

Predation by calanoid copepods on the appendicularian *Oikopleura dioica*

Abstract—Appendicularians have some of the highest growth rates among metazoans but they are usually outnumbered by the slower growing copepods in mesozooplankton communities. We present experimental evidence that the eggs and juveniles of the appendicularian *Oikopleura dioica* are actively consumed by various copepod species. Clearance rates of *Calanus helgolandicus*, *Candacia armata*, *Centropages typicus*, *Eucalanus crassus*, and *Temora longicornis* on eggs of *O. dioica* were usually above 300 ml copepod⁻¹ d⁻¹. The ingestion rates of *C. helgolandicus* on *O. dioica* eggs did not reach saturation even at the highest egg concentrations (4,560 eggs L⁻¹). Although *C. helgolandicus*, *C. typicus*, and *C. armata* preyed actively on 1-mm-long *O. dioica* (approximately 0.2 mm in trunk length), predatory pressure decreased with increasing appendicularian size. We suggest that the association of dense appendicularian populations with phytoplankton blooms could be explained by their opportunistic response to beneficial conditions before copepod densities become high enough to cause a decline in appendicularian populations due to predation. Our results indicate that, in addition to the direct shunt of biomass from picoplankton to fish, appendicularians can occupy a similar role to that of microzooplankton in the ocean. They represent an intermediate step in the less efficient, picoplankton–appendicularia–copepod–fish food chain.

Appendicularians are one of the major mesozooplankton groups in marine ecosystems (Sommer and Stibor 2002). They mediate a direct shunt of biomass from picoplanktonic producers to fish, which represents a more efficient chain than that flowing from picoplankton through ciliates to copepods to fish (Gorsky and Fenaux 1998). Although appendicularians grow close to an order of magnitude faster than copepods (Hopcroft et al. 1998; López-Urrutia et al. 2003), they are usually outnumbered by copepods (e.g., Vargas et al. 2002). Competitive interactions between copepods and appendicularians are unlikely to be responsible for this general pattern of copepod dominance because each group uses different food (e.g., Sommer et al. 2002). The growth rates of appendicularians become food limited at lower concentrations than those of copepods (López-Urrutia et al. 2003). This suggests that bottom-up interactions are not responsible for their lower abundance and indicates that they might be under higher predatory control (Hopcroft et al. 1998; López-Urrutia et al. 2003).

Adult appendicularians are eaten by many planktonic organisms (Gorsky and Fenaux 1998), but the sources of mortality of appendicularian eggs and juveniles have not been fully considered. Appendicularians are semelparous organisms that release their eggs freely into the water. The diameter of appendicularian eggs varies between 44 and 130 μ m (Galt 1987), which lies within the optimal food-size range of many copepods. Our aim was to determine if the copepods *Calanus helgolandicus*, *Candacia armata*, *Centropages typicus*, *Eucalanus crassus*, and *Temora longicornis* can feed on the eggs of *Oikopleura dioica*, a widespread

appendicularian species. We also determined the functional response of the calanoid copepod *C. helgolandicus* on *O. dioica* eggs and tested whether copepods are equally efficient predators on *O. dioica* of different sizes.

Materials and methods—General experimental procedures: Copepods and appendicularians were collected from a coastal station in the English Channel off Plymouth (station L4). *O. dioica* cultures were maintained and experiments conducted in a constant temperature room at 15°C with a simulated 12:12 day:night cycle. Cohorts of cultured *O. dioica* (maintained according to Fenaux and Gorsky 1985) were used to obtain eggs and juvenile appendicularians. To prevent fertilization of eggs, adult female *O. dioica* were separated from the males and maintained in 5-liter beakers filled with 30- μ m-filtered seawater until they were ripe enough to expect spawning within a few hours. The females were then repeatedly transferred into GF/F-filtered seawater and finally placed with 5 ml of filtered seawater into tissue culture flat-bottom, 6-well plates where spawning occurred. The dead female and its house were removed from the well and the eggs maintained at 4°C until the experiments, which took place within 24 h of spawning. The copepods used as predators were collected with a WP-2 net. Adult female copepods were sorted under the binocular microscope and maintained in 5-liter beakers filled with GF/F filtered seawater for approximately 6–8 h until the experiments started. The experiments were conducted in 300-ml Duran® laboratory bottles mounted on a plankton wheel rotating at 1 rpm. Average prey concentrations during the incubations (C^*) were calculated from the number of prey at the beginning (C_1^*) and end (C_2^*) of the experiments using the equation given by Kiørboe et al. (1982),

