $\mu\text{m}$ )	$F_{\max}$ (ml ind. <sup>-1</sup> d <sup>-1</sup> )	$I_{\max}$ (cells ind. <sup>-1</sup> d <sup>-1</sup> )	$I_{\max}$ (% body C d <sup>-1</sup> )	$K_m$ (cells ml <sup>-1</sup> )	$C_{90}$ (cells ml <sup>-1</sup> )
NII–III	139 $\pm$ 2	0.36 $\pm$ 0.02	1623 $\pm$ 46	213 $\pm$ 6.5	2272 $\pm$ 138	6815
NV–VI	238 $\pm$ 2	1.29 $\pm$ 0.06	5623 $\pm$ 185	207 $\pm$ 6.5	2188 $\pm$ 136	6563
CI–II	457 $\pm$ 3	6.25 $\pm$ 0.34	21649 $\pm$ 659	265 $\pm$ 7.6	1733 $\pm$ 120	5198
CIII–IV	632 $\pm$ 2	15.7 $\pm$ 0.98	52761 $\pm$ 1290	195 $\pm$ 5.4	1684 $\pm$ 121	5051
Ad males	922 $\pm$ 1	8.98 $\pm$ 0.46	67772 $\pm$ 1858	68 $\pm$ 1.9	3773 $\pm$ 243	11318
Ad females	1052 $\pm$ 3	15.9 $\pm$ 0.57	218457 $\pm$ 6401	124 $\pm$ 3.3	6877 $\pm$ 368	20632

title counter. Initial and final copepod sizes were determined by photographing 30–40 nauplii or copepodites and 20–25 adults with an inverted microscope and measuring their body (nauplii) or prosome (copepodites, adults) lengths with ImageJ software (Schneider et al. 2012). Copepod sizes were calculated for each prey concentration as the arithmetic mean between their initial and final mean lengths.

### 2.3. Data analysis

Average prey concentrations and copepod feeding rates (clearance and ingestion rates) were determined according to equations in Frost (1972).

Holling Type III curves were fitted to copepod feeding rates as a function of prey concentration using the software package SigmaPlot v.14.0. Curve fitting was carried out by non-linear regression following the equations in Helenius & Saiz (2017):

$$F = \frac{I_{\max}C}{C^2 + K_m^2} \quad (1)$$

and

$$I = \frac{I_{\max}C^2}{C^2 + K_m^2} \quad (2)$$

where  $F$  is the clearance rate,  $I$  is the ingestion rate,  $I_{\max}$  is the maximum ingestion rate,  $C$  is the prey concentration, and  $K_m$  is the half-saturation constant. Estimates of  $I_{\max}$ ,  $K_m$  and prey concentration at which 90% of the maximum ingestion rate was reached ( $C_{90}$ ) were obtained directly from the Holling Type III model. Maximum clearance rates ( $F_{\max}$ ) were calculated as described in Helenius & Saiz (2017):

$$F_{\max} = \frac{I_{\max}}{2K_m} \quad (3)$$

Carbon-specific feeding rates were calculated using the conversion factor 0.221 pg C  $\mu\text{m}^{-3}$  for

*R. salina* (Helenius & Saiz 2017) and the length–weight relationships for *P. grani*:  $W = 3.24 \times 10^{-7} L^{2.34}$  for nauplii and  $W = 1.12 \times 10^{-10} L^{3.58}$  for later stages (E. Saiz et al. unpubl. data), where  $W$  is the copepod mass in  $\mu\text{g C}$ , and  $L$  is the body (nauplii) or prosome (copepodites and adults) length in  $\mu\text{m}$ .

The relationships between copepod body mass and maximum feeding rates (clearance and ingestion rates) were adjusted to a power function. The power fits were obtained from linear regression after log transformation of the variables using the software KaleidaGraph 4.5.4. To improve the robustness of the fitting, for this analysis, we added additional estimates of  $I_{\max}$  of *P. grani* obtained from unpublished experiments (M. Olivares et al. unpubl. data) conducted under similar conditions.

