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**Feeding performance of the copepod *Clausocalanus lividus***  
**(Frost and Fleminger 1968)**

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**Keywords:** copepod, *Clausocalanus lividus*, feeding, functional response, size selection

**ABSTRACT**

*Clausocalanus* is a small-sized copepod genus that is widespread in the world ocean, but it has been poorly investigated from a biological and ecophysiological point of view. In this study we targeted the species *Clausocalanus lividus*, one of the less studied circumglobally occurring congeners of the genus, to explore a number of aspects of its feeding. We examined the functional feeding response of adult wild females to seven monospecific diets with prey items differing in terms of size (ESD: 4-28  $\mu\text{m}$ ) and motility. *C. lividus* did not significantly clear the small flagellate, *Isochrysis* sp., while for the larger-sized food items offered (ESD>5  $\mu\text{m}$ ), it exhibited a type II functional feeding response. Its maximum daily carbon intake ranged from 54 to 137 % of its body carbon and was generally higher on prey with ESD>15  $\mu\text{m}$ , being up to 17  $\mu\text{g C cop}^{-1} \text{ day}^{-1}$  for the diatom *Thalassiosira weissflogii*. The clearance maxima (10 to 308  $\text{mL cop}^{-1} \text{ day}^{-1}$ ) were generally associated with prey size (increasing with the ESD). The estimated feeding rates of *C. lividus* are discussed in relation to the concentration and size of food and compared to findings for other congeners.

## INTRODUCTION

One major paradigm in copepod ecology and biological oceanography in recent years has been the overwhelming numerical dominance of small-sized copepods in planktonic communities (e.g., Calbet *et al.*, 2001; Gallienne and Robins, 2001; Turner, 2004; Zervoudaki *et al.*, 2006). This perception seems to challenge the view that we have had for the last 50 years about the ecological role of planktonic copepods in marine ecosystems (e.g., Mauchline, 1998), because most of the scientific effort directed toward elucidating the biogeochemical impact of this group has been focused on a very small number of copepod species: both large-sized copepods, (i.e. *Calanus*) and medium-sized representatives of shelf and coastal waters (Saiz and Calbet, 2007). Due to the bias in the body size structure of copepod communities and the disproportionate importance given to some particular species, there is an obvious need to extend research relevant to future estimations of copepod-mediated fluxes and to consider the functional diversity encompassed within the “neglected” smaller copepod taxa. This is particularly the case in relation to future scenarios of climate forcing, in which phenological and distributional changes in zooplankton communities may involve shifts to smaller-sized copepods (e.g., Batten and Welch, 2004).

A typical representative of this widespread copepod size fraction is the calanoid genus *Clausocalanus* (♀ total length: 0.66-1.90 mm but usually <1 mm) (Frost and Fleminger, 1968), which has been regarded as a worldwide genus with a high ecological success. It is distributed circumglobally with 13 congeners (Frost and Fleminger, 1968), forming an important numerical component of epipelagic mesozooplankton communities both in terms of abundance and biomass in different trophic environments, from low- to high-latitude ecosystems (e.g., Webber and Roff, 1995: up to 32% of copepod biomass in tropical oceans; Calbet and Agusti, 1999: up to 30% of copepod abundance in the Atlantic; Peralba, 2008: up to 55% and 73% in the eastern and western Mediterranean respectively, up to 57% of copepod abundance in the Atlantic).

Existing information on fundamental ecological aspects of the genus, such as species-specific distribution patterns (e.g., Fragopoulou *et al.*, 2001; Paffenhöfer and Mazzocchi, 2003; Peralba and Mazzocchi, 2004), seasonal cycles (e.g., Mazzocchi and Ribera d' Alcala, 1995; Siokou-Frangou, 1996; Peralba and Mazzocchi, 2004) and reproductive parameters (Peralba, 2008), has considerably broadened our insight into the niche characterisation of several *Clausocalanus* species (Peralba and Mazzocchi, 2004; Peralba, 2008). Nonetheless, our knowledge regarding many behavioural and physiological mechanisms of the genus remains scarce. Substantial difficulties related to the taxonomic distinction among its congeners (Blanco-Bercial and Álvarez-Marqués, 2007) and the cultivation of these species (Mazzocchi and Paffenhöfer, 1998) have made this particular genus less

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2 attractive for laboratory experimentation and have discouraged in-depth, species-specific  
3 ecophysiological studies.  
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5 During the last three decades some assessments of *Clausocalanus* vital rates (i.e., egg  
6 production, respiration, grazing, gut evacuation, growth) have been sporadically included in  
7 published studies estimating a number of biological processes of field copepod assemblages (e.g.,  
8 Sazhina, 1985; Landry *et al.*, 1994; Webber and Roff *et al.*, 1995; Hopcroft and Roff 1998; Saiz *et*  
9 *al.*, 1999; Mayzaud *et al.*, 2002). However, the first laboratory research purely focused on the  
10 biological mechanisms of the genus *Clausocalanus* was conducted by Mazzocchi and Paffenhöfer  
11 (1998, 1999). These authors, targeting the species *Clausocalanus furcatus*, provided preliminary  
12 experimental data on the feeding and swimming behaviour of the genus, along with some  
13 information on its reproductive and developmental processes. Through a detailed observation of the  
14 swimming trajectories of the species (Mazzocchi and Paffenhöfer, 1999; Uttieri *et al.*, 2008a), a  
15 unique motion strategy was discovered for small planktonic copepods, which is not only displayed  
16 by *C. furcatus*, but presumably by the other congeners as well. This strategy involves a rapid (ca. 10  
17 body lengths  $s^{-1}$ ), continuous movement in convoluted small loops and the capture of  
18 dinoflagellates while swimming at high speed, with no evidence of feeding current generation. This  
19 foraging tactic also implies that food is perceived within a restricted horizon by direct encounter  
20 (intercept feeding), which is a feature that has been argued to be an efficient adaptation of the  
21 species in the oligotrophic areas (Uttieri *et al.*, 2008a).  
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35 Although in recent years there has been an increasing interest in the variables regulating  
36 population dynamics of *Clausocalanus* species (e.g., Buttino *et al.*, 2004; Bi and Benfield, 2006;  
37 Cornils *et al.*, 2007a; Peralba, 2008), no thorough studies describing the feeding performance and  
38 prey size spectrum of this copepod genus have yet been conducted. To the best of our knowledge,  
39 since the pioneering works by Mazzocchi and Paffenhöfer (1998, 1999), dietary studies on  
40 *Clausocalanus* congeners have involved mainly *in situ* trials with the natural particle composition  
41 and concentration (Batten *et al.*, 2001 and Broglio *et al.*, 2004: on *Clausocalanus* spp; Paffenhöfer  
42 *et al.*, 2006: on *C. furcatus*; Cornils *et al.*, 2007b: on *C. farrani* and *C. furcatus*).  
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50 In this paper, we deal with the first experimental data on the functional feeding response of  
51 this genus, targeting one of the larger sized congeners, *C. lividus*. This species is characterised by an  
52 antitropical distribution in the Atlantic (Williams and Wallace, 1975; Peralba, 2008) and Pacific  
53 Ocean (Frost and Fleminger, 1968). In the Mediterranean, it occurs at relatively low abundances  
54 compared with smaller congeners, though a more significant presence has been reported during  
55 spring in the less oligotrophic western part of the basin (Peralba, 2008). Thus far, *C. lividus* has  
56 attracted attention due to its different spawning behaviour (free spawner) compared to the rest of its  
57 small and medium sized congeners (sac spawners) (Saiz and Calbet, 1999; Peralba, 2008).  
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2 However, there is no information about the biological mechanisms (e.g., feeding behaviour) that  
3 define the success of this species and shape its distribution patterns.  
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6 With the aim of shedding some light on this topic, we exploited the spring-early summer  
7 population of *C. lividus* off the Barcelona coast (NW Mediterranean) to explore the single-resource  
8 feeding functional response of wild females on prey differing in size and motility. Feeding rates  
9 were estimated as a function of the food concentration and the relevance of prey-specific  
10 characteristics in the maximum feeding capacity of *C. lividus* were evaluated. We consider the  
11 information provided in this paper to be a prerequisite that will allow future comparisons of the  
12 feeding behaviour and requirements among congeners and will facilitate our understanding of the  
13 ecological interactions of this widespread genus and the functional role of its species.  
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## 22 **METHOD**

