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Predation by a carnivorous marine copepod, *Euchaeta norvegica* Boeck, on eggs and larvae of the North Atlantic cod *Gadus morhua* L.

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Abstract: The predatory behavior of a carnivorous marine copepod, *Euchaeta norvegica* Boeck, feeding on eggs and larvae of the North Atlantic cod *Gadus morhua* L. was examined. In the laboratory, adult females of *Euchaeta norvegica* did not feed on eggs. Predation rates on yolk-sac larvae and starved post-yolk-sac larvae did not vary significantly with age up to 14 days old because of little change in size or activity of the larvae. This differs from *E. elongata* Esterly, a temperate congener, which selectively feeds on middle yolk-sac-stage larvae of the Pacific hake *Merluccius productus* Ayres. The subarctic congener *Euchaeta norvegica* appeared to detect tailbeats of the cod larvae. The functional response was measured for *E. norvegica* feeding on 2–4-day-old yolk-sac larvae. Maximum ingestion was achieved at 5 larvae $\cdot l^{-1}$ with a rate of 6.3 ± 1.2 larvae $\cdot$ copepod$^{-1} \cdot$ day^{-1} or 10.5% of its body weight. Estimates of short-term feeding rates, determined from gut-evacuation curves, indicate that *E. norvegica*, when preying on cod larvae only, must feed for at least 4 h to achieve this maximum ingestion rate. Presence of copepods as alternative prey for *E. norvegica* depresses its predation rate on cod, although the ingestion of cod greatly supplements the ration consumed. Copepods fed cod larvae form black melanin-pigmented fecal pellets in which larval cod otoliths have been found. Approximately 0.5 larva was required to form one fecal pellet. The last three developmental stages of the predatory copepod were able to ingest larvae and form dark-pigmented fecal pellets. The feeding of this carnivorous marine copepod may contribute to the mortality noted in the larval stages of cod because *E. norvegica* is numerous in the center of the cod-spawning area of Skrova in the Lofoten Islands, northern Norway.

Key words: Predatory copepod; Fish larva; Recruitment; *Euchaeta norvegica*

Introduction

The assessment of recruitment of marine fishes requires an understanding of the factors which contribute to the massive mortality experienced by fish in their larval stages. Two major factors affecting survival of fish larvae are starvation and predation (Blaxter, 1969; Hunter, 1981; Rothschild *et al.*, 1982). After the larvae hatch, however, they go through a yolk-sac stage in which they are not dependent on an external food supply; the yolk prevents them from starving. Because mortality is high during this stage (Ahlstrom, 1965; Hunter, 1981) and there is no apparent increase in mortality when

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larvae begin feeding (Table 1 in May 1974; Harding *et al.*, 1978), predation, instead, must be the primary factor operating at this stage (Hunter, 1982).

Fish eggs and larvae, which are small and have limited locomotory and sensory capability, are extremely vulnerable to predation by a wide variety of fish (Hunter & Kimbrell, 1981; Webb, 1981) and invertebrates (Lillelund & Lasker, 1971; Theilacker & Lasker, 1974; Westerhagen & Rosenthal, 1976; Purcell, 1981; 1984; Bailey & Yen, 1983; Bailey, 1984; Brewer *et al.*, 1984). Although planktivorous fish can consume large quantities of larvae and eggs and thereby cause considerable mortality on the population, invertebrate predators, due to their great abundance, may exert a significant predation pressure (Kawai & Ishbasi, 1981; Purcell, 1981; 1984; Bailey & Yen, 1983; Moller, 1984). Purcell (1984) found that larval fish constituted 70–100% of the natural diet of siphonophores and one of these siphonophores accounted for 28% of mortality on the larval population. Bailey & Yen (1983) noted that in late spring, when the carnivorous copepod *Euchaeta elongata* is abundant, it has the potential to consume 100% of the yolk-sac hake larvae in an enclosed bay.