### 3. RESULTS

The average size of the copepods used in the functional response experiments ranged from 139  $\mu\text{m}$  in early nauplii to 1052  $\mu\text{m}$  in adult females (Table 1). Mean prey size was similar in all experiments (range 7.1–7.4  $\mu\text{m}$  ESD). All stages of *Paracartia grani* showed a Holling Type III feeding functional response when grazing on *Rhodomonas salina*. Clearance rates peaked at an intermediate prey concentration and decreased at lower and higher concentrations (Fig. 1).  $F_{\max}$  increased with stage/size, from 0.36 ml ind.<sup>-1</sup> d<sup>-1</sup> for early nauplii to 15.9 ml ind.<sup>-1</sup> d<sup>-1</sup> for adult females; the  $F_{\max}$  values for adult males were, however, lower than the estimates for late copepodites and females (Table 1). Ingestion rates increased with prey concentration following a sigmoid curve and became steady after reaching food saturation (Fig. 1).  $I_{\max}$  increased from ca. 1600 cells ind.<sup>-1</sup> d<sup>-1</sup> (ca. 0.08  $\mu\text{g C}$  ind.<sup>-1</sup> d<sup>-1</sup>) in early nauplii to ca. 218 000 cells ind.<sup>-1</sup> d<sup>-1</sup> (ca. 9.12  $\mu\text{g C}$  ind.<sup>-1</sup> d<sup>-1</sup>) in adult

