Predation by omnivorous copepods on early developmental stages of *Calanus finmarchicus* and *Pseudocalanus* spp.

Abstract—Predation is thought to be an important source of mortality in the early life stages of fish and copepods on Georges Bank. Omnivorous copepods may be predators on copepod eggs and nauplii, but data on feeding rates or selectivity are scarce. As part of the GLOBEC Georges Bank program, we generated functional response curves for the omnivorous copepods *Metridia lucens, Centropages typicus,* and *Temora longicornis* feeding on the eggs and nauplii of *Calanus finmarchicus* or *Pseudocalanus* spp. in shipboard predation trials. Neither *C. typicus* nor *M. lucens* reached saturation feeding on *Calanus* eggs until prey concentration was >400 L^{-1}. Individual *M. lucens* and *C. typicus* ingested up to 34 ± 9 (mean ± SD, $n = 3$) and 24 ± 14 eggs d^{-1}, respectively (6°C). *T. longicornis* was more abundant in late spring, when they ingested *Calanus* eggs at rates similar to those of *C. typicus*. At ambient prey concentrations, ingestion rates of *Calanus* nauplii were higher than rates of *Calanus* eggs for the predator *M. lucens* but were similar for *C. typicus*. Advanced naupliar stages were less susceptible to predation than young stages. *Pseudocalanus* nauplii moved faster and were ingested at lower rates than similarly sized *Calanus* nauplii. Predation rates increased with increasing temperature for the warm-water species *C. typicus* but decreased for the cold-water species *M. lucens*. These results may contribute to models predicting the development of copepod populations and their availability to larval fish.

Calanus finmarchicus and *Pseudocalanus* spp. are key species in the Georges Bank ecosystem (Davis 1987) because they dominate the zooplankton community in spring (Kane 1993). Their high abundance at that time is essential for the successful recruitment of spring-spawning fish on the bank (Lough and Mountain 1996). All life stages of both species are prey for larval cod and haddock, with eggs of *C. finmarchicus* and *Pseudocalanus* spp. being the most abundant (Kane 1984; Lough 1984). Lynch et al. (1998) concluded from earlier work on Georges Bank (Davis 1984; Madin et al. 1996; Sullivan and Meise 1996) that predation is likely to be the dominant source of mortality of *C. finmarchicus* on the Bank. They estimated minimal mortality to be 20% d^{-1} for *C. finmarchicus* eggs and 15% d^{-1} for nauplii. For both *Calanus* and *Pseudocalanus,* predation on the early life stages appears to be the most important contribution to total population mortality (Davis 1984).

The sources of mortality of eggs and nauplii of these two species are not yet entirely understood (McGillicuddy et al. 1998; Miller et al. 1998). Predictions of abundance based on the known rates of egg production, the available food resources, the hydrographic conditions, and the known sources of mortality overestimate the naupliar densities, compared with what is observed. The most likely explanation is that predators other than fish cause more mortality of copepods than has been previously recognized, thereby also diminishing the food supply for larval fish.

We investigated whether predation by omnivorous copepods could be an important source of mortality for the early life stages of *C. finmarchicus* and *Pseudocalanus* spp. Omnivory presumably is an inherent capability of most calanoids (Paffenhöfer and Knowles 1980) and might be a particularly opportunistic feeding strategy in environments with a variable food supply (Ohman and Runge 1994). Haq (1967) found that *Metridia lucens* was a voracious predator that strongly preferred zooplankton to phytoplankton when offered both together. *Centropages typicus* is broadly omnivorous and has been assumed to interfere with the food resources for larval fish on Georges Bank during spring (Davis 1987).

We measured predation rates on early life stages of *C. finmarchicus* and *Pseudocalanus* spp. by three omnivorous copepods, *M. lucens, C. typicus,* and *Temora longicornis,* that were abundant on Georges Bank during spring and early summer (April through June) of 1999. Quantification of their potential impact could determine whether this class of predators is a significant factor affecting population development of key species in the Georges Bank ecosystem and similar nursery grounds for fish.

Shipboard predation trials—In 15 shipboard predation experiments, we exposed eggs and nauplii of the calanoid copepods *C. finmarchicus* and *Pseudocalanus* spp. to omnivorous copepods. Experiments were performed during two cruises on the Southern Flank of Georges Bank (between 40°52′N–41°36′N and 66°01′W–67°39′W): R/V *Endeavor* cruise EN 322 (17 April–2 May 1999) and R/V *Edwin Link* cruise EL 9905 (10–29 May 1999).