### 23 **Sample collection**

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25 Live zooplankton were collected ca. five nautical miles from the coast of Barcelona, Spain  
26 (41°20'N, 002°15'E; ca. 100 m depth) on five dates from April to June 2009 (Table I). Oblique  
27 slow-speed tows of a 100- $\mu$ m mesh plankton net were deployed for five minutes at an approximate  
28 depth of 40 m order to collect live material. The end of the net was equipped with a non-filtering  
29 cod-end (plastic bag) that, upon retrieval, was transferred to an isothermal container filled with  
30 surface seawater, and tied with a string to avoid the presence of an air interface to which  
31 *Clausocalanus* might stick on. In the laboratory, zooplankton were concentrated and adult females  
32 of *C. lividus* were sorted with a wide-mouth Pasteur pipette under a dissecting microscope.  
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### 42 **Feeding experiments**

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44 The feeding functional response of *C. lividus* was explored on seven monospecific diets  
45 (Table I). The prey selected ranged in size (equivalent spherical diameter, ESD) from 4  $\mu$ m to 28  
46  $\mu$ m and were kept in batch cultures growing exponentially at 20°C under a 12:12 h light:dark cycle.  
47 Autotrophic prey were grown in f/2 medium with silicon added for the maintenance of the diatom  
48 *Thalassiosira weissflogii*. Heterotrophic dinoflagellates (i.e. *Gyrodinium* sp. and *Oxyrrhis marina*)  
49 were grown on the cryptophyte *Rhodomonas salina*, whereas the ciliate *Strombidium sulcatum* was  
50 fed on the small-sized (ca. 2  $\mu$ m ESD) autotrophic flagellates *Micromonas* sp.  
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56 Food suspensions in all of the experiments were prepared in 0.2  $\mu$ m filtered sea water (FSW)  
57 using stock cultures; in some cases, prior to their use the cultures were screened through a larger  
58 mesh to remove any cell aggregates. In the case of *T. weissflogii*, three days before the initiation of  
59 the experiments cultures were aerated to induce the removal of cell spines because these structures  
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2 have been reported to influence copepod feeding behaviour (Gifford *et al.*, 1981). Heterotrophic  
3 prey stocks were not fed on the day preceding the experiment to ensure that food algae were grazed  
4 down, and hence, our results would not be associated with a potential presence of algae. The  
5 concentrations of the stock cultures and the cell volume were determined using a Beckman Coulter  
6 Multisizer III electronic particle counter. For each food item, the adjustment of the initial  
7 suspensions to the desired concentrations was achieved through successive dilutions. Finally all  
8 suspensions (autotrophic, heterotrophic) were enriched with 5 mL of f/2 medium per litre of  
9 suspension to (a) avoid a difference in algal growth among the treatments with or without copepods  
10 due to nutrient excretion by the copepods and (b) assure the same conditions in experiments with  
11 autotrophs or heterotrophs. While preparing the ciliate suspension, EDTA  
12 (ethylenediaminetetraacetic acid 10  $\mu\text{M}$ ) was added to the FSW before the inclusion of the prey to  
13 ensure their survival (Jonsson and Tiselius, 1990)  
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23 Each experiment consisted of six consecutively doubled food levels (Table I). A total of five  
24 replicate 625-mL Pyrex screw-cap bottles were prepared per food level. Once the bottles were filled  
25 near the neck with the appropriate algal suspensions, copepods (4-12, the number was inversely  
26 dependent on the food concentration and according to copepod size, which was found to vary  
27 significantly among the different experiments) were added to only two of the bottles (experimental:  
28 2 x Exp), while the other three served as initial (1 x I) and control bottles (2 x C). The copepods  
29 used in the experiments had been acclimated for the preceding 24 h at the experimental temperature  
30 and light conditions and exposed to a prey concentration equal to the corresponding mean value of  
31 the range of concentrations to be used during the experiment. After the addition of copepods, all the  
32 bottles were filled to the top and prior to the tightening of the screw-cap, a plastic film was placed  
33 over their mouth to prevent bubble formation. The initial bottles corresponding to each  
34 experimental concentration were sampled as described below, whereas both the experimental and  
35 control bottles were incubated on a slowly rotating plankton wheel (0.2 rpm) for 24 h at 16°C with a  
36 light: dark cycle of 12h:12h. At the end of each experiment, the content of all bottles were carefully  
37 poured through a 200- $\mu\text{m}$  mesh, and the actual number and condition of copepods was checked.  
38 The mortality of females was negligible in our experiments, with one or two dead animals  
39 occasionally being observed (not considered for calculations). After mixing the contents of each  
40 bottle well, a sample of 50 mL (or of a higher volume in the case of ciliates) was preserved with 2%  
41 Lugol solution. The abundance of *S. sulcatum* in the experiment was corrected for 25% fixation  
42 losses according to Broglio *et al.* (2003). Cell numbers were counted visually by inverted  
43 microscopy, except for the smallest prey item, *Isochrysis* sp for which the food concentrations at the  
44 termination of grazing experiments were determined with a Beckman Coulter Multisizer III fitted  
45 with a 70- $\mu\text{m}$  aperture tube.  
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The clearance and ingestion rates as well as average food concentrations, were computed for each food level according to the equation of Frost (1972). Carbon-specific ingestion rates for each food were also estimated taking into account the average copepod carbon content in each experiment and the cell carbon content of the prey. For copepods as well as the algae *Heterocapsa* sp. and *Isochrysis* sp. the carbon content was determined with a CHN analyser. For the other prey items the carbon content was obtained by the conversion of the cell volume (as obtained using the Multisizer III) with different equations found in the literature (Table I).

To assess the functional response to food concentration, an exponential decay equation ( $F = F_{\max} * e^{-bC}$ ) was fitted to the weighted clearance rates (using the inverse of the standard error as weight), where  $F_{\max}$  is the maximum clearance rate ( $\text{mL cop}^{-1} \text{d}^{-1}$ );  $b$  is a prey-specific constant; and  $C$  is the food concentration ( $\text{cells mL}^{-1}$ ). Regarding ingestion rates, asymptotic maxima were estimated by fitting the data (after weighting with the inverse of the standard error) to the model described by Ivlev (1961):  $I = I_{\max} * (1 - \exp^{-aC})$ , where  $I_{\max}$  is the asymptotic maximum ingestion rate,  $a$  is a constant defining the rate at which ingestion ( $I$ ) approaches the maximum ingestion ( $I_{\max}$ ); and  $C$  is the food concentration ( $\text{cells mL}^{-1}$  or  $\mu\text{g C L}^{-1}$ ).

The maximum clearance rates of *C. lividus* were plotted against the ESD of the prey to examine the effect of prey size in the feeding behaviour of the females of the species. Additionally, to compare the capability of the copepods to approach saturation (i.e., the shape of the curve) under the different diets, we computed the parameter  $C_{I_{\max}/2}$  (Fig. 2C), which is the concentration at which ingestion equals half of the maximum rate ( $C_{I_{\max}/2} = \ln(0.5)/-a$ ); equivalent to  $K_m$  in the Michaelis-Menten equation).