$$C^* = \frac{C_2^* - C_1^*}{\ln \frac{C_2^*}{C_1^*}}$$

Copepod predation was expressed in terms of daily clearance (F) according to the equation

$$F = \frac{V}{t} \times \ln \left(\frac{C_2}{C_2^*} \right)$$

where V is the volume of the bottles, C_2 and C_2^* are the final prey concentration in the control and treatment bottles and t is the incubation time (days). Ingestion rates were estimated as the average prey concentration times clearance rates (Kiørboe et al. 1982). The size of the eggs and juveniles of *O. dioica* and the total length of the copepods was measured from digital photographs using image-analysis software. Photographs were taken with an inverted microscope at magnifications ranging from $\times 20$ to $\times 200$ using a SONY SSC color video camera connected to a computer.

Predation on *O. dioica* eggs: To study the functional response of *C. helgolandicus* feeding on *O. dioica* eggs, eight bottles were filled with 0.2- μm -filtered seawater. The eggs were transferred from the multiwell plates into the bottles using a Pasteur pipette at initial concentrations ranging from 250 to 8,000 eggs L^{-1} . All the eggs transferred into each bottle were counted, which ensured that the error in the estimation of initial concentrations was minimal ($<1\%$). One adult female *C. helgolandicus* was introduced into each bottle and incubated for 12 h. At the end of the experiment, the contents of the bottles were filtered under low vacuum (<10 mm Hg) onto 2- μm membrane filters (Nucleopore). The bottles and filtration units were repeatedly rinsed with 0.2- μm -filtered seawater. The filters were placed on microscope slides with a drop of filtered seawater and all the eggs immediately counted under an inverted microscope. The filtration unit was further rinsed with 0.2- μm -filtered seawater onto a Petri dish that was checked under a binocular microscope for any remaining eggs. Because preliminary trials showed that this protocol resulted in $<5\%$ of eggs being lost, we used no control bottles for this experiment and assumed that the final egg concentration in the control bottles would have been equal to egg concentrations at the beginning of the experiment. Egg diameters were measured both at the beginning and end of the experiments and egg concentrations in carbon units were calculated using an egg carbon to volume ratio of $2.96 \times 10^{-8} \mu\text{g C } \mu\text{m}^{-3}$ (obtained from data in King et al. 1980).

Similar experiments at a fixed initial egg concentration of 400 eggs L^{-1} were conducted with *C. helgolandicus*, *C. armata*, *C. typicus*, *T. longicornis*, and *E. crassus* as predators. To test whether the use of filtered seawater to maintain the copepods prior and during the experiments could bias the measurement of the clearance rate, we included an additional treatment consisting of *C. helgolandicus* fed a mixed suspension of *O. dioica* eggs and the dinoflagellate *Gymnodinium sanguineum* (50 μm in diameter) added at a concentration of 120 $\mu\text{g C } \text{L}^{-1}$. The *Calanus* used in this latter treatment were maintained in the *Gymnodinium* suspension for 6–8 h prior to the experiment. The experiments consisted of 24-h incubations in triplicate control (without copepods) and treatment (with one copepod) bottles.