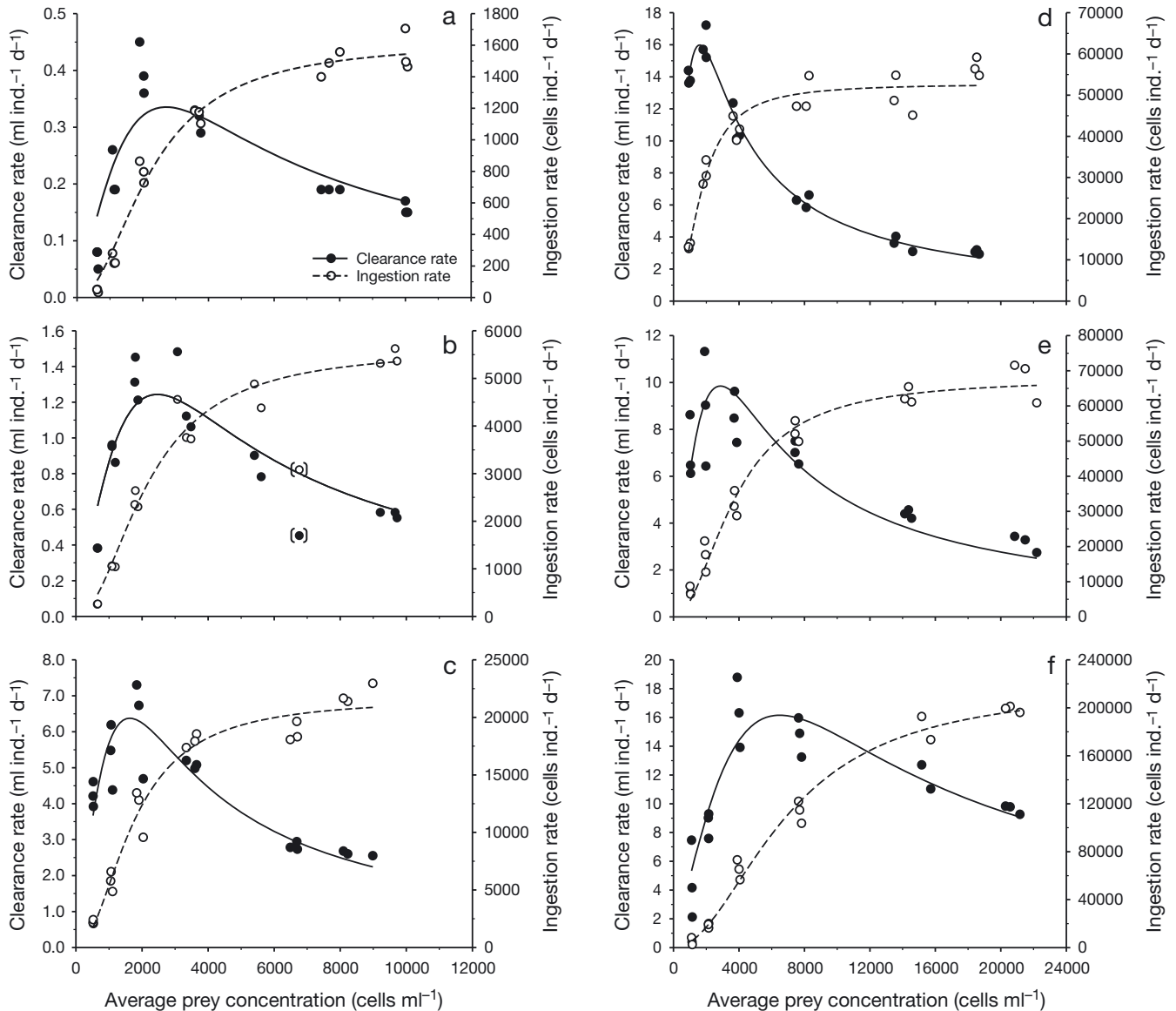


Fig. 1. Functional responses of (a) nauplii II–III, (b) nauplii V–VI, (c) copepodites I–II, (d) copepodites III–IV, (e) adult males, and (f) adult females of *Paracartia grani* feeding on *Rhodomonas salina*. Holling Type III curves were fitted to the clearance and ingestion rates as a function of the average prey concentration. Data in brackets are excluded from the model

females (Table 1). The  $I_{\max}$  values for females were approximately 3 times higher than those of males.

Fig. 2 shows the power fits between copepod body mass and copepod  $F_{\max}$  ( $r^2 = 0.991$ ,  $p < 0.01$ ; Fig. 2a) and  $I_{\max}$  ( $r^2 = 0.967$ ,  $p < 0.001$ ; Fig. 2b).  $F_{\max}$  of nauplii and copepodites increased with body mass with a scaling factor of  $1.09 \pm 0.07$ , whereas the fit between body mass and  $I_{\max}$  had an exponent of  $0.83 \pm 0.05$  considering all copepod life stages.  $F_{\max}$  of adults did not follow the general pattern observed for nauplii and copepodites.

In terms of mass-specific rates, the maximum daily ingestion ranged from ca. 210% of the body carbon

in nauplii to 265% of the body carbon in early copepodites and then declined to 68 and 124% of the body carbon in adult males and females, respectively (Fig. 3, Table 1). Adults became satiated at much higher prey concentrations than copepodites and nauplii:  $K_m$  values were 3773 cells  $\text{ml}^{-1}$  (ca.  $170 \mu\text{g C l}^{-1}$ ) and 6877 cells  $\text{ml}^{-1}$  (ca.  $290 \mu\text{g C l}^{-1}$ ) for males and females, respectively, and less than 2300 cells  $\text{ml}^{-1}$  (ca.  $110 \mu\text{g C l}^{-1}$ ) for juvenile stages (Table 1). The  $K_m$  values for copepodites (CI–II and CIII–IV) were lower than those for nauplii. The food concentrations at which 90% of satiation (i.e. the maximum ingestion rate) was attained ( $C_{90}$ ) followed a similar pattern to