## RESULTS

The feeding response of *C. lividus* on the different food particles as a function of resource density is presented in Fig. 1. Two-way ANOVA tests showed significant consumption in the experimental bottles for all of the tested prey ( $P < 0.01$ ), except for the autotrophic flagellates *Isochrysis* sp. ( $\text{ESD} < 5 \mu\text{m}$ ), the smallest item offered. For this reason we only computed clearance and ingestion rates for the other prey items tested.

*C. lividus* cleared the other offered food resources ( $\text{ESD} > 5 \mu\text{m}$ ) at different rates, ranging from  $3 \text{ mL cop}^{-1} \text{day}^{-1}$  (for *R. salina* at an average concentration of ca.  $2000 \text{ cells mL}^{-1}$ ) to  $323 \text{ mL cop}^{-1} \text{d}^{-1}$  (for *S. sulcatum* at a mean concentration of ca.  $1 \text{ cell mL}^{-1}$ ) (Fig. 1). The clearance rates ( $F$ ,  $\text{mL cop}^{-1} \text{d}^{-1}$ ) of *C. lividus* typically declined with increasing food concentration (Fig. 1). The parameters of the fitted exponential decay equations for each prey are shown in Table II. The maximum clearance rates ranged from 10 to  $308 \text{ mL cop}^{-1} \text{day}^{-1}$  and increased with food particle

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2 size. Among the offered prey, the lowest clearance rates were found for the autotrophic flagellate *R.*  
3 *salina* and the highest for the ciliate, whereas dinoflagellates ranging from 13 to 17  $\mu\text{m}$  in ESD  
4 were cleared at rates that increased with the size (i.e., *Heterocapsa* < *Gyrodinium* sp. < *Oxyrrhis*  
5 *marina*) (Fig. 2A). The diatom *T. weissflogii* was cleared more efficiently than expected on the  
6 basis of its size, with an  $F_{\text{max}}$  ca.  $166 \text{ mL cop}^{-1} \text{ day}^{-1}$ .  
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11 With respect to ingestion, the estimated rates of *C. lividus* on prey larger than 5  $\mu\text{m}$  generally  
12 increased with prey concentration up to a feeding plateau, resembling an asymptotic Type II  
13 functional response (Gentleman *et al.*, 2003). The tendency towards saturation was more evident for  
14 the species *Rhodomonas salina*, *Heterocapsa* sp. and *Oxyrrhis marina* (Fig. 1), while in the rest of  
15 the cases the satiating conditions seemed to exceed our highest food levels. The observed ingestion  
16 rates varied considerably among food types and concentrations, ranging from 215 to 166,004 cells  
17  $\text{cop}^{-1} \text{ mL}^{-1}$  and between 0.36 and  $15.25 \mu\text{g C cop}^{-1} \text{ day}^{-1}$  in terms of cells and carbon respectively  
18 (Fig. 1, 3A). Incubations with the ciliate *Strombidium sulcatum* at an average concentration of ca. 1  
19 cell  $\text{mL}^{-1}$  (corresponding to  $1 \mu\text{g C L}^{-1}$ ) resulted in the lowest ingestion records during our study.  
20 The highest rates in cell units were exhibited when feeding on the flagellate *Rhodomonas salina*  
21 (when offered at an average concentration  $59,096 \text{ cell mL}^{-1}$ ), whereas when carbon units were  
22 considered the diatom *T. weissflogii* resulted in the highest ingestion rates. The estimated  
23 parameters of the Ivlev models fitted to the ingestion rate functional responses are provided in  
24 Table II. Maximum ingestion rates ranged from 8,112 to 169,960 cells  $\text{cop}^{-1} \text{ day}^{-1}$  and were lower  
25 when feeding on *S. sulcatum* and higher in the case of *R. salina*. The estimated maxima appeared to  
26 be quite similar for the three dinoflagellates, whereas the diatom *T. weissflogii* was unexpectedly  
27 ingested at rates more than two times higher compared to dinoflagellates (Table II). When  
28 expressed in terms of carbon, the maximum intake per individual was higher overall on prey with  
29 an  $\text{ESD} > 15 \mu\text{m}$ .; however a maximum value of  $17 \mu\text{g C cop}^{-1} \text{ day}^{-1}$  was found for the diatom  
30 species tested (Table II, Fig. 3A). Daily ration curves (% body C  $\text{day}^{-1}$ ) are shown in Fig. 3B. The  
31 carbon ingestion in relation to body carbon ranged from 2-33 % in the lowest food concentrations  
32 and between 49.2 to 112.5 % in the highest (Fig. 3B), with maximum ingestion ranging from 54 to  
33 137 % body C  $\text{day}^{-1}$  (Table II). When the maximum carbon daily rations were plotted against prey  
34 size (Fig. 2B), no clear trend was shown, though *C. lividus* displayed the highest ingestion rates  
35 when offered *T. weissflogii* and *Gyrodinium* sp.  
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57 When we compared the capability of the copepod to approach saturation under the different  
58 diets tested (Fig. 2C), we also found no clear pattern in relation to size and dinoflagellates and  
59 ciliates resulted in lower  $C_{\text{Imax}/2}$  values.  
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## DISCUSSION

### Feeding rates of *C. lividus*: effect of resource density

The available feeding rates reported for the genus in the literature, which were based on few observations and primarily focused on *C. furcatus*, were estimated mainly via bottle incubation experiments (but also see Mazzocchi and Paffenhöfer, 1999) using either the natural prey assemblage of oligotrophic environments (NW Spain: Batten *et al.*, 2001; NW Mediterranean: Broglio *et al.*, 2004; subtropical ocean: Paffenhöfer *et al.*, 2006; Gulf of Aqaba: Cornils *et al.*, 2007b) or cultured monospecific diets (Mazzocchi and Paffenhöfer, 1998; Montresor *et al.*, 2003). The food resources utilised in all previous studies involved only a small variation in the food density, which was always within the ranges of oligotrophy (Table III). Hence, there is no comprehensive information regarding the ability of this genus to perform in the richer environments that they can also inhabit (e.g. Valdés *et al.*, 2007). In addition, even in the most trophically poor environments, the ephemeral patchiness of resources at small spatial scales within the water column is likely to be encountered by copepods (Tiselius, 1992; Saiz *et al.*, 1993). In this regard, Uttieri *et al.* (2008a, b), taking into consideration the peculiar swimming behaviour of *C. furcatus* and the sensory structure of the A1 and A2 antennae, hypothesised that *Clausocalanus* might be especially suited to profit from food patches. Thus, it would be also of particular ecological interest to consider how extreme feeding conditions (e.g., towards satiation) would be perceived by this presumably “intercept feeder” and test its physiological response.

Except for *Isochrysis*, which was not ingested, *C. lividus* typically exhibited an asymptotic, density-dependent feeding pattern (Type II, Gentleman *et al.*, 2003): ingestion rates increased up to satiation with increasing food concentration, whereas clearance rates showed the opposite trend. The ranges of prey concentrations chosen for conducting the experiments did not allow full satiation in some cases. This was, in part, a consequence of the restrictions in the stock cell densities that we were able to reach for the slow-growing heterotrophic prey (*S. sulcatum*, *Gyrodinium* sp.). For this reason, in these cases, the maximum feeding rates of *C. lividus* obtained by the fit of Ivlev’s model must be taken as a proxy for the prey-specific maximum potential of the species.