During the course of the cruises, live copepods were caught in vertical net hauls, mostly with a 333-μm ring net or large cod-end net (Reeve 1981). We transferred adult females of *M. lucens, C. typicus,* and *T. longicornis* into cultures for use as the predators and adult female *C. finmarchicus* and *Pseudocalanus* spp. for obtaining eggs (*Calanus*) and nauplii (both species) as the prey. We held all copepods at 3.5–5°C, except for egg-bearing females of *Pseudocalanus,* which we kept at 12°C in order to accelerate the longer egg development times and obtain nauplii. We changed the cultures of *Calanus* 1–2 times daily to collect eggs, which we either used directly or kept to hatch nauplii. All other cultures were changed at intervals of several days. Starting at the first feeding, naupliar instar (III), *Calanus,* and *Pseudocalanus* were fed daily with cultured phytoplankton (*Thalassiosira weissflogii* and *Heterocapsa triquetra*), grown at 15–20°C. Predators were fed ad libitum with the same phytoplankton over a period of at least 24 h before the experiments, to prevent overestimates of predation rates due to starvation. Occasionally, we used predator individuals more

than once but allowed feeding on phytoplankton for at least 24 h between trials.

Bottles were filled with freshly filtered seawater and different combinations of prey and predators and incubated for ~24 h in a plankton wheel on deck, to keep the prey in suspension. A transparent flow-through water bath that used surface seawater provided ambient temperature and exposure to the natural light:dark cycle. During cruise EN 322, the experimental temperature stayed constantly at 6°C. During EL 9905, changing ambient water temperatures were recorded every 1–2 h, and predation rates related to the average temperature during the period of incubation. Incubations were in 2.35-liter bottles (or 1.15-liter bottles for highest prey densities), with triplicates of three or four predation treatments, differing in prey concentrations, prey type, or predator type. All incubations included triplicate controls (bottles without predators), which contained one of the prey concentrations represented in the experimental treatments. Predator concentrations were 4.3 L^{-1}. *Calanus* eggs were offered at concentrations from 0 to >400 eggs L^{-1}, with emphasis on the lower half of this range, which we assumed to be most relevant in the field. Eggs used were <12 h old when we started to prepare for the incubation, to prevent hatching during the experiment (egg development time of *C. finmarchicus* at 5°C is 2.6 d, Campbell et al. in press). Immediately after terminating each experiment, we preserved the eggs with vinegar (0.1 solution; Joly pers. comm.), to prevent the eggs from hatching in response to light and increased temperature during counting.

In predation trials with nauplii, we mainly used concentrations of 10–50 nauplii L^{-1}, representing concentrations often found in the field (e.g., Lough and Mountain 1996), but added several treatments with up to 350 nauplii L^{-1} to test for saturation effects. When terminating the incubations, we counted nauplii live and preserved subsamples to determine developmental stages. Naupliar stages used were N1–N4 for *Calanus* and *Pseudocalanus*; for details, see figure legends. In experiments on stage-specific predation by *Centropages* and *Temora*, nauplii labeled "N3" were 97% N3 (body length 0.26–0.29 mm), "N4" were 76% N4 (0.32–0.38 mm), 21% N3, and 3% N2; temperature 11.6 ± 0.7°C (median and range between three experiments).

Analyses of functional responses over a wide range of prey concentrations required that results from two or three experiments be combined for each species (as in Fig. 1). Data were only plotted in the same graph if the mean experimental temperatures differed by a maximum of 1°C between two or 1.5° among three incubations. Ingestion and clearance rates were calculated according to the method of Kiørboe et al. (1982) and given as mean ± SD of three replicates. Curves for ingestion rates were fitted to a Holling functional response with $[y = ax^\theta/(1 + abx^\theta)]$ (Holling 1959). To distinguish between Holling type II and III responses, we compared the curve fits for $\theta = 1$ and $\theta = 2$ and chose the better fitting model for each respective predator.