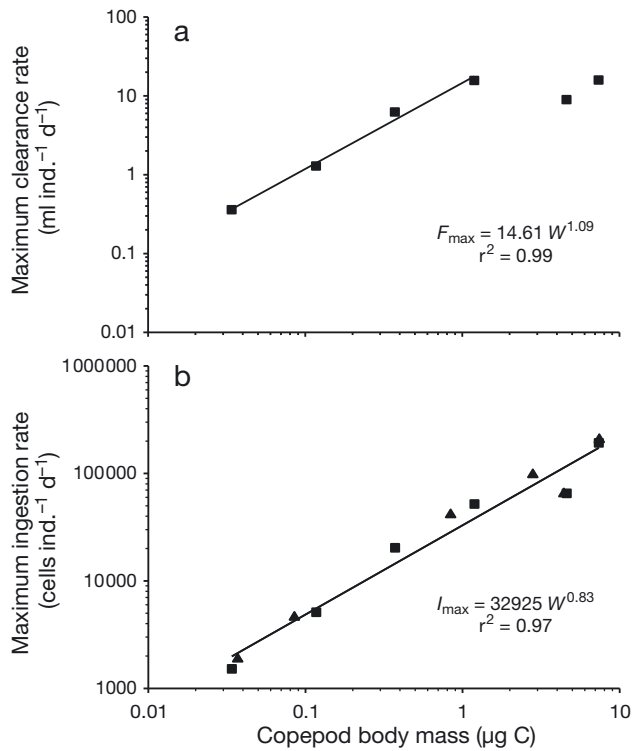


Fig. 2. (a) Maximum clearance rates ( $F_{\max}$ ) and (b) maximum ingestion rates ( $I_{\max}$ ) of *Paracartia grani* feeding on *Rhodomonas salina* with increasing copepod body mass ( $W$ ). Power function fits and corresponding equations are shown. Note that for the clearance rates, only data on nauplii and copepodites are used for the fit. For the ingestion rates, data from the functional response experiments (■) and additional unpublished trials (▲) are pooled together

that of  $K_m$ : decreasing from nauplii to copepodites and substantially increasing in adults (Table 1).

## 4. DISCUSSION

### 4.1. Ontogenetic changes in the feeding functional response

We examined changes in the feeding functional response of the marine copepod *Paracartia grani* through ontogeny and focused on relevant ecological aspects, such as the shape and key parameters of the functional response (i.e.  $I_{\max}$ ,  $F_{\max}$ ,  $K_m$ ). Previous studies have also addressed ontogenetic changes in feeding patterns of marine copepods, but they focused on other aspects of feeding, such as the prey size spectrum (Berggreen et al. 1988), or did not analyse functional responses through the whole developmental range from nauplii to adults (Almeda et al. 2010, Saiz et al. 2014).

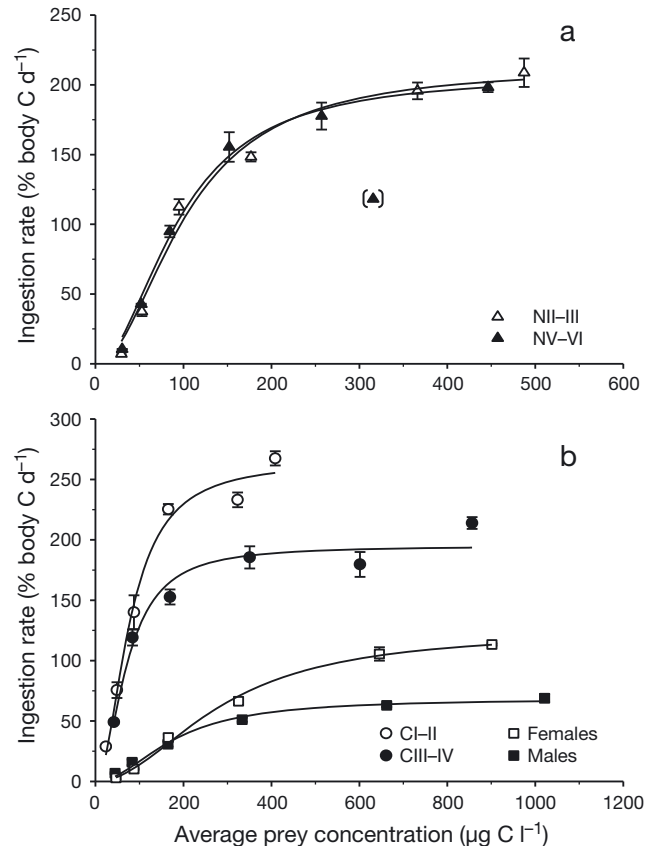


Fig. 3. Carbon-specific functional responses of (a) nauplii and (b) copepodites and adults of *Paracartia grani* feeding on *Rhodomonas salina*. Holling Type III curves were fitted to the carbon-specific ingestion rates as a function of the average prey concentration. Means and SE bars are shown. Data in brackets are excluded from the model