In this article, I examine predation by the large carnivorous copepod *Euchaeta norvegica* Boeck on eggs and larvae of the North Atlantic cod *Gadus morhua* L. I describe the attack response of the predator to the activity of the larvae and investigate the effects of larval age, prey concentration, and presence of alternative prey on ingestion rate by the copepod on cod-fish larvae. Short-term predation rates were estimated by monitoring fecal pellet production by the copepod when fed fish larvae. This method is described as a potentially useful means for assessing in situ predation rates of invertebrates feeding on fish larvae.

METHODS

SOURCE OF ANIMALS

Euchaeta norvegica were taken in March–June from a deep fjord, Korsfjorden, in western Norway (60°12′N:5°13′E, 690 m maximum depth). *E. norvegica* are found between 300–500 m during the day (pers. obs.) where temperatures typically range from 6 to 8 °C (Bakke & Sands, 1977). The copepods were collected with a 1-m^2 plankton trawl having a 500-μm mesh netting attached to a 4-1 cod end. The large cod end lacked drainage holes so that live specimens remained immersed in seawater. The net was towed horizontally at 500 m for 10 min followed by a slow oblique haul to 300 m when it was closed. Adult females of *E. norvegica* were sorted into 4-1 jars filled with chilled (7.5 °C) coarse-filtered (73-μm screen) seawater. Animals were brought back to the laboratory and maintained at 7.5 °C on a diet of small copepods, collected in Raunefjorden, adjacent to Korsfjorden.

Cod eggs were obtained periodically from the Marine Research Institute's Aquaculture Station at Austevoll, University of Bergen, Norway. Eggs were placed in square glass containers having 333-μm mesh at the bottom suspended in a large tank of flowing

seawater kept in a 7.5 °C cold room. Eggs hatched within 12 days. Yolk-sac larvae were not fed. Eggs and larvae of specified ages (batches were maintained separately) were sorted out for experiments. Lengths of live animals, anesthetized with *m*-aminobenzoic acid ethyl ester methanesulfonate (MS-222, CalBiochem; 8–10 drops · 50 ml^{-1} of a 2% solution), were taken using an ocular micrometer on a dissecting microscope. Dry weights of animals, dried for at least 3 days at 60 °C, were measured on a CAHN electrobalance.

PREDATION EXPERIMENTS

Each experiment, whether measuring feeding rates on a specific larval stage or at a specific larval concentration, consisted of five to eight experimental jars and two control jars. The jars were filled with 73-μm filtered seawater at 7.5 °C. A designated number of eggs or larvae were transferred from the stocks into all jars. One or two predators were similarly transferred into the experimental jars. Two predator-free jars were randomly selected as controls to monitor natural mortality in the absence of predators. The jars were filled with seawater, sealed with plastic lids, and placed on a mixing device which slowly rotates jars along its long axis at 2.4 rpm (Yen, 1982). Larvae are phototactic so that experiments were done in the dark to maintain an even distribution. Also, *E. elongata*, a congener, is known to feed only in the dark (Yen, 1982). After 24 h, predators were removed and the number of live larvae and carcasses were counted. The difference between the number of larvae in the controls minus the number of live larvae and carcasses (90% intact) in the experimental containers gave daily ingestion rates (I) for the predators. Attack rates were determined as in Bailey & Yen (1983) from, m, the instantaneous rate of handling and mortality in the absence of predators, as determined from the controls using the equation:

$$C = C_0 e^{-mt},$$

where C is the number of larvae alive in controls after time t (24 h) with initial concentrations of C_0, and from, p, the instantaneous predation rate, as determined in the experimental jars using the equation:

$$N = N_0 e^{-(m+p)t},$$

where N is the number of larvae alive after time t (24 h) with initial concentrations of N_0. The number of larvae attacked, A, was thus:

$$A = pN_0[(1 - e^{-(m+p)t}) \cdot (m + p)^{-1}].$$

This differs from the number of larvae ingested (I) because it includes those larvae that were killed by attacks but not completely ingested. Mortality in the absence of predators

(0–15%) was always less than predator mortality. Ingestion efficiency (E_I) was computed as follows:

$$E_I = 1 - [(A - I) \cdot A^{-1}],$$

where A is the attack rate and I is the ingestion rate.