To determine weight-specific ingestion rates, carbon content of the predators was measured with a C/N analyzer (Fysons, Model 1108), by using pooled samples of five individuals each. A total of 13 samples for *Metridia*, 13 for
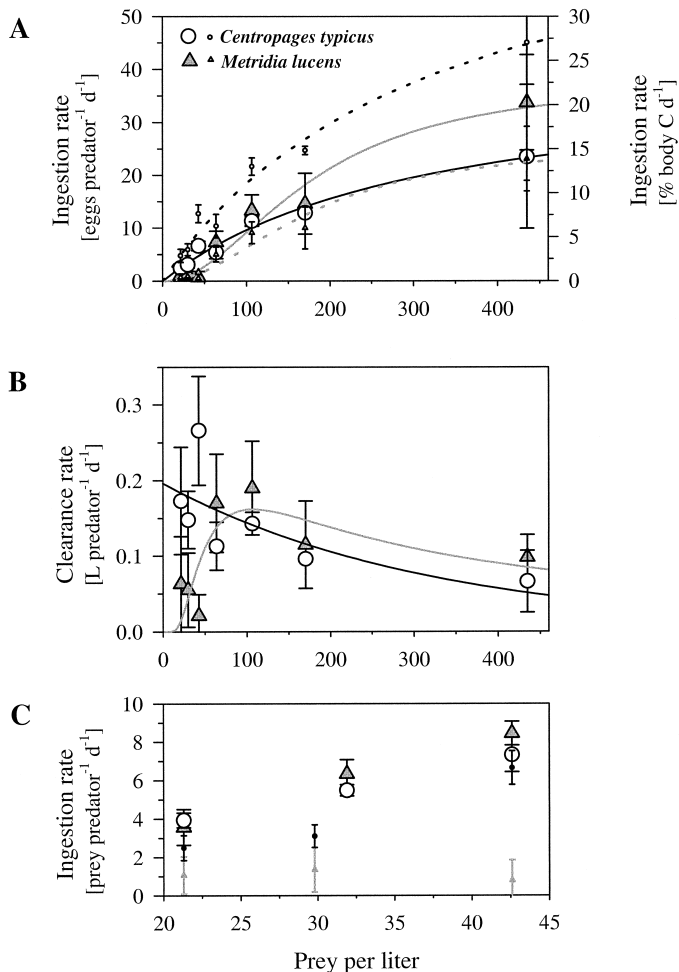

Fig. 1.   Ingestion (A) and clearance rates (B) for *Calanus* eggs preyed upon by *C. typicus* and *M. lucens.* Large symbols and solid regression lines represent individual-based rates, small symbols and dotted lines weight-specific rates. Curves fitted to Holling type II (*Centropages*) and type III (*Metridia*) functional response. (A) *C. typicus* $[y = ax/(1 + abx)]$, with $a = 0.126$, $b = 0.0246$; and *M. lucens* $[y = ax^2/(1 + abx^2)]$, $a = 0.0012$, $b = 0.0261$. (B) *C. typicus* $[y = ae^{-bx}]$, $a = 0.1963$, $b = 0.0031$; and *M. lucens* $[y = ax^{-1}e^{-b/x}]$, $a = 47.0929$, $b = 106.9250$. (C) Ingestion rates for *Calanus* nauplii (large symbols), compared with rates for eggs (small symbols, data from A). Body lengths of nauplii used: 0.17–0.30 mm (N1–N3). (A–C) Experimental temperature = 6°C.

Centropages, and 3 for *Temora* were analyzed, giving mean carbon content per individual of 56 ± 10, 20 ± 3, and 24 ± 5 μg C, respectively. Body size (cephalothorax length) was measured on the same 145 individuals, resulting in mean sizes (±SD) of 2.08 ± 0.13 mm for *Metridia,* 1.41 ± 0.08 mm for *Centropages,* and 1.17 ± 0.07 mm for *Temora.* For transformation to weight-specific rates, we used a carbon content of the prey of 0.23 μg C for *Calanus* eggs (Ohman and Runge 1994), 0.16 for N1, 0.22 for N2, and 0.45 for N3, and for *Pseudocalanus,* 0.10 μg C for N1, 0.13 for N2, 0.21 for N3, and 0.29 or N4 (Davis 1984).

A Q_{10} value of clearance rates (L ind^{-1} d^{-1}) was calculated for *Centropages* predation on *Calanus* eggs as:

Table 1. Two-way ANOVAs testing the dependence of individual-based (top) and weight-specific ingestion rates (bottom) on prey concentration (eggs L^{-1}) and predator species (*M. lucens* and *C. typicus*); data as in Fig. 1a. Experimental temperature = 6°C.

Source of variation	SS	df	MS	F	P
Individual-based					
Prey concentration	3,284	6	547	24.01	8×10^{-10}
Predator species	10	1	10	0.44	0.51
Interaction	222	6	37	1.63	0.18
Within	638	28	23		
Total	4,155	41			
Weight-specific					
Prey concentration	2,992,897	6	498,816	13.59	4×10^{-7}
Predator species	838,759	1	838,759	22.85	5×10^{-5}
Interaction	259,150	6	43,192	1.18	0.35
Within	1,027,790	28	36,707		
Total	5,118,596	41			

$$Q_{10} = \left(\frac{F_1}{F_2}\right)^{[10/(t_1 - t_2)]},$$

where F_1 and F_2 are clearance rates at experimental temperatures t_1 and t_2. We determined the Q_{10} values for the average clearance rate over a range of prey concentrations below saturation. *T. longicornis* was excluded from this analysis because experiments did not include identical predator-prey combinations at different temperatures.