The functional response of an organism shows its capability to exploit environmental resources and the potential flux of energy into secondary production (somatic growth, egg production). We found that the feeding functional response of *P. grani* grazing on *Rhodomonas salina* consistently followed a Holling Type III pattern in all life stages. Holling Type III responses have been traditionally linked to predator-prey systems where predators may control prey densities by switching to alternative prey types according to relative prey abundances, exploiting the more abundant resources and thereby ensuring a basal level of prey diversity in the system (Gismervik & Andersen 1997, Van Leeuwen et al. 2007). However, Holling Type III responses are not restricted to multiple-prey systems, as they have been reported in numerous single-prey experiments (Kiørboe et al. 2018). In our study, we conducted experiments with one algal species and inferred a clear Type III response in all cases. The interpretation of Type III

responses in single-prey scenarios is that predators stop actively searching for prey when the energy gained by feeding would not compensate for the energy invested in capturing prey (in our study, this threshold would correspond to approximately 2000 cells ml<sup>-1</sup> for nauplii and copepodites, and 4000–6000 cells ml<sup>-1</sup> for adults). Accordingly, this foraging strategy has been proposed to be adaptive for copepods associated with productive environments where prey availability is high, such as coastal environments (Paffenhöfer & Stearns 1988). A recent analysis by Kiørboe et al. (2018) noted that in single-prey environments, Holling Type III responses are more typical of copepods with feeding strategies that involve higher metabolic costs (for instance, creating feeding currents to enhance the encounter rate with prey), while less active swimmers, such as ambush-feeding copepods, generally show a Holling Type II response. Adults of *Acartia* species (sensu lato) normally produce feeding currents when feeding on relatively small prey (Jonsson & Tiselius 1990, Saiz & Kiørboe 1995). The fact that we observed the same feeding functional pattern throughout the whole ontogeny of *P. grani* suggests that active foraging occurs not only in adults but also in the juvenile stages of this marine species. Nauplii of *P. grani* are known to perform continuous hopping movements during foraging and show a Type III response for a wide range of prey types (Henriksen et al. 2007, Helenius & Saiz 2017). There are no detailed reports regarding the underlying mechanisms involved in *P. grani* nauplii feeding, but in the case of the related species *Acartia tonsa*, nauplii are able to detect a prey item remotely and then capture it by using temporary feeding currents generated by the second antennae and mandibles (Paffenhöfer et al. 1996, Bruno et al. 2012).

Although previous studies (Almeda et al. 2010, Saiz et al. 2014) and our results indicate that the feeding functional response follows the same pattern through copepod development, Santer & van den Bosch (1994) reported ontogenetic differences in the freshwater copepod species *Cyclops vicinus*. They found that the naupliar and early copepodite stages of *C. vicinus* exhibited a Holling Type II response, whereas late copepodites and adults responded in more of a rectilinear pattern. However, their observations must be taken with caution because the rectilinear response in late copepodites and adults might be a consequence of not reaching satiating conditions in the experimental food concentrations. Moreover, it is often difficult to accurately distinguish between Type II and Type III responses in data sets, either because

very low food concentrations might not be included in the experimental range or because the large variance in counts at low concentrations masks a Type III response.

#### 4.2. Changes in $F_{\max}$ through ontogeny

The  $F_{\max}$  that we estimated for nauplii II-III (0.36 ml ind.<sup>-1</sup> d<sup>-1</sup>) was very similar to the value reported by Helenius & Saiz (2017) for the same copepod species, stage, and prey species (0.33 ml ind.<sup>-1</sup> d<sup>-1</sup>). These values were also comparable to the  $F_{\max}$  estimated by Henriksen et al. (2007) for *P. grani* nauplii II-III grazing on larger prey organisms (0.39 and 0.41 ml ind.<sup>-1</sup> d<sup>-1</sup> for *Thalassiosira weissflogii* and *Heterocapsa* sp., respectively).

The  $F_{\max}$  of *P. grani* increased with body mass from nauplii to late copepodites to the power of 1.09, which is in accordance with the scaling factor of 0.93 determined for the clearance rates of the closely related species *A. tonsa* when grazing on *Rhodomonas baltica* (Berggreen et al. 1988) and the value of 1 reported for  $F_{\max}$  across various zooplankton taxa (Kiørboe 2011, Kiørboe & Hirst 2014).  $F_{\max}$  describes the capability of a predator to locate and capture prey at low prey densities when factors such as handling time or gut filling are not relevant. Compared to nauplii, copepodites have more developed feeding appendages that can produce larger and stronger feeding currents to capture prey and scan larger volumes of water (Paffenhöfer 1971). Therefore, higher feeding efficiency in copepodites may result in a steeper increase in  $F_{\max}$  with body mass compared to the typical allometric scaling factor of 0.75 found for other parameters, such as  $I_{\max}$  (see Section 4.3).