Response of copepod predation to *O. dioica* size: Incubations consisted of triplicate control and treatment (with one copepod) bottles with *C. helgolandicus*, *C. armata*, and *C. typicus* as predators and eggs and juvenile *O. dioica* of different sizes as prey. To allow the appendicularians to feed during the experiments, the bottles were filled with 5- μm -filtered natural seawater. Juveniles and eggs were added at a concentration of 50 *O. dioica* L^{-1} . Because the juvenile *O. dioica* were normally feeding inside their filter houses and growing during the incubations both in treatment and control bottles, their average body size was calculated as the geometric mean of animals measured from control bottles at the start and end of the incubation. The tail, trunk length (from mouth to upper gonad end), and width of juvenile appendicularians were measured from digital photographs. The total length of the juvenile *O. dioica* was expressed as the sum of appendicularian trunk (from mouth to distant gonad end)

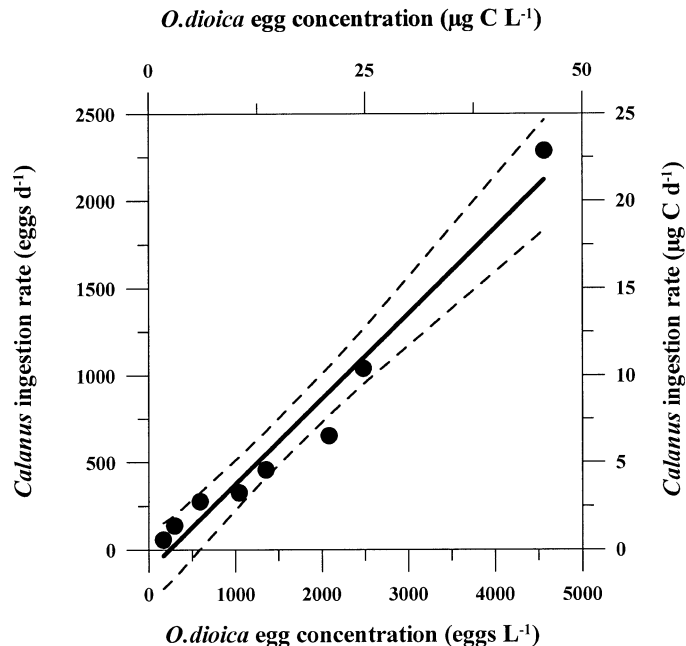


Fig. 1. *Calanus helgolandicus* feeding on *Oikopleura dioica* eggs. Lines represent the least square regression (slope = 0.490 ± 0.039 ; intercepts = $-1.16 \pm 0.82 (\mu\text{g C } \text{d}^{-1})$ and $116 \pm 82 (\text{egg } \text{d}^{-1})$; $\pm \text{SE}$; $r^2 = 0.96$; $n = 8$; $P < 0.001$) and 95% confidence limits for the parameter estimates (dashed lines).

and tail length, which is approximately equivalent to the diameter of the appendicularian filter house (E. Palacios and J. L. Acuña, pers. comm.).

Results—Ingestion rates of *C. helgolandicus* on the eggs of *O. dioica* increased linearly with increasing egg concentration and did not saturate even at the highest prey densities (4,560 egg L^{-1} , Fig. 1). There was no significant relationship between the clearance rates on *O. dioica* eggs and copepod body size (Fig. 2). The number of eggs we were able to obtain for experiments restricted the use of large experimental containers and required us to use 300-ml bottles to obtain realistic egg concentrations. At times, this reduced volume resulted in a decrease in egg concentration greater than 30%, which could cause clearance rate to vary during the experiment. Nevertheless, the low egg concentration used (approximately 4 $\mu\text{g C } \text{L}^{-1}$) fell within the linear part of the functional response of *C. helgolandicus*, and consequently, clearance rates should remain constant. Although we do not know whether the functional response for other copepod species is similar and the extent to which our clearance rates could be underestimated, most copepod species preyed on *O. dioica* eggs at clearance rates $>200 \text{ ml ind}^{-1} \text{ d}^{-1}$, which are relatively high when compared with maximum recorded clearance rates of copepods of similar body size (Mauchline 1998; Fig. 2). The clearance rates of *C. helgolandicus* feeding on a mixture of eggs and the large dinoflagellate *G. sanguineum* were similar to treatments with the same concentration of eggs in filtered seawater (t -test; $t = 0.38$, $P = 0.57$, degrees of freedom = 4; Fig. 2). Thus, the use of filtered seawater to maintain the copepods prior to and dur-