*Clausocalanus* feeding rates on single nutritional resources have previously been quantified by supplying dinoflagellates or flagellates at concentrations resembling oligotrophic field conditions: (a) *Gymnodinium nelsoni* and *Rhodomonas* sp. to individuals of *C. furcatus* and copepodites of *Clausocalanus* (Mazzocchi and Paffenhöfer, 1998) and (b) *Scrippsiella trochoidea* and *Scrippsiella ramonii* to *C. lividus* (Montresor *et al.*, 2003). In the current study, when *C. lividus* was offered three dinoflagellate species (*Heterocapsa* sp., *Gyrodinium* sp. and *Oxyrrhis marina*) at carbon concentrations within the range employed by Mazzocchi and Paffenhöfer (1998) and

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2 Montresor *et al.* (2003), the estimated feeding rates compared well to those reported in these  
3 previous studies. Our data also agree with those for *Clausocalanus* spp. (Broglia *et al.*, 2004), *C.*  
4 *furcatus* (Paffenhöfer *et al.*, 2006; Cornils *et al.*, 2007b) and *Clausocalanus farrani* (Cornils *et al.*,  
5 2007b) under natural particle composition and concentration (Table III).  
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10 Food limitation is considered to be the main factor that limits the feeding rates of copepods in  
11 the field with respect to their potential maxima, with this effect being more pronounced in the case  
12 of more oligotrophic environments and for the larger-sized species (Saiz and Calbet, 2007). The  
13 capability of *Clausocalanus lividus* to exploit food resources ( $C_{I_{max/2}}$ ) seems to be inversely  
14 dependent on prey size overall, reaching satiation at lower food concentrations when prey is larger  
15 (Fig. 3C), as observed in other copepod species (Frost, 1972; Uye and Kayano, 1994; Støttrup and  
16 Jensen, 1990). One can tentatively estimate the metabolic needs of *C. lividus* to assess the critical  
17 food concentration at which their metabolic demands can be satisfied. Using the equation of Ikeda  
18 *et al.* (2001) to estimate oxygen consumption as a function of body mass and temperature, and  
19 assuming a respiratory quotient of 0.97 (Omori and Ikeda, 1984), *C. lividus* metabolic demands are  
20 on the order of 11.5 % of body carbon respired per day (for an average body mass of  $14.9 \mu\text{g C ind}^{-1}$   
21 at  $16^\circ\text{C}$ ). However, this figure is probably in the lower range because is based on 24h incubations  
22 in filtered seawater and there is evidence that under feeding conditions, respiration rates can  
23 increase up to 2.3 times (Almeda *et al.*, 2010). For the sake of the comparison, Fig. 3B shows the  
24 ingestion rates (assuming 90% assimilation efficiency) required to satisfy the metabolic demands of  
25 *C. lividus* both under starved conditions and under feeding conditions (assuming a 2.3-fold  
26 increase). The critical concentrations obtained are relatively high (ca.  $14\text{--}70 \mu\text{g C L}^{-1}$  for prey with  
27 an  $\text{ESD} > 15 \mu\text{m}$ ;  $> 49 \mu\text{g C L}^{-1}$  for prey with an  $\text{ESD} < 15 \mu\text{m}$ ) compared to what is expected in  
28 oligotrophic natural environments. The above calculations may also provide a reasonable  
29 explanation for the rarity of *C. lividus* in the more oligotrophic eastern part of the Mediterranean  
30 (Fragopoulou *et al.*, 2001; Peralba, 2008). Interestingly, within the boundaries of the oligotrophic  
31 Ionian waters (Eastern Mediterranean), where *C. lividus* is usually recorded only in low numbers,  
32 Peralba (2008) demonstrated the association of high fluorescence waters offshore the Calabrian  
33 coast (“the Calabrian bloom” in the NW Ionian Sea) with a distinct *Clausocalanus* assemblage,  
34 mainly comprising of *C. lividus* and copepodites of the genus. This appears to contrast with what  
35 has been assumed for the smaller sized *C. furcatus*, the basal metabolism of which may be satisfied  
36 even under the particularly limited food resources of the subtropical open ocean (Paffenhöfer *et al.*,  
37 2006). Hence, one can assume that under low food conditions, the energetic demands of *C. lividus*  
38 may not be satisfied to the same extent as those of its lower body weight congeners.  
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2 In contrast to the low daily rations of the species observed when prey availability was low, at  
3 saturation levels the ingestion rates increased up to  $17.12 \mu\text{g C cop}^{-1} \text{ day}^{-1}$ , representing a daily food  
4 ration equal to 137% of body carbon. The satiating feeding rates of *C. lividus* estimated during our  
5 study (Table II) compare well with those reported for other calanoid copepods with a body mass in  
6 the range of *C. lividus* (daily ration: average=102% body C  $\text{d}^{-1}$ , range=53 to 189% body C  $\text{d}^{-1}$ ,  
7 computed from Appendix A1.2 in Saiz and Calbet, 2007).  
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### 16 **Feeding rates of *C. lividus*: the effect of food size**