EFFECT OF DEVELOPMENTAL STAGE

To test the effect of larval stage on ingestion rates, at least two stages were fed to the predator simultaneously in separate experiments. All ingestion rates were measured at a prey concentration of 40 larvae in 4 l of filtered seawater with one to two predators per jar. Eggs and yolk-sac larvae (up to 9 days old) and 14-day-old starved first-feeding larvae were cultured in the laboratory. Older cod larvae, 20–30 days old, were obtained from fish ponds and cultures maintained at the Marine Research Institute's Aquaculture Station at Austevoll. These large larvae were fed to *E. norvegica* at 5 larvae $\cdot l^{-1}$.

EFFECT OF LARVAL CONCENTRATION

For experiments testing the effect of larval concentration on ingestion rates, four concentrations of 2–4-day-old larvae were tested simultaneously in two separate experiments with four to eight replicates per concentration. In the first set the concentrations were 2, 5, 10, and 20 $\cdot l^{-1}$, and in the second set 1, 5, 10, and 30 $\cdot l^{-1}$. One-liter jars were used for the higher concentrations (10, 20, and 30 $\cdot l^{-1}$) and 4-l jars for the lower concentrations (1, 2, and 5 $\cdot l^{-1}$) to keep the total number of larvae available $\cdot$ jar^{-1} at similar levels.

On one occasion, live larvae were removed from a ripe female *Sebastes* and fed to *Euchaeta norvegica* at 10 $\cdot l^{-1}$.

SENSORY ASPECTS

To test the effect of prey movement on predator ingestion rates, heat-killed larvae were offered to *E. norvegica*. To determine if the first antennae are needed for prey detection, feeding rates on cod larvae by *E. norvegica* with and without antennae were measured. Antennae were gently pinched off adult females of *E. norvegica* that had been anesthetized. These copepods survived in the laboratory for >2 wk without their antennae.

INGESTION AND EGESTION

The daily ingestion rates estimated in laboratory feeding experiments were compared to the hourly ingestion rates estimated by monitoring the rate of gut evacuation of copepods fed fish larvae, assuming that the rate of egestion is equivalent to the rate of ingestion. Gut-evacuation rates of *E. norvegica* were determined by prefeeding copepods overnight on 2–4-day-old cod larvae. Copepods that had consumed larvae, obvious by

the darkly pigmented distended guts, were sorted individually into 30-ml containers of filtered seawater. The number of fecal pellets produced at 15–60-min intervals were recorded until the gut was completely empty. These data described the gut-evacuation curves. The hourly ingestion rate (I) was computed from the following equation:

$I = SRt$ (Doble & Eggers, 1978; Elliott & Persson, 1978),

where S = weight of stomach contents which, in this case, was not weight but the total number of fecal pellets evacuated multiplied by a conversion factor (number of larvae ingested · fecal pellet egested^{-1}); R = the instantaneous gut-evacuation rate derived from the exponent of an exponential decay equation, $N = N_0 e^{-Rt}$, fitted to the gut-evacuation curves and t = the duration, which should not be applied for periods longer than the gut-evacuation time due to possible variations in feeding rates over longer periods.

The conversion factor, or number of larvae consumed · fecal pellet egested^{-1}, was ascertained by offering *E. norvegica* a known number of larvae of a certain stage in 4-l experimental jars containing filtered seawater, larvae at 10 · l^{-1}, and predators. After 24 h of feeding, the copepods were transferred into jars of clean filtered seawater and allowed to empty their gut over the next 12 h. The number of larvae in the experimental jars were counted and compared with the number in the controls to determine the number of larvae eaten. The number of fecal pellets defecated in the first 24 h plus the number of pellets defecated in the next 12 h after removing the copepods from their food, were summed. The ratio of the number of larvae consumed to the total number of fecal pellets egested was computed. The copepods do not reingest their fecal pellets.