The  $F_{\max}$  of adults did not follow the general pattern observed in juvenile stages, as the  $F_{\max}$  of males and females (ca. 9 and 16 ml ind.<sup>-1</sup> d<sup>-1</sup>, respectively) were not higher than that of late copepodites (ca. 16 ml ind.<sup>-1</sup> d<sup>-1</sup>). We think that this discordance in adult clearance rates is due to the relatively small size of the prey, *R. salina*. It is known that the optimal prey size of marine copepods changes with body size and through ontogeny (Berggreen et al. 1988, Landry & Fagerness 1988, Saiz et al. 2014). It could be argued that the use of the same prey type throughout development may affect the interpretation of our results. In fact, our estimates of the  $F_{\max}$  for adult females were 4–7 times lower than those previously reported for *P. grani* females feeding on larger prey organisms, such as *T. weissflogii* (ca. 13 µm ESD, 70 ml female<sup>-1</sup> d<sup>-1</sup>; Saiz et al. 1992), *Heterocapsa* sp.

(ca. 13  $\mu\text{m}$  ESD, 66 ml female<sup>-1</sup> d<sup>-1</sup>; Isari et al. (2013), and *Oxyrrhis marina* (ca. 17  $\mu\text{m}$  ESD, 111 ml ind.<sup>-1</sup> d<sup>-1</sup>; Calbet et al. (2007)). In Table 1, we can also see that adults showed the highest  $K_m$  and  $C_{90}$  values through development, indicating that the discrepancy between optimal prey size and predator size was the greatest among all life stages. Therefore, it is likely that if we had used larger prey in the experiments with adults,  $F_{\text{max}}$  would have conformed to the power-of-1 scaling pattern throughout development.

#### 4.3. Changes in $I_{\text{max}}$ through ontogeny

Although the  $I_{\text{max}}$  that we estimated for nauplii II-III was comparable to the value reported by Helenius & Saiz (2017) for the same copepod species, stage, and prey species (1623 and 1234 cells ind.<sup>-1</sup> d<sup>-1</sup>, respectively), our estimate of the carbon-specific  $I_{\text{max}}$  (ca. 213 % body C d<sup>-1</sup>) was much higher than the value found in their study (74 % body C d<sup>-1</sup>). This large difference in mass-specific rates relies mostly on the fact that the carbon biomass that we extrapolated for our nauplii (34 ng C ind.<sup>-1</sup>) was substantially lower than the measured biomass in their study (62 ng C ind.<sup>-1</sup>), even though the average naupliar sizes were very similar (139 and 143  $\mu\text{m}$ , respectively). Our estimate, nonetheless, was closer to the maximum daily ingestions reported by Henriksen et al. (2007) for *P. grani* nauplii feeding on *T. weissflogii* and *Heterocapsa* sp. (185 and 299 % body C d<sup>-1</sup>, respectively). In this regard, Henriksen et al. (2007) determined that *P. grani* nauplii, with an average body length of 165  $\mu\text{m}$ , contained 40 ng C animal<sup>-1</sup>, which indicates that the carbon content values measured by Helenius & Saiz (2017) might have been anomalously high.

The maximum daily ration that we estimated for adult females (124 % body C) fell within the range of 103–188 % d<sup>-1</sup> found in the literature for the closely related species *A. tonsa* at same experimental temperature and when provided with the same prey species (Kiørboe et al. 1985, Toudal & Riisgård 1987, Støttrup & Jensen 1990, Thor & Wendt 2010). This value was also close to the specific rates reported for *P. grani* feeding on other prey, such as *Heterocapsa* sp. (ca. 13  $\mu\text{m}$  ESD, 147 % d<sup>-1</sup>; Isari et al. 2013) and *Oxyrrhis marina* (ca. 17  $\mu\text{m}$  ESD, 149 % d<sup>-1</sup>; Calbet et al. 2007). It is worth noting that across prey sizes, maximum mass-specific ingestion rates show a much narrower range of variability in comparison with  $F_{\text{max}}$ , which can differ by a factor of up to 7 (see Section 4.2). In this regard, Frost (1972) previously reported that the  $F_{\text{max}}$  of *Calanus pacificus* varied between 91