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18 Feeding rates of planktonic copepods have been considered to be the outcome of a complex  
19 multi-factorial influences, associated with prey characteristics (e.g., cell size, motility, palatability,  
20 food quality) and structural properties of the food assemblage (i.e., species and size distribution), as  
21 well as the predator itself (i.e., previous feeding history) (as reviewed by Paffenhöfer, 1988;  
22 Mauchline, 1998). Among these parameters, the role of cell size in prey selection has been the  
23 central subject of debate over the last 40 years, often prompting laboratory estimations of the food-  
24 particle size spectra in different species (e.g., Frost, 1972, 1977; O' Connors *et al.*, 1980; Bartram,  
25 1981; Vanderploeg *et al.*, 1984; Berggreen *et al.*, 1988). The study of feeding as a function of  
26 particle size has provided the chance to make comparisons among species regarding important  
27 aspects of ecology (i.e., the lower, optimum and higher limit in food size).  
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35 The prey items selected for the present study had a 4-28  $\mu\text{m}$  ESD size range. Although this is  
36 rather restricted when compared to other studies (e.g., Vanderploeg *et al.*, 1984: natural assemblage;  
37 Berggreen *et al.*, 1998: ESD= 1.90 to 247  $\mu\text{m}$ ), this choice actually encompasses the majority of  
38 food items abundant in oligotrophic environments. For instance, the particle range 10-20  $\mu\text{m}$  is  
39 considered to represent a major component of the material ingested by *C. furcatus* in the subtropical  
40 open ocean due to a combination of high clearance rates and particle concentration in this size range  
41 (Paffenhöfer *et al.*, 2006). In our study, the flagellates *Isochrysis* sp., located at the lower end (ca. 4  
42  $\mu\text{m}$ ) of the food size spectrum offered, were not significantly consumed and represent the lower  
43 threshold in the particle capture efficiency of *C. lividus*. Copepods are not passive filter feeders  
44 (Koehl and Strickler, 1981; Paffenhöfer *et al.*, 1982; Price *et al.*, 1983), as their feeding appendages  
45 work like paddles but also as leaky sieves under certain circumstances (see Koehl, 2004). In this  
46 regard our finding fits well with the 15% retention of particles  $\leq 5 \mu\text{m}$  calculated by Boyd (1976) for  
47 *C. arcuicornis* based on the intersetular distance measurements made by Nival and Nival (1973).  
48 Unfortunately the *in situ* feeding measurements on *Clausocalanus* species (i.e., *C. furcatus*, *C.*  
49 *farrani*) did not provide any information on this topic, because inefficient feeding on particles < 5  
50 or 6  $\mu\text{m}$  had been considered a priori (Paffenhöfer *et al.*, 2006; Cornils *et al.*, 2007b). Similar or  
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2 even lower values of the lower size limit have been reported for adult females of other copepod  
3 species e.g., ca. 2  $\mu\text{m}$  for *Acartia tonsa* (Berggreen *et al.*, 1998; Bartram, 1981), 1.5  $\mu\text{m}$  for  
4 *Paracalanus parvus* (Bartram, 1981), and 3 to 4  $\mu\text{m}$  for *Diaptomus sicilis* females (Vanderploeg *et*  
5 *al.*, 1984). In this regard, it is quite puzzling to understand how *Clausocalanus*, which is reportedly  
6 unable to create feeding currents and behaves as a fast-swimming intercept feeder (Mazzocchi and  
7 Paffenhöfer, 1999; Uttieri *et al.*, 2008a), can manage to capture relatively small prey (<15  $\mu\text{m}$  ESD:  
8 *R. salina*, *T. weissflogii*, *Heterocapsa* sp.) at rates comparable to those exhibited by feeding-current  
9 copepods (see review in Saiz and Calbet, 2007). Further studies using high-speed video will be  
10 required to provide better insights into the particular feeding mechanisms of *Clausocalanus*.  
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19 In contrast to the small cell *Isochrysis* sp., all of the larger prey items offered (ESD>5  $\mu\text{m}$ )  
20 were consumed by *C. lividus* and cleared at rates proportional to the prey size. Hence, the  
21 maximum clearance was lower on *Rhodomonas salina* (ESD= 7  $\mu\text{m}$ ), increased successively with  
22 prey size and was found to be highest for the larger-sized cell, the ciliate *S. sulcatum* (ESD= 28  
23  $\mu\text{m}$ ). The prey size spectra for the other copepod species, resembling either increasing (Frost, 1977;  
24 Bartram, 1981) or bell-shaped curves (Vanderploeg *et al.*, 1984; Berggreen *et al.*, 1998), showed  
25 similar size-dependent clearance patterns, which can be explained by an increase in realised  
26 encounter rate due to a higher percentage of individual cell detections with size (Price and  
27 Paffenhöfer, 1985) and to a prey size-dependent capture efficiency.  
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35 Nevertheless, a discrepancy to the above-mentioned pattern was also observed in our study  
36 due to the feeding performance of *C. lividus* on the diatom *T. weissflogii*. The clearance rates on this  
37 food species showed a three-fold increase compared to the similarly sized autotrophic dinoflagellate  
38 *Heterocapsa* sp. Additionally, *C. lividus* cleared the diatoms at rates 2 and 1.3 times higher than the  
39 larger dinoflagellates *Gyrodinium* sp. and *O. marina* respectively. Although the estimated clearance  
40 values on this particular prey are realistic in the overall context of copepod feeding rates, this  
41 finding has to be treated cautiously because this particular observation seems to challenge not only  
42 the “anticipated” influence of size on copepod feeding but also an anticipated positive stimulus of  
43 prey motility on the feeding procedure (Paffenhöfer, 1988). A similar deviation from what is  
44 expected on the basis of size was observed for females of *A. tonsa*, which cleared the dinoflagellate  
45 *Scrippsiella faröense* less efficiently than expected (Berggreen *et al.*, 1998). This result was  
46 attributed to copepod “taste preferences”, implying a rejective behaviour to chemical substances  
47 excreted by dinoflagellates (e.g., Huntley *et al.*, 1986). Similarly, the nutritional characteristics or  
48 chemical properties of the diatom may make it more “preferable” prey item, but this speculation  
49 deserves further study.  
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Although the series of experiments described here allows conclusions related to the lower prey  
size limit of *C. lividus*, as well as the relationship between  $F_{\text{max}}$  vs. prey size, unfortunately the

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2 largest prey sizes tested (28  $\mu\text{m}$  ESD) did not allow us to estimate the upper limit of the prey size  
3 range. Reviewing their own data on *Acartia tonsa* and published studies on *Calanus pacificus* and  
4 *Diaptomus sicilis*, Berggreen *et al.* (1998) suggested an optimum particle size for copepods equal to  
5 ca. 2-5% their body length. Taking into account the average prosome length of *C. lividus* found in  
6 our experiments (1.16 mm), the optimum particle range in our case would be 23-58  $\mu\text{m}$ . Thus,  
7 among the prey examined, only the ciliate *S. sulcatum* (ESD 28  $\mu\text{m}$ ) might fall within the optimum  
8 particle range. Regarding the other *Clausocalanus* congeners, the feeding selectivity in terms of size  
9 has been recently investigated for females of the species *C. furcatus* and *C. farrani* in the very  
10 oligotrophic waters of Red Sea (Cornils *et al.*, 2007b). These authors concluded that both species  
11 mainly feed on small-sized food items between 5 and 20  $\mu\text{m}$  in terms of abundance, whereas the  
12 main carbon uptake was observed in the size classes larger than 20  $\mu\text{m}$ .

21 We must also take into account that apart from the cell size, the food items we utilised varied  
22 in terms of nutritional mode (autotrophs vs. heterotrophs), motility (motile vs. immotile) and  
23 phylogeny (flagellates, dinoflagellates, diatoms, ciliates), and it is not only cell dimensions that may  
24 have influenced the feeding performance of *C. lividus* in our experiments. For instance, we cannot  
25 exclude the possibility that the high clearance rates on the ciliate *S. sulcatum* could be a combined  
26 function of a size and taxon selectivity of *C. lividus*. Ciliates form an important component in the  
27 diet of copepods (Calbet and Saiz, 2005) and represent a selected prey for a variety of copepod  
28 species (Broglia *et al.*, 2004). Taxon-related selectivity in the feeding of the genus *Clausocalanus*  
29 was examined during in situ feeding studies of congeners (*C. furcatus* and *C. farrani* in Cornils *et*  
30 *al.*, 2007b; *Clausocalanus* spp. in Broglia *et al.*, 2004), but the responses were rather contradictory.  
31 Incubation experiments coupled with fatty acid and stable isotope analysis, were employed by  
32 Cornils *et al.* (2007b) to study this phenomenon, and both methods revealed no apparent selectivity  
33 for the major taxa (e.g. diatoms, ciliates, dinoflagellates) comprising the natural particle  
34 assemblage. This overall finding was interpreted as a reflection of the strategy adopted by the  
35 species in the very oligotrophic waters of the Red Sea (Cornils *et al.*, 2007b). However, Broglia *et*  
36 *al.* (2004) observed a clear selection for ciliates by individuals of the genus in the NW  
37 Mediterranean, in accordance with what has been shown for many other copepod species in their  
38 and other studies (e.g., Atkinson, 1996; Batten *et al.*, 2001; Calbet and Saiz, 2005). Similarly, gut  
39 pigment analysis in *Clausocalanus* sp. also revealed high carotenoid concentrations of animal and  
40 dinoflagellate origin (Kleppel *et al.*, 1988).