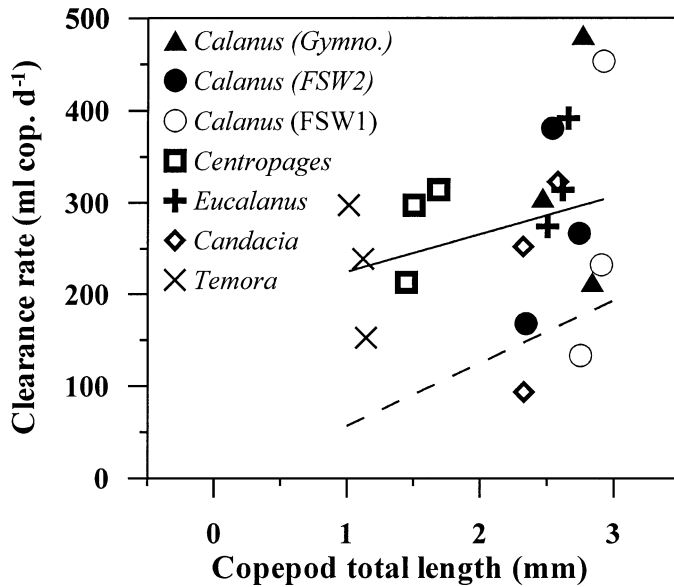


Fig. 2. Clearance rate of different calanoid copepod species on *Oikopleura dioica* eggs in relation to copepod total length. All experiments were performed in filtered seawater (FSW) except one experiment with *Calanus helgolandicus*, in which *G. sanguineum* ($120 \mu\text{g C L}^{-1}$) was added to the egg suspension (Gymno.). Solid line represents the linear regression between clearance rate and copepod size ($F_{1,19} = 0.67$, $P = 0.45$, $r^2 = 0.03$), dashed line represents the regression equation between maximum recorded clearance rates and body length of copepods obtained by Mauchline (1998).

ing the experiments did not introduce any bias in the clearance rates.

The clearance rates of *C. helgolandicus* preying on newly hatched *O. dioica* were higher than when feeding on eggs, but then declined for larger sizes (Fig. 3A) approaching zero for *O. dioica* with a total length greater than $1,000 \mu\text{m}$ (corresponding to an *O. dioica* 3 d old with a trunk length of $300 \mu\text{m}$). Clearance rates of *C. armata* showed a less pro-

nounced decrease with increasing *O. dioica* size, and this species was able to prey efficiently even on larger *O. dioica* (Fig. 3B). Although the experiment with *C. typicus* covered a narrower *O. dioica* size range and copepod clearance rates were more variable, *C. typicus* cleared over $300 \text{ ml ind}^{-1} \text{ d}^{-1}$ on appendicularians with a total length of $1,200 \mu\text{m}$ (Fig. 3B).

Discussion—The importance of copepod predation on appendicularian population dynamics: The high growth rates of appendicularians allow them to respond faster than copepods to favorable conditions and therefore to take opportunistic advantage of phytoplankton blooms (Troedsson et al. 2002). Even when food is limited, the intrinsic rate of natural population increase (r) of *O. dioica* at 15°C is 0.69 d^{-1} (Troedsson et al. 2002). With this high reproductive potential, it is surprising that mesozooplankton communities are not dominated by appendicularians. Our results suggest that predation by copepods on appendicularian eggs and juveniles (Figs. 1–3) could limit appendicularian population growth rates. The importance of this predatory impact will depend on the abundance of copepods and their clearance rate on appendicularians. Given that, during the first 3 d of the life cycle of *O. dioica* this clearance rate is approximately $0.3 \text{ L ind}^{-1} \text{ d}^{-1}$ (see Results and Fig. 2) and that the generation time of *O. dioica* at 15°C is 7.2 d (Troedsson et al. 2002), the copepod clearance rate integrated during one generation of *O. dioica* is approximately $0.125 \text{ L ind}^{-1} \text{ d}^{-1}$ ($0.3 \text{ L ind}^{-1} \text{ d}^{-1}$ times 3 divided by 7.2). To calculate the total copepod population predatory impact, we should then multiply $0.125 \text{ L ind}^{-1} \text{ d}^{-1}$ by the copepod population densities (ind L^{-1}). At copepod densities higher than 5.52 ind L^{-1} (obtained by dividing $r = 0.69 \text{ d}^{-1}$ by $0.125 \text{ L ind}^{-1} \text{ d}^{-1}$), the copepod predatory impact would be sufficient to equal the intrinsic rate of natural population increase of *O. dioica* and limit appendicularian population growth rates. This estimated copepod density threshold is close to the observed densities of calanoid copepods, $<5\text{--}10 \text{ ind L}^{-1}$, at