RESULTS

EFFECTS OF DEVELOPMENTAL STAGE AND DENSITY ON PREDATION RATES

Adult females of *Euchaeta norvegica* (3 mg dry weight, 5.7 mm prosome length) consumed only 0.75 ± 0.79 (95% CI, unless otherwise stated) cod eggs · preda-

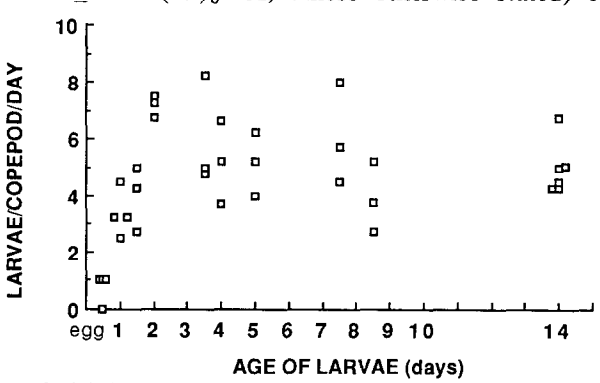

Fig. 1. Ingestion rates of adult females of *Euchaeta norvegica* fed eggs and various stages of the larvae of *Gadus morhua* at a prey concentration of 10 larvae · l^{-1} in 4-l containers. Yolk-sac stage lasts 9 days at 7–9 °C.

tor^{-1} · day^{-1} (Fig. 1). The rates were slightly higher on 1-day-old larvae (4.0 ± 3.0 larvae · predator^{-1} · day^{-1} at 10 larvae · l^{-1}). After the larvae were older than 2 days, feeding rates of 6.2 ± 0.7 larvae · predator^{-1} · day^{-1} did not vary for the yolk-sac stages (2–9 day) of the larvae. The rates were slightly reduced to 5.0 ± 1.0 larvae · predator^{-1} · day^{-1} if copepods were fed the starved first-feeding larvae (14 days old). Cod larvae did not vary significantly in length, ranging from 3.7 to 4.5 mm. The average length of 8-day-old larvae was 4.05 mm ± 4.5% (coefficient of variation) and widths between tail and head ranged between 350 and 775 μm. The swimming speeds, however, do change (Fig. 2) where an increase in activity is noted at 2–3 days when the larval eye becomes functional.

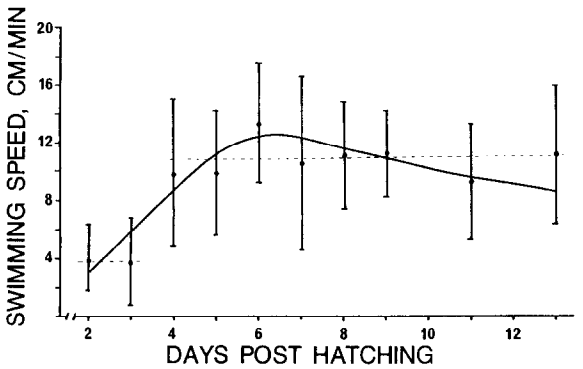

Fig. 2. Swimming speeds of various stages of the larvae of *Gadus morhua*. Solid line represents data of S. Tilseth (unpubl.) showing a peak in activity at 6 days while the dashed line represents an alternative interpretation of his data indicating increased activity at 2–3 days when the larval eye becomes functional.

Feeding rates increased with increasing prey concentration (Fig. 3). At 1 larva · l^{-1}, mean ingestion rates were 1.5 ± 2.0 larvae · predator^{-1} · day^{-1}. At 2 · l^{-1}, rates increased to 3.6 ± 1.4 larvae · predator^{-1} · day^{-1}. These rates are three times those measured by Bailey (1984) for *E. norvegica* feeding on yolk-sac cod larvae at a

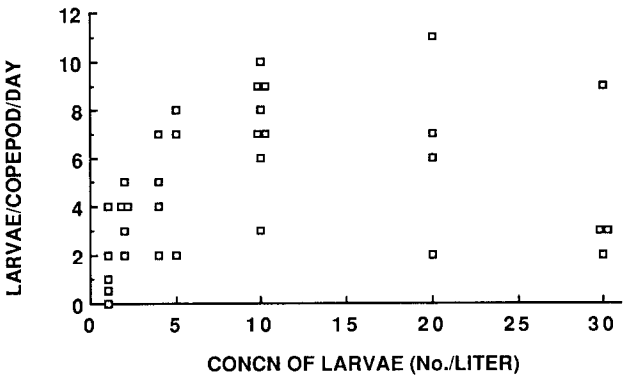

Fig. 3. Ingestion rates of adult females of *Euchaeta norvegica* fed varying concentrations of 2–4-day-old yolk-sac larvae of *Gadus morhua*.