51 Although the present study provided preliminary information with respect to the feeding  
52 processes of *C. lividus*, an in-depth understanding of these processes would be advanced by the  
53 observation of free-swimming animals in different trophic regimes in terms of prey size and  
54 concentration. Future studies should include the performance of selective feeding experiments in  
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2 which certain food types at varying concentrations are offered concurrently, as well as observations  
3 of the behavioural responses of both predator and prey.  
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## 22 TABLE AND FIGURE LEGENDS

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25 **Table I:** Overview of the experiments conducted. Equivalent spherical diameter (ESD) was  
26 estimated in live cells with a Beckman Coulter Multisizer III. Prey carbon contents were estimated  
27 by (a) application of conversion factors found in the literature, (b) through CHN analysis carried out  
28 either within the present study or during previous experimental studies using the same strains and  
29 growing conditions. Date<sup>Samp</sup>: sampling date, Date<sup>Exp</sup>: date of experiment, T: sea surface  
30 temperature.  
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37 **Table II:** Maximum ingestion ( $I_{\max}$ ) and clearance ( $F_{\max}$ ) rates estimated by the Ivlev model  
38 [ $I=I_{\max}*(1-\exp^{-aC})$ ] and the exponential decay equation ( $F=F_{\max}*e^{-bC}$ ), respectively. Parameters  $a$   
39 and  $b$  of the equations are also given.  
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45 **Table III:** Feeding rates of the genus *Clausocalanus* on natural field assemblages or monospecific  
46 diets compiled from the literature (C:ciliate; D: dinoflagellate; Dia: diatom; F: flagellate).  
47 Information on body mass (B. M.), temperature (Temp), food type (size fraction of natural  
48 assemblage or species in the single diets) and food concentration (F. C.) have also been provided.  
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53 **Fig. 1:** Functional feeding response of *C. lividus* (♀) on six different-sized food items. Clearance  
54 rates ( $\text{mL cop}^{-1} \text{ day}^{-1}$ ) and ingestion rates ( $\text{cells cop}^{-1} \text{ day}^{-1}$ ) are presented as a function of the  
55 average food concentration ( $\text{cells mL}^{-1}$ ). Parameters of the fitted models are provided in Table II.  
56 Error bars indicate the standard errors of the mean values.  
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2 **Fig. 2:** Maximum clearance rates (A) and daily ration (B) of *C. lividus*, as well as the  $C_{I_{max}/2}$   
3 (concentration at which ingestion equals half the maximum rate), plotted against the equivalent  
4 spherical diameter (ESD) of the different prey items (Iso: *Isochrysis* sp., Rho: *Rhodomonas salina*,  
5 Hete: *Heterocapsa* sp., Thala: *Thalassiosira weissflogii*, Gyro: *Gyrodinium* sp., Oxy: *Oxyrrhis*  
6 *marina*, Stro: *Strombidium sulcatum*).  
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12 **Fig. 3:** Comparative presentation of the carbon intake of *C. lividus* (♀) on prey of equivalent  
13 spherical diameter (ESD) smaller and larger than 15  $\mu\text{m}$ . Ingestion rates expressed as  $\mu\text{g C cop}^{-1}$   
14  $\text{day}^{-1}$  (A) and carbon-specific ingestion rates (% of body carbon  $\text{day}^{-1}$ ) (B) are presented in relation  
15 to the mean food concentration ( $\mu\text{g C L}^{-1}$ ). The curves correspond to the fitting of Ivlev's model to  
16 the data (estimated parameters for each prey item are provided in Table II). Horizontal dashed lines  
17 correspond to the required ingestion rates to satisfy the metabolic demands of *C. lividus* (assuming  
18 90% assimilation efficiency), both under starved (12.8%) and feeding conditions (29.4%).  
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**Table I.** Overview of the experiments conducted. Equivalent spherical diameter (ESD) was estimated in live cells with a Beckman Coulter Multisizer III. Prey carbon contents were estimated by (a) application of conversion factors found in the literature, (b) through CHN analysis carried out either within the present study or during previous experimental studies on the same strains and growing conditions.

Date<sup>Samp</sup>: sampling date, Date<sup>Exp</sup>: date of experiment, T: sea surface temperature

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Date <sup>Samp</sup>	T (°C)	Date <sup>Exp</sup>	Taxon	FOOD ITEMS			COPEPODS	
				ESD (µm)	Carbon content (x10 <sup>-6</sup> µg cell <sup>-1</sup> )	Range of initial food concentrations (cells mL <sup>-1</sup> )	Mean prosome length (mm)	Body carbon content (µg C cop <sup>-1</sup> )
07/4/2009	13.9	08/4/2009	<i>Oxyrrhis marina</i>	17.1	323.9 <sup>(1)</sup>	61-1331	1.25	19.9
		10/4/2009	<i>Strombidium sulcatum</i>	27.8	1699.1 <sup>(2)</sup>	1.6-78	1.22	18.1
20/5/2009	18.2	22/5/2009	<i>Heterocapsa</i> sp.	13.6	287.7 <sup>(3)</sup>	148-4620	1.19	17.3
		24/5/2009	<i>Rhodomonas salina</i>	6.8	55.0 <sup>(4)</sup>	1692-56753	1.19	17.3
03/6/2009	20.0	04/6/2009	<i>Gyrodinium</i> sp.	16.2	416.2 <sup>(1)</sup>	38-1192	1.07	10.1
		06/6/2009	<i>Thalassiosira weissflogii</i>	14.0	220.5 <sup>(5)</sup>	161-5250	1.08	12.5
10/6/2009	20.0	11/6/2009	<i>Isochrysis</i> sp.	4.3	11.3 <sup>(3)</sup>	4251-105450	1.11	9.7

<sup>1</sup>:  $0.76 \times V^{0.819}$  equation for dinoflagellates from Menden-Deuer and Lessard, 2000

<sup>2</sup>:  $0.15 \text{ pg C } \mu\text{m}^{-3}$  based on the ratios ( $C/\text{vol}_{\text{Lugol}} = 0.19 \text{ pg C } \mu\text{m}^{-3}$  &  $\text{vol}_{\text{Lugol}} = 78\% \text{ vol}_{\text{live cell from coulter counter}}$ ) found in Putt and Stoecker, 1989

<sup>3</sup>: CHN analysis in this study

<sup>4</sup>: Broglio *et al.*, 2003

<sup>5</sup>: Henriksen *et al.*, 2007

**Table II.** Maximum ingestion ( $I_{\max}$ ) and clearance ( $F_{\max}$ ) rates estimated by the Ivlev model [ $I=I_{\max}*(1-\exp^{-aC})$ ] and the exponential decay equation [ $F=F_{\max}*e^{-bC}$ ], respectively. Parameters  $a$  and  $b$  of the equations are also given.

Food type	Clearance rates						Ingestion rates					
	$\text{mL}^{-1} \text{cop}^{-1} \text{day}^{-1}$			$\text{cells cop}^{-1} \text{day}^{-1}$			$\mu\text{g C cop}^{-1} \text{day}^{-1}$			% body carbon $\text{day}^{-1}$		
	$F_{\max}$	$b$ ( $\times 10^{-3}$ )	$r^2$	$I_{\max}$	$a$ ( $\times 10^{-3}$ )	$r^2$	$I_{\max}$	$a$ ( $\times 10^{-3}$ )	$r^2$	$I_{\max}$	$a$ ( $\times 10^{-3}$ )	$r^2$
<i>Isochrysis</i> sp.	No model was fitted			No model was fitted			No model was fitted			No model was fitted		
<i>Rhodomonas salina</i>	10.49	0.02	0.86	169960	0.06	0.99	9.35	1.16	0.99	54	1.16	0.99
<i>Heterocapsa</i> sp.	52.55	0.77	0.99	32298	1.58	0.99	9.29	5.49	0.99	54	5.49	0.99
<i>Thalassiosira weissflogii</i>	166.41	1.72	0.99	77627	0.26	0.77	17.12	1.19	0.77	137	1.19	0.77
<i>Gyrodinium</i> sp.	77.197	1.48	0.88	30255	1.84	0.99	12.59	4.43	0.99	125	4.43	0.99
<i>Oxyrrhis marina</i> *	120.43	1.74	0.97	29412	3.67	0.84	14.15	7.64	0.84	71	7.64	0.84
<i>Strombidium sulcatum</i>	307.84	24.39	0.77	8112	23.08	0.99	13.78	13.58	0.99	76	13.58	0.99

\* the second concentration has been omitted for the sake of a more realistic fit of the models



**Table III.** Feeding rates of the genus *Clausocalanus* on natural field assemblages or monospecific diets compiled from the literature (CIL: ciliate; DIN: dinoflagellate; DIA: diatom; F: flagellate; HNF: heterotrophic nanoflagellates). Information on copepod body mass (B.M.), experimental temperature (Temp), food type (size fraction of natural assemblage or species in the single diets) and food concentration (F. C.) have also been provided.