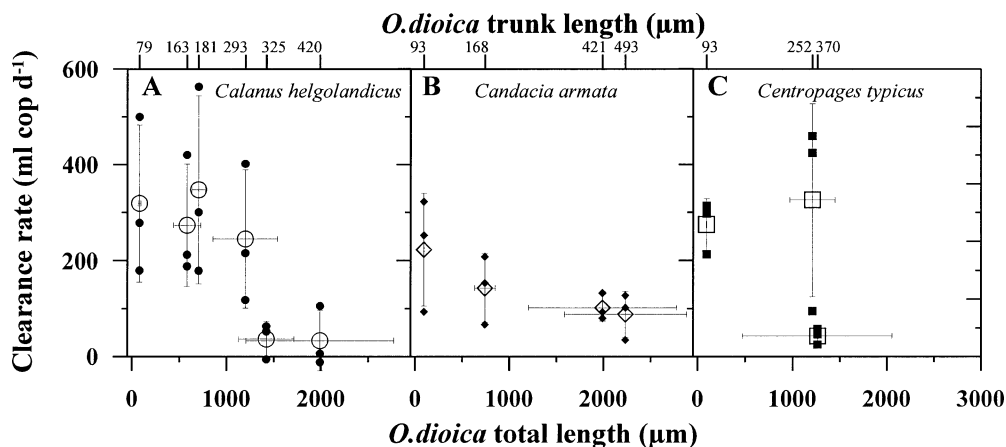


Fig. 3. Clearance rate of (A) *Calanus helgolandicus*, (B) *Candacia armata*, and (C) *Centropages typicus* in relation to the size of *Oikopleura dioica*. The first x-axis data points represent the diameter of *O. dioica* eggs. Solid symbols represent the measured clearance rates and open symbols represent their mean. Vertical and horizontal error bars are the standard deviation of clearance rates and *O. dioica* size, respectively.

which appendicularians start to bloom in the field and during copepod exclusion mesocosm experiments (Sommer et al. 2003).

Appendicularians as a food source for copepods: Carnivorous feeding can allow copepods to maintain their reproductive rates when phytoplankton concentrations are low (Ohman and Runge 1994). Our results show that appendicularian eggs and juveniles represent an alternative food source for copepods. Record densities of *O. dioica* in nature are close to 100 ind L⁻¹, the proportion of individuals larger than 200 μ m in trunk length being approximately 15% (Nakamura 1998). Even if we assume that all these large appendicularians spawn simultaneously, egg concentrations would only be around 3,600 eggs L⁻¹ (if each adult produces 240 eggs; Troedsson et al. 2002), i.e., lower than the highest concentration in our functional response experiment. The egg and juvenile densities in carbon units would be 56 and 7 μ g C L⁻¹, respectively (using carbon weights in King et al. 1980). Given a clearance rate of 0.3 L ind⁻¹ d⁻¹ (Figs. 1 and 2), a copepod would obtain 18.9 μ g C d⁻¹ from the ingestion of the eggs and juvenile *O. dioica*. Although we lack knowledge on how nutritious and digestible appendicularians are, for a copepod 40 μ g C like *C. helgolandicus*, this ingestion rate represents approximately a daily ration of 47% and five times the carbon requirements for metabolism (3.43 μ g C d⁻¹, obtained using the equation in Ikeda et al. 2001). Although such high appendicularian densities are not common (e.g., Nakamura 1998; Sommer et al. 2003), appendicularians can be, at times, an important supplement to the copepod diet. Moreover, appendicularians swim actively toward the surface to spawn, which results in aggregation of eggs in the surface at concentrations as high as 150,000 eggs L⁻¹ (approximately 2,325 μ g C L⁻¹; Alldredge 1982). Therefore, appendicularian eggs could form vertical patches of high food concentrations, what may also serve as a way to reduce predation risk due to saturation of copepod ingestion rates.