Predation on Calanus *eggs*—Individual *Metridia* ingested up to 34 ± 9 and *Centropages* up to 24 ± 14 eggs per day (Fig. 1a; 6°C). The individual-based ingestion rates for eggs did not differ significantly between predator species (Table 1, top), and neither of the predators reached saturation within the range of prey concentrations offered (21–435 eggs L^{-1}). In contrast, predator species as well as prey concentration had highly significant effects on weight-specific ingestion rates of eggs (Table 1, bottom), with maximum values being 14% ± 4% body carbon d^{-1} for *Metridia* females and 28% ± 16% d^{-1} for *Centropages* (Fig. 1a). *Metridia* predation followed the Holling type III functional response. For *Centropages,* the type II model fitted slightly better than the type III model. Clearance rates for *Metridia* were highest at intermediate prey concentrations ~100 eggs L^{-1} with 0.19 ± 0.06 L predator^{-1} d^{-1}. *Centropages* had highest clearance rates of 0.27 ± 0.07 L predator^{-1} d^{-1} at lowest concentrations. *T. longicornis* was more abundant in late spring and was only investigated as a potentially important predator during the May cruise. Ingestion rates of *Calanus* eggs did not vary significantly between *Temora* and *Centropages,* either on the individual basis (1-way ANOVA, $F = 0.054$, df = 1, $P = 0.82$), or weight-specific (4%–14% body carbon d^{-1} for *Centropages* and 4%–12% d^{-1} for *Temora* at 21–64 eggs L^{-1} offered).

Predation on Calanus *nauplii*—Individual-based ingestion rates of *Calanus* nauplii also were similar for *Metridia* and *Centropages*. For 21–43 nauplii L^{-1}, representing concentrations found on Georges Bank in the upper mixed layer and particularly in the thermocline, ingestion rates increased
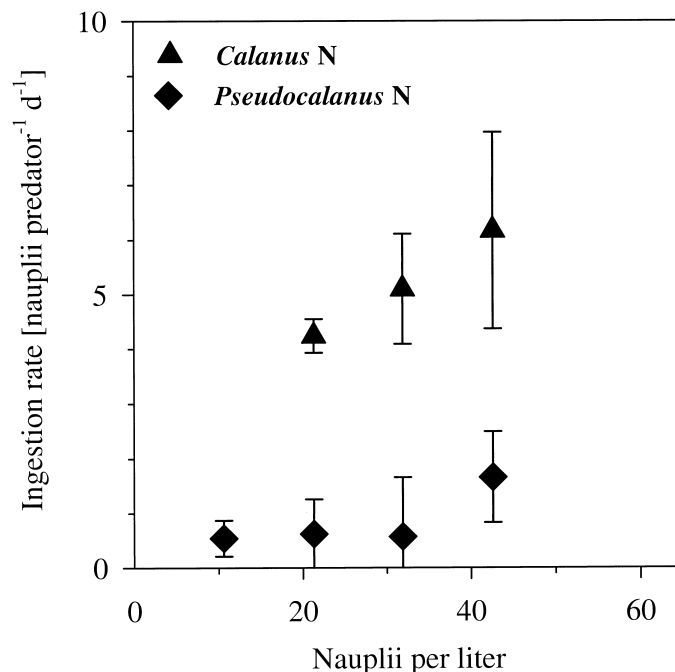

Fig. 2. Ingestion rates of *M. lucens* feeding on *Calanus* or *Pseudocalanus* nauplii. Nauplii offered with mean size of 0.28 ± 0.01 mm for *Calanus* (3% N2, 97% N3), and 0.24 ± 0.04 mm for *Pseudocalanus* (mixture of stages with 3% N1, 49% N2, 39% N3, and 9% N4), respectively. Experimental temperatures: 9.1°C (*Calanus* nauplii) and 9.8°C (*Pseudocalanus* nauplii).

from ~4 to 7–8 nauplii per predator per day (Fig. 1c), with clearance rates remaining ~0.4 L ind^{-1} d^{-1}. At very high concentrations (348 nauplii L^{-1}), individual *Centropages* ingested 24.9 ± 7.4 nauplii predator^{-1} d^{-1} (11°C; for temperature effects see below). As for eggs, weight-specific ingestion rates of nauplii were significantly, on average 2.6 (±0.4) times, greater for *Centropages* than for *Metridia* (ANOVA, $F = 34$, df = 1, $P = 3 \cdot 10^{-5}$). *Metridia* ingested nauplii at significantly higher rates than eggs (ANOVA, $F = 39$, df = 1, $P = 1 \cdot 10^{-5}$; both at 6°C), but there was no such difference in *Centropages* ($F = 3.09$, df = 1, $P = 0.098$). Between *Temora* and *Centropages* later in spring (11°C), there was no significant difference in individual-based ($F = 0.11$, df = 1, $P = 0.75$) or weight-specific ingestion rates ($F = 1.16$, df = 1, $P = 0.31$) for prey concentrations of up to 45 nauplii L^{-1}. *Temora* ingestion rates for eggs (4.3 ± 0.1 and 7.8 ± 0.7 eggs predator^{-1} d^{-1}, at 21 and 43 eggs L^{-1}, respectively) were significantly higher than for nauplii (3.4 ± 0.3 and 5.8 ± 1.3 nauplii predator^{-1} d^{-1}; *t*-test: two-sample assuming unequal variances; $t = 4.60$, df = 2, $P = 0.022$ and $t = 2.40$, df = 3, $P = 0.048$).