Taxon	B.M. ( $\mu\text{g C cop}^{-1}$ )	Temp ( $^{\circ}\text{C}$ )	Food type	F. C. ( $\mu\text{g C L}^{-1}$ )	Clearance rate ( $\text{mL}^{-1}\text{ cop}^{-1}\text{ day}^{-1}$ )	Ingestion rate ( $\mu\text{g C cop}^{-1}\text{ day}^{-1}$ )	%BC $\text{d}^{-1}$
<i>Natural assemblage</i>							
<i>Clausocalanus</i> spp. <sup>1</sup>	2.26; 1.40	21.8; 23.1	total particles (autotrophic + ciliates)	10.00; 38.00	-	0.12; 0.48	5.18; 34.64
<i>Clausocalanus</i> spp. <sup>2</sup>	-	18	CIL: 16-20 $\mu\text{m}$ ; 21-30 $\mu\text{m}$	0.92 (16-30 $\mu\text{m}$ )	36; 74.4	-	-
			DIN: 16-20 $\mu\text{m}$ ; 21-30 $\mu\text{m}$ ; 31-45 $\mu\text{m}$	0.32(Din+HNF)	49.92; 38.16; 35.76	-	-
			HNF: 2-5 $\mu\text{m}$ ; 5-20 $\mu\text{m}$			$\approx$ 5.38; 1.89	-
♀ <i>C. farrani</i> <sup>3</sup>	4.20	21- 25.5	particles >5 $\mu\text{m}$	1.58	134.00	0.48	13.00
♀ <i>C. furcatus</i> <sup>3</sup>	3.69	21-24	particles >5 $\mu\text{m}$	1.41	50.00	0.01	1.94
♀ <i>C. furcatus</i> <sup>4</sup>	2.74	23	6-8 $\mu\text{m}$ ; 8-10 $\mu\text{m}$ ; 10-20 $\mu\text{m}$ ; 20-40 $\mu\text{m}$	1.07; 0.93; 3.11; 1.18	56; 71; 114; 218	-	-
<i>Monospecific diets</i>							
<i>Clausocalanus</i> spp. <sup>5</sup>	-	20	F <i>Rhodomonas</i> sp.	29.67	9.60	0.28	-
"	"	"	DIN <i>Gymnodinium nelsoni</i>	17.42; 29.03	29.04; 31.68	0.51; 0.92	-
♀ <i>C. furcatus</i> <sup>5</sup>	3.60	20	"	12.90; 25.80	29.00; 47.00	0.37; 1.21	10.30; 33.60
♀ <i>C. lividus</i> <sup>6</sup>	-	20	" <i>Scrippsiella trochoidea</i>	55.95	-	$\approx$ 2.93	-
"	"	"	" <i>Scrippsiella ramonii</i>	56.65	-	$\approx$ 1.58	-
♀ <i>C. lividus</i> <sup>7</sup>	9.7-19.9*	16	" <i>Heterocapsa</i> sp.	42.58	48.27	1.75	10.08
"	"	"	" <i>Gyrodinium</i> sp.	15.82	80.78	0.90	8.99
"	"	"	" <i>Oxyrrhis marina</i>	19.76	115.50	3.28	16.43
"	"	"	F <i>Isochrysis</i> sp.	48.04	n.s. consumed	n.s. consumed	n.s. consumed
"	"	"	" <i>Rhodomonas salina</i>	93.06	10.40	1.13	6.50
"	"	"	DIA <i>Thalassiosira weissflogii</i>	35.50	128.81	4.15	33.35
"	"	"	CIL <i>Strombidium sulcatum</i>	2.72	323.22	0.36	2.01

<sup>1</sup>: NW Mediterranean (Broglio *et al.*, 2004)

<sup>2</sup>: NW Spain (Batten *et al.*, 2001)

<sup>3</sup>: Gulf of Aqaba: averaged data of four and seven experiments with *C. furcatus* and *C. farrani* respectively (Cornils *et al.*, 2007)

<sup>4</sup>: subtropical Atlantic Ocean: averaged data of six experiments in subtropical (Paffenhöfer *et al.*, 2006)

<sup>5</sup>: S.E. USA (Mazzocchi and Paffenhöfer, 1998)

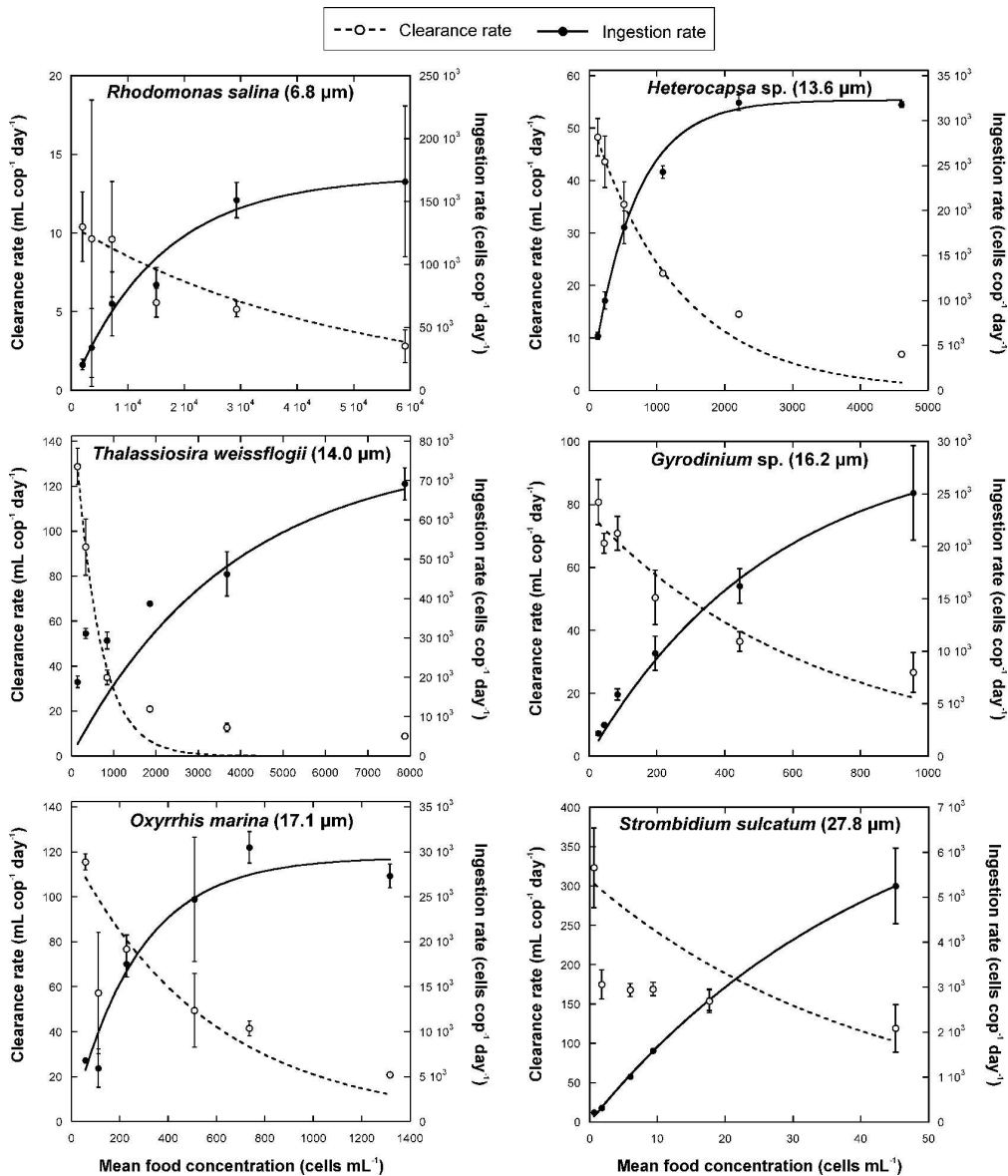
<sup>6</sup>: Gulf of Naples: values correspond to vegetative forms that have been approximately ( $\approx$ ) extracted from their Fig. 1 (Montresor *et al.*, 2003)