Copepod and appendicularian behavior: Different copepod species show different ability for carnivory, which is reflected in differences in feeding behavior and morphologies of sensory and prey capture appendages rather than in body size (Landry and Fagerness 1988). Although carnivorous Candaciids can selectively prey on large appendicularians with a tail length of 1,030–3,680 μ m (Ohtsuka and Onbé 1989), omnivorous copepods switch between herbivory and carnivory depending on the relative abundance of plant and animal food in the environment (Landry 1981). This switching strategy is beneficial not only for the copepod but also for the prey because it can find refuge from predation when the concentration of other food is high (Landry 1981). Therefore, appendicularians may benefit from decreased predatory pressure during high phytoplankton concentrations. This could explain why reports of high appendicularian densities are mainly limited to highly eutrophic, neritic waters and to phytoplankton blooms (e.g., Hopcroft et al. 1998; Nakamura 1998). However, copepod egg mortality rates in the field are independent of the biomass of other prey types (Ohman and Hirche 2001) and the predation rates

on *O. dioica* eggs were similar in the presence or absence of *G. sanguineum* (Fig. 2). Copepod switching is a counterbalance between the time spent in suspension feeding and ambush feeding modes (Kjørboe et al. 1996). The juvenile *O. dioica* are captured by ambush predation (pers. observation) and could benefit from the presence of phytoplankton and the switch to a suspension-feeding behavior. However, the eggs are mainly captured by suspension feeding; therefore, predation pressure on eggs will not be decreased by the presence of phytoplankton unless food concentration is high enough to saturate copepod suspension-feeding rates. At the end of the bloom, when the density of copepods is high and phytoplankton concentrations decline, the predation by copepods could be responsible for high appendicularian mortalities and a decline in appendicularian populations.

The behavior and morphology of both predator and prey are likely to affect the shape of the predation response to appendicularian size. Appendicularians exhibit one of the most complex behavioral patterns in planktonic organisms (Alldredge 1976). After hatching, appendicularians start to feed and produce an external filter structure, commonly known as the house, which decreases predation due to the increase in overall size. However, the tail-beat that they use to create the feeding current generates a hydromechanical signal that can be detected by rheotactic predators and counteracts the benefit from the increase in size. This hydromechanical signal could explain why newly hatched *O. dioica*, although larger in size, are preyed at similar rates as eggs (Fig. 3). With development, the appendicularian house continues to increase in size, protecting them from predators and causing clearance rates to decrease (Fig. 3A). The house is discarded every few hours and the appendicularian swims actively for a few minutes until a new house is produced (Alldredge 1976). The encounter rate between copepods and appendicularians is likely to differ for each of these phases and therefore also the predation risk. The escape behavior is also different for each of these phases. Outside the house, appendicularians may escape by swimming rapidly. When attacked inside the house, they either abandon or remain inside it depending on a complex cost-benefit behavior (pers. observations, see the discussion in Alldredge 1976). All these fascinating predator avoidance strategies are much more complex than those exhibited by copepod nauplii (e.g., Titelman 2001) and current knowledge is still too limited to allow us to fit a plausible curve to the data presented in Fig. 3.

The role of appendicularians and copepods in pelagic food webs: Copepods play a flexible role in the pelagic food web. They may act as secondary or tertiary consumers depending on whether phytoplankton or heterotrophs are the main part of their diet (Sommer and Stibor 2002). They are also able to feed on the eggs and nauplii of other copepods and conspecifics and to control their own population dynamics (e.g., Ohman and Hirche 2001). Our results show that copepods are active appendicularian predators, which suggests a new role of copepods in pelagic food webs and that the trophic role of appendicularians should be also considered to be flexible. In the absence of copepod predation, appendicularians would represent the traditional shunt in which their produc-

tion is channeled directly toward fish and other, more traditional, tertiary consumers. When copepods are abundant, appendicularians become an intermediate step in a longer, energetically less efficient picoplankton–appendicularia–copepod–fish chain.

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