Species-specific and stage-specific predation on nauplii—*Calanus* nauplii were more vulnerable to omnivorous copepods than *Pseudocalanus*. Within the same size class, *Pseudocalanus* nauplii were ingested at significantly lower rates by *Metridia* than were *Calanus* nauplii (Fig. 2; Wilcoxon two-sample test for prey concentrations >20 nauplii L^{-1}, $U_s = 81$, $U_{0.001[9,9]} = 74$, $P < 0.001$). Ingestion of *Calanus* increased from 4.4 (±0.4) to 6.1 (±1.6) nauplii pred-

ator^{-1} d^{-1} as prey concentration increased from 21 to 43 nauplii L^{-1}. The corresponding ingestion rates for *Pseudocalanus* were 0.6 ($\pm$0.6) and 1.7 ($\pm$0.8) nauplii predator^{-1} d^{-1}. Whereas 52% of the *Pseudocalanus* nauplii were still N2 and N1, 97% of the *Calanas* nauplii had advanced to N3. These are the first feeding stages and are likely to have much better escape responses than N2 of the same species.

For a particular predator, predation rates on *Calanus* nauplii varied with developmental stage of the prey. *Temora* ingested smaller nauplii (N3) at higher rates than larger and stronger swimming ones (N4). Average clearance rates were 0.25 $\pm$ 0.07 (for N3, $n = 6$) and 0.11 $\pm$ 0.05 L predator^{-1} d^{-1} (for N4, $n = 9$) within the range of 20–43 nauplii L^{-1}. Individual-based clearance rates on instar N3 were similar for *Centropages,* with 0.30 $\pm$ 0.12 L predator^{-1} d^{-1}, but weight-specific rates were somewhat higher in this predator ingesting up to 15.3 $\pm$ 1.1% body weight d^{-1} at 43 N3 nauplii L^{-1}, as opposed to 10.8 $\pm$ 2.5% in *Temora.*

Temperature-dependence of predation rates—The influence of temperature on predation rates differed between *C. typicus* and *M. lucens.* For *C. typicus,* ingestion and clearance rates of *Calanus* eggs increased with increasing temperature (Fig. 3a). At densities of <65 prey L^{-1}, average clearance rates per predator were 0.18 and 0.39 L d^{-1} at 6°C and 11°C, respectively. This corresponded to a Q_{10} value of 4.87. The clearance rate of naupliar prey at 6°C (Fig. 3b) was 0.35 L d^{-1}, twice the rate for eggs (0.18 L d^{-1}; Fig. 3a). However, unlike the case for eggs, ingestion rate for nauplii did not vary with temperature (ANOVA, df$_{between}$ = 1, df$_{within}$ = 16, $F = 0.41$, $P = 0.53$) and was similar to the rate for eggs at 11°C. For *M. lucens,* predation rates on equal-sized nauplii decreased significantly with increasing temperature (Fig. 3c) temperature (ANOVA for ingestion rates, df$_{between}$ = 2, df$_{within}$ = 24, $F = 10.65$, $P = 5 \times 10^{-4}$). Clearance rates were 0.44, 0.35, and 0.12 L d^{-1} at 6°C, 9°C, and 13°C, respectively.

Functional relationships between omnivorous copepods and their prey—Neither *C. typicus* nor *M. lucens* reached saturation of ingestion rates within the naturally occurring range of prey concentrations. Naupliar densities as found in a 1981 study on the southern flank of Georges Bank in April–May were between 5 and 25 prey L^{-1} in general and 50 prey L^{-1} in the thermocline at a strongly stratified site (Lough 1984). In May of 1992, Incze et al. (1996) found similar and higher densities of nauplii on the southern flank, 7–80 nauplii L^{-1} in the upper mixed layer and 22–160 nauplii L^{-1} within the thermocline.