and 223 ml ind.<sup>-1</sup> d<sup>-1</sup> across a range of prey diameters between 11 and 87  $\mu\text{m}$ , whereas  $I_{\text{max}}$  remained fairly constant between 24.2 and 27.1  $\mu\text{g C ind.}^{-1} \text{d}^{-1}$ .  $F_{\text{max}}$  is very dependent on the predators' perception of prey, which is particularly sensitive to prey size and motility (Saiz et al. 2014, Almeda et al. 2018). In contrast,  $I_{\text{max}}$  appears to be not greatly influenced by prey size (Frost 1972) and is more constrained by factors such as copepod gut volume, digestion time, and gut turnover rate (Hassett & Landry 1988, Henriksen et al. 2007). Handling times, as a parameter in Holling equations, are typically also considered for the satiation effect, but in copepods they are generally too short to constrain food intake (Tiselius et al. 2013, Kiørboe et al. 2016). The fact that specific  $I_{\text{max}}$  values are not very dependent on prey size helps to explain the exponent of 0.83 in our allometric analysis. This exponent, although slightly higher, was not significantly different from the expected value of 0.75 ( $t$ -test,  $p > 0.05$ ) according to the 3/4 power law accepted for most organisms, including marine calanoid copepods (West & Brown 2005, Saiz & Calbet 2007, Kiørboe & Hirst 2014). Thus, it appears that the use of a single prey size in our experiments did not result in any substantial bias in the estimation of  $I_{\text{max}}$ .

In relation to sex differences, mass-specific  $I_{\text{max}}$  values for males were ca. 1.8 times lower than those of females (68 and 124 % of body C d<sup>-1</sup>, respectively). Sex-related differences in feeding rates have been previously reported for the same copepod species (Saiz et al. 1992) and other copepod species (Saage et al. 2009, van Someren Gréve et al. 2017b). On the one hand, some authors have attributed the relatively lower feeding rates of males to size differences between the sexes (Bautista et al. 1988, van Someren Gréve et al. 2017b). However, our allometric analysis (Fig. 2) shows that  $I_{\text{max}}$  values for *P. grani* males were lower than expected for a copepod of their size. In fact, the feeding rates of late copepodites were also higher than those of males. On the other hand, previous studies state that in some copepod species, adult males are more active swimmers than females and spend a substantial fraction of their time searching for a mate to the detriment of feeding (Kiørboe 2007, Almeda et al. 2017, van Someren Gréve et al. 2017a). We do not know whether sex-related differences in swimming activity could explain the low feeding rates found in *P. grani* males, but it seems unlikely given that the males and females of the related species *A. tonsa* appear to display similar swimming patterns (Bagøien & Kiørboe 2005). We think that the differences in maximum feeding rates between the sexes may not rely on their swimming behaviour but



rather on differences in the allocation of energy to the reproductive process. In this regard, *P. grani* females can exhibit high reproductive output under optimal food conditions that would require higher ingestion rates (Saiz et al. 2015, Saiz et al. 2017).

## 5. CONCLUSIONS

Our study provides empirical data about the ontogenetic changes that marine copepods show in the exploitation of food resources. The insights obtained can help improve modelling capabilities to estimate energy transfer through copepod populations with different stage compositions in pelagic food webs. We have shown that the functional response of the copepod *Paracartia grani* when feeding on *Rhodomonas salina* followed a common pattern (Holling Type III) from early nauplii to adults.  $F_{\max}$  increased with body mass with a power scaling factor of 1, except for the adult stages, which deviated from that common allometric trend, presumably due to the relatively small prey size.  $I_{\max}$  scaled to body mass with a factor of 0.8, close to the typical value of 0.75 found in many animals. In this case, prey size did not seem to substantially affect our estimates of  $I_{\max}$  along ontogeny. We suggest that future studies addressing feeding activity of copepods should also consider the changes in prey size spectrum along ontogeny. In addition, we think that plankton dynamic models would benefit from assessments in multiple resource scenarios, in which selectivity patterns and switching responses can modulate the foraging behaviour of marine copepods.

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