<sup>7</sup>: NW Mediterranean (present study; \*: range of body carbon in our experiments; n.s.: not significantly)

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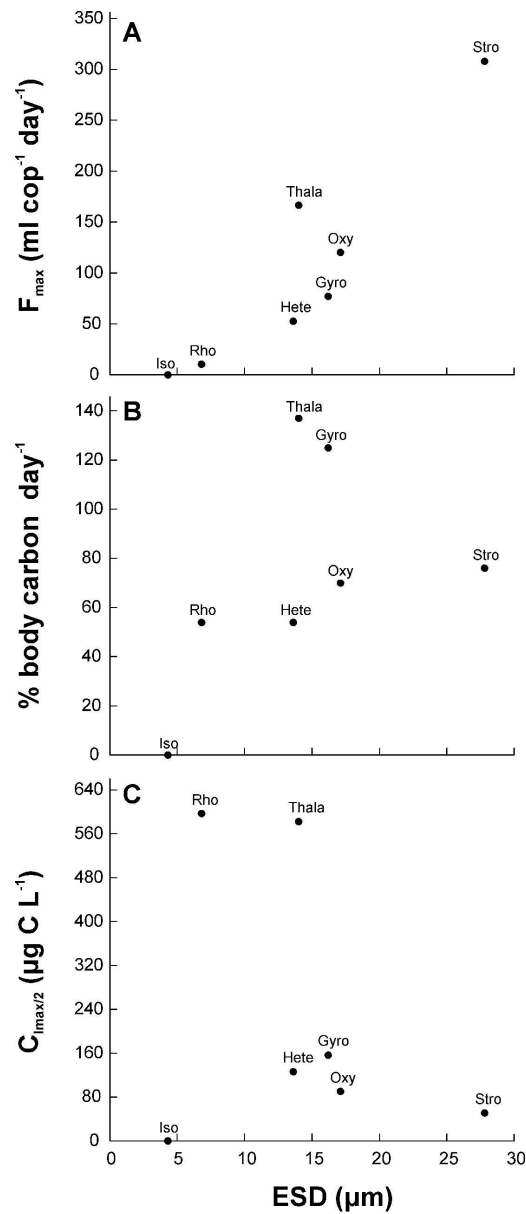
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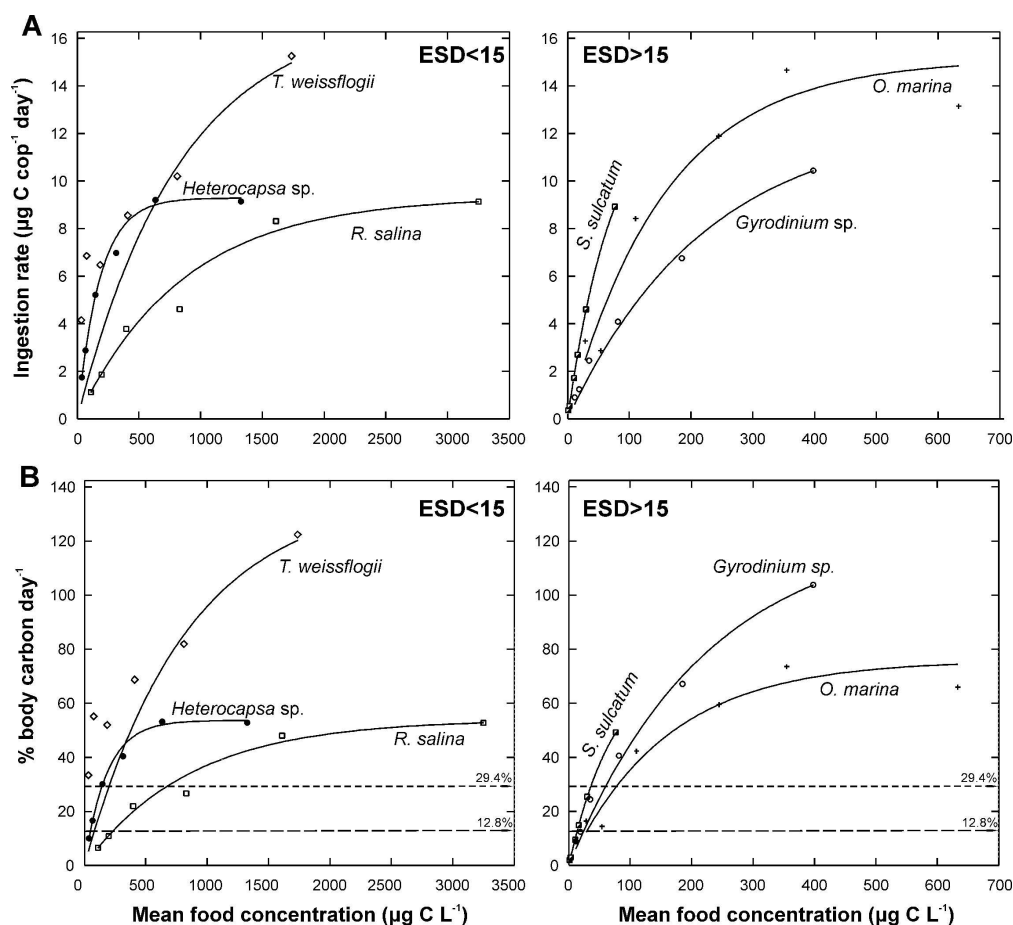
Functional feeding response of *C. lividus* (♀) on six different-sized food items. Clearance rates (mL cop<sup>-1</sup> day<sup>-1</sup>) and ingestion rates (cells cop<sup>-1</sup> day<sup>-1</sup>) are presented as a function of the average food concentration (cells mL<sup>-1</sup>). Parameters of the fitted models are provided in Table II. Error bars indicate the standard errors of the mean values.

213x249mm (600 x 600 DPI)



Maximum clearance rates (A) and daily ration (B) of *C. lividus*, as well as the  $C_{Imax/2}$  (concentration at which ingestion equals half the maximum rate), plotted against the equivalent spherical diameter (ESD) of the different prey items (Iso: *Isochrysis* sp., Rho: *Rhodomonas salina*, Hete: *Heterocapsa* sp., Thala: *Thalassiosira weissflogii*, Gyro: *Gyrodinium* sp., Oxy: *Oxyrrhis marina*, Stro: *Strombidium sulcatum*).

93x219mm (600 x 600 DPI)



Comparative presentation of the carbon intake of *C. lividus* (♀) on prey of equivalent spherical diameter (ESD) smaller and larger than 15  $\mu\text{m}$ . Ingestion rates expressed as  $\mu\text{g C cop}^{-1} \text{ day}^{-1}$  (A) and carbon-specific ingestion rates (% of body carbon  $\text{day}^{-1}$ ) (B) are presented in relation to the mean food concentration ( $\mu\text{g C L}^{-1}$ ). The curves correspond to the fitting of Ivlev's model to the data (estimated parameters for each prey item are provided in Table II). Horizontal dashed lines correspond to the required ingestion rates to satisfy the metabolic demands of *C. lividus* (assuming 90% assimilation efficiency), both under starved (12.8%) and feeding conditions (29.4%).

192x175mm (600 x 600 DPI)