Nonsaturating responses were also observed by Paffenhöfer and Knowles (1980) for adult females of the omnivores *Centropages furcatus* and *Temora stylifera* feeding on copepod nauplii at densities up to 120 nauplii L^{-1}. Most observations on the effect of temperature on feeding rates of calanoid copepods have shown an increase of feeding activity with increasing temperatures. The Q_{10} value of 4.87 for clearance rates by *C. typicus* measured in our study is at the top of the range of values observed for a variety of species and metabolic rates (Kiørboe et al. 1982; Hirche 1987).
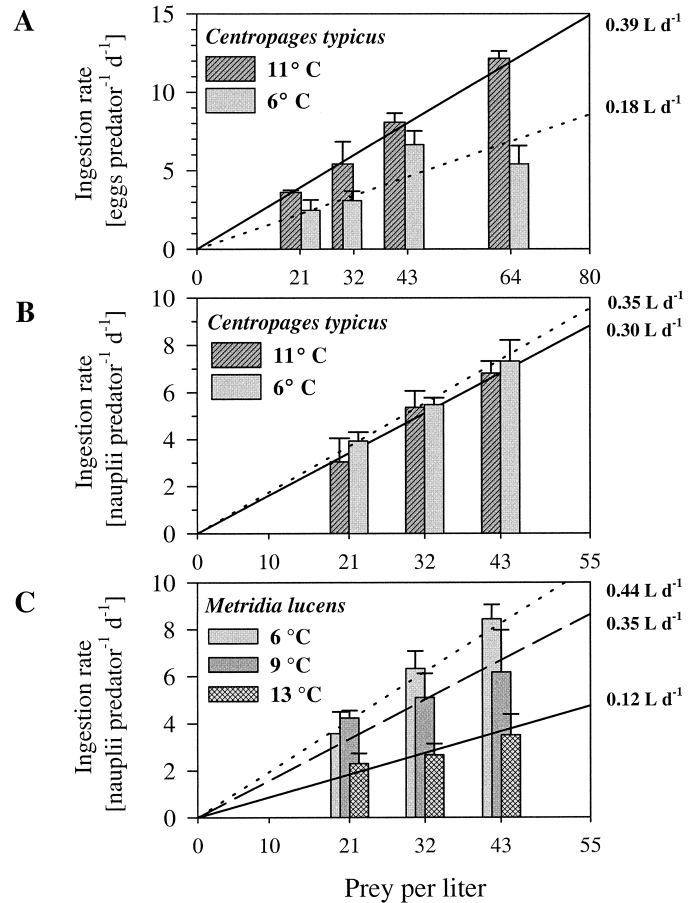

Fig. 3. Ingestion rates at two different temperatures for *C. typicus* feeding on *Calanus* eggs (A) and nauplii (B). (C) Ingestion rates at three temperatures for *M. lucens* feeding on *Calanus* nauplii. Because there was no indication for saturation of ingestion rates in the shown concentration range, linear regressions were applied (forced through the origin) and clearance rates calculated as their slopes (values on right margin). Nauplii in (B, C) were N3 (0.26–0.30 mm), except for the treatments with 32 ind L^{-1} at 6°C, which also included several N1 and N2 (0.17–0.22 mm).

For clearance rates on nauplii, a Q_{10} value cannot be calculated directly as it can for eggs, because the temperature increase also affects the swimming of the prey. The unchanged ingestion and clearance rates of *Centropages* at higher temperatures may reflect both increased motility and/or metabolism of the predator and increased motility and escape capability in the prey. Under nonsaturating prey concentrations, and under the assumption that activity of the predator is increased by the same Q_{10} effect as in the experiments with eggs, a *Centropages* individual would be expected to clear at 11°C ~ twice the volume that it clears at 6°C (Fig. 3a). With nonmotile prey, one predator individual clearing 0.35 L d^{-1} at 6°C should clear 0.76 L d^{-1} at 11°C; however, the observed average clearance rate for nauplii was only 0.30 L d^{-1} (Fig. 3b). We attribute this lower observed value to the increased activity and escape ability of the nauplii at the higher temperature.

Clearance rates for *M. lucens* decreased more than can be explained by increased naupliar escapes. Unlike for *Centro-*

pages or for the naupliar prey, the higher temperatures are disadvantageous for *M. lucens* and caused decreased feeding—that is, a $Q_{10} < 1$. The decrease in ingestion rates between 6°C and 13°C implies that the cold-water inhabiting *M. lucens* may be beyond its physiological optimum at temperatures >6–9°C. This finding is in contradiction to Batchelder and Williams (1995), who modeled the population dynamics of *M. lucens* in the North Atlantic and included a Q_{10} value for ingestion rates of 2.5. However, the function for temperature dependence used in their model was originally developed for a warm-water species (*Euterpina acutifrons;* Carlotti and Nival 1992) and may not hold for *M. lucens* on Georges Bank. *M. lucens* undergoes diel vertical migration and appears to have a broad temperature tolerance, but it tends to live in deeper waters in the southern part of its distribution area. On Georges Bank, *M. lucens* is typically abundant during the cold season in the deeper waters (Kane 1993), although during spring at nighttime, *M. lucens* can reach very high abundance at the surface (Durbin pers. comm.). Haq (1967) observed that *M. lucens* in the Gulf of Maine became sluggish, reduced their oxygen consumption, and eventually died at temperatures >14–18°C. Hirche (1987) noted that respiration rates in *M. longa* increased up to 11°C and decreased beyond that temperature. More experimental data are needed to verify whether *M. lucens* is inhibited at the higher temperatures occurring in late spring and summer on Georges Bank. We assume that there is some variability in temperature preference depending on geographical occurrence and on the general physiological state of the animals but that, in general, *Metridia* species are adapted to live in a lower temperature range than *Centropages* spp. or *T. longicornis.*

Vulnerability to a predacious copepod depends partly on the prey's body size. *Calanus* is most vulnerable to a large predacious calanoid like *Euchaeta elongata* during the first copepodite stage (Yen 1983), whereas vulnerability to the smaller predators in our study is maximal during earlier stages. With *Temora,* size-dependent vulnerability may be greater for eggs than for nauplii. In addition to relative size, the behaviors of predator and prey affect prey vulnerability. Suspension feeders are most efficient in catching nonmoving prey (Tiselius and Jonsson 1990). We found that *Calanus* eggs were more vulnerable than their nauplii to predation by *Temora,* and smaller nauplii (N3) were more vulnerable than larger nauplii (N4). *Temora* creates a strong, constant feeding current suitable for the capture of predominantly nonmoving prey (Paffenhöfer and Knowles 1980; Tiselius and Jonsson 1990). At the same time, the current may allow detection and avoidance of *Temora* by larger, motile animal prey (Paffenhöfer and Knowles 1980). This feeding behavior can explain our results for *Temora* of lower predation rates on *Calanus* nauplii, particularly on the older and stronger swimming naupliar stages.

M. lucens is an ambush predator that, according to models of foraging behavior, should be most efficient at capturing moving prey (Greene 1986; Kiørboe and Saiz 1995). In our study, *Metridia* had significantly higher ingestion rates of *Calanus* nauplii than of both *Calanus* eggs and *Pseudocalanus* nauplii. Since offered nauplii of both species were identical in size, we conclude that the different vulnerability was determined by their escape abilities. Although ~50% of the *Pseudocalanus* nauplii were one stage behind in ontogenetic development, they appeared capable of stronger swimming, compared with that of *Calanus* N3. While predation rates on nauplii may be governed by a combination of stage-specific and species-specific behavior, nauplii of *Pseudocalanus* clearly had a species-specific advantage over equal-sized *Calanus* nauplii.

The foraging behavior of *Centropages* appears intermediate between *Metridia* and *Temora,* particularly since *Centropages* can switch between two behavioral modes (Kiørboe and Saiz 1995). *Centropages* is a cruising predator and thus experiences greater encounter rates than the other two predators, particularly for slow-moving prey (Tiselius and Jonsson 1990). Tiselius and Jonsson stated that cruising predators could approach their prey with less hydrodynamic signal than stationary suspension feeders like *Temora* and may be able to capture slow nauplii more efficiently. The weight-specific ingestion rates for small nauplii confirm that the predator *Centropages* captured them most efficiently. We did not find a significant difference between ingestion rates of *Calanus* eggs and nauplii by *Centropages* at either 6°C or 11°C, which supports its position of prey preference between *Metridia* and *Temora.*

Potential impact of omnivorous copepods on recruitment of Calanus *and* Pseudocalanus—Predation by omnivorous copepods could theoretically have as significant an effect on populations of *Pseudocalanus* as it does on those of *Calanus,* despite the lower vulnerability of the former. Even moderate mortality rates affect *Pseudocalanus* strongly, because production rates of nauplii in egg-carrying calanoids like *Pseudocalanus* are low, compared with production rates of free-spawning species (Kiørboe and Sabatini 1994). Individual females of *C. finmarchicus* in the North Atlantic during May/June produce 11–62 eggs d^{-1} (Ohman and Runge 1994); on Georges Bank in April 1999 they produced 11–86 eggs d^{-1} (Runge et al. unpubl. data from cruise EN 322). For *Pseudocalanus minutus,* Corkett and McLaren (1969) estimated a total of 180 eggs to be produced during the lifetime of one female. Commonly, egg production rates in *Pseudocalanus* spp. are in the range of 1–10 eggs female^{-1} d^{-1}.

It has been suggested that larval fish are not likely to control growth rates of copepod populations, particularly on Georges Bank, because of their low abundance and slow numerical response (Cushing 1983; Davis 1984). In contrast, numerical responses in omnivorous copepods (*Centropages* spp. in the model in Davis 1984) are fast enough to allow for population control of other copepods. Davis's model suggests that the summer decline of the *Pseudocalanus* population on the Bank is due to the combined activity of several invertebrate predators but cannot be explained without the predation by omnivorous copepods. Similarly, Dong et al. (1994) attributed unexplained loss of calanoid eggs to consumption by omnivorous copepods. The abundance of *C. typicus* on Georges Bank increases over the summer, whereas that of both *C. finmarchicus* and *Pseudocalanus* spp. declines (Kane 1993). This is consistent with our experimental

results. The predation rates we have measured for *Centropages, Temora,* and *Metridia* feeding on eggs and nauplii or *Calanus* and *Pseudocalanus* indicate the capacity of these species to affect or even control population sizes of the prey species. The three omnivorous species complement each other in their preferences for prey type and water temperature and hence may not directly compete in predation on *Calanus* eggs or nauplii. We conclude that omnivorous copepods on Georges Bank have a highly significant effect on calanoid recruitment. High predation rates by omnivores may limit the available food resources in copepod eggs and nauplii for fish larvae. We consequently assume that on Georges Bank copepod populations are more likely to be limiting the growth of larval fish than larval fish are likely to limit the growth of copepod populations. In exceptional cases, copepods also prey on fish larvae themselves (Lillelund and Lasker 1971). We believe that our results will contribute to population models investigating the effect of predation by omnivorous copepods and its implications for the prey field available to larval fish.

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Turbulence avoidance: An alternate explanation of turbulence-enhanced ingestion rates in the field

Abstract—Field observations supporting the hypothesis that wind-driven mixed-layer turbulence enhances the prey ingestion by larval fish tend not to have the resolving power to distinguish an alternative hypothesis: that the fish larvae and their prey avoid the turbulence by swimming or sinking downward to the calmer waters, thereby enhancing their concentrations and increasing encounter rates of predator and prey. Here, evidence is supplied supporting the notion of the turbulence-avoidance hypothesis, and some rough calculations are made to estimate the conditions under which it might apply, how large its effect might be, and the types of organisms that might benefit from it. It is suggested that the turbulence-avoidance behavior could lead to significant increases in predator and prey concentrations below the mixed layer only hours after the onset of wind-driven mixing. Larger larval and juvenile fish are expected to benefit the most from such a behavior because they are stronger swimmers and eat larger prey, which might also exhibit the turbulence-avoidance behavior.

In the wake of Rothschild and Osborn's (1988) paper outlining how turbulence might enhance predator–prey contact rates in the ocean, numerous models have been developed exploring the effects of turbulence on encounter and ingestion rates of larval fish or copepods (MacKenzie and Leggett 1991; MacKenzie et al. 1994; Kiørboe and Saiz 1995). The encounter rate per predator, *e,* is a function of the prey concentration, *C,* and factors affecting the relative motion between the predator and prey, β (the 'behavioral kernel' with units similar to a clearance rate of cm^3 s^{-1}).

$$e = \beta C \qquad (1)$$

Most models concentrate on refining β because it contains the information about the immediate effects of turbulent motions. Here, I suggest that attention must also be paid to the effects of turbulence on the prey concentration *C,* which may undergo significant changes due to turbulence-induced behaviors in the field. It is important to test whether these latter effects outweigh the influence of turbulence-enhanced contact rates.

Testing the influence of turbulence on encounter, ingestion, and growth rates of fish larvae in the field has led to equivocal results (reviewed in MacKenzie 2000). Although several studies have found a positive effect (Sundby and Fossum 1990; Sundby et al. 1994; Dower et al. 1998), other investigations have found no or even negative effects. Laboratory experiments using fish larvae preying on copepods (MacKenzie and Kiørboe 1995; 2000) or copepods preying on diatoms or ciliates (Saiz and Kiørboe 1995) have shown enhancement of encounter rates at moderate levels of turbulence and depressed ingestion at higher levels of turbulence, although pursuit success of fish larvae was significantly depressed by all levels of turbulence. Extrapolating such results to the field, however, is problematic: the laboratory conditions do not allow the organisms a refuge from the turbulent motions and thus restrict their natural range of behaviors.

An alternative explanation for the enhanced ingestion and growth rates of copepods and larval fish in turbulent mixed layers is that the organisms actively avoid the turbulent waters by swimming downward. Such a behavior could lead to increased plankton concentrations below the mixing layer if the organisms swim into a thinner layer than they previously occupied. Such behaviorally enhanced concentrations could lead to increased encounter and ingestion rates of predators in the submixed layer region compared to the surface-mixed layer prior to the increase in mixing. If the refuge region below the mixed layer is relatively thin—say, 5 m or less—most conventional sampling schemes would not be able to distinguish it from the mixed layer, leading to the interpre-