concentration of 3 larvae $\cdot l^{-1}$, possibly because the Norwegian type is slightly larger than the type found in the Scottish lochs. At 5, 10, and 20 $\cdot l^{-1}$, rates were not significantly different (overlapping 95% CI) and averaged 6.3 $\pm$ 1.2 larvae predator$^{-1} \cdot$ day^{-1}. At this maximum feeding rate, *E. norvegica* consumed the equivalent of 10.5% of the body weight $\cdot$ day^{-1} assuming the dry weight of a cod larva is 50 μg (Ellertsen *et al.*, 1980). At 30 $\cdot l^{-1}$, there was a slight depression in the feeding rate to 3.6 $\pm$ 3.6 larvae $\cdot$ predator$^{-1} \cdot$ day^{-1}.

E_I (Fig. 4) was high at concentrations $< 10 \cdot l^{-1}$ (0.69 $\pm$ 0.12) and declined at higher concentrations of 20–30 prey $\cdot l^{-1}$ (0.34 $\pm$ 0.31). When feeding was inefficient at the higher prey concentrations, the prey parts remaining were usually the anterior portion or eyes of the larvae. Tails, apparently, were consumed first.

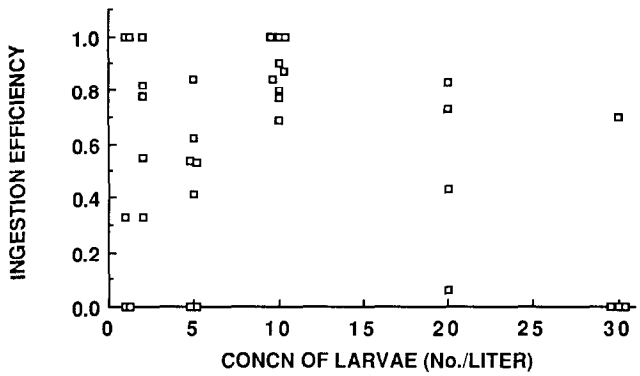

Fig. 4. E_I of adult females of *Euchaeta norvegica* feeding at varying concentrations of 2–4-day-old yolk-sac larvae of *Gadus morhua*.

Euchaeta norvegica cannot consume healthy 20–30-day-old juvenile cod (7–30 mm) but, if the larvae were weakened (starved or injured in collection), the copepod did kill and partially consume them. The fecal pellets produced by the predators consuming these older larvae were lighter in color due to the reduced amount of melanin $\cdot$ amount of fish ingested^{-1}. *E. norvegica* also did not capture large *Sebastes* larvae (6.58 $\times$ 1.40 mm).

SENSORY ASPECTS

Euchaeta norvegica did not feed on heat-killed larvae (Table I). Prey movement appears necessary for prey detection and predator–prey encounters. *E. norvegica* without their first antennae fed at rates five times lower than predators with antennae. The antennae apparently were needed for detecting prey movement in water.

MIXED-PREY EXPERIMENTS

Feeding rates in a mixed-prey experiment were compared with rates on single species (Table II). The rates on cod and preferred copepod prey *Pseudocalanus* sp. were high

in single-species experiments. When offered both cod and *Pseudocalanus* together with two other copepod prey, the rates were reduced on both cod and *Pseudocalanus* sp. The predation rates on each prey type in mixed-prey experiments were 42–79% the rates achieved in single-species experiments. The total dry weight ingested in the mixed-prey experiment (319 μg) was slightly less than the amount consumed as cod only in the single-species experiments, but much more than that ingested as only copepods.

TABLE I

Effect of heat-killing of prey or removal of first antennae of predator on mean predation rates ($\pm$ 95% CI) of adult females of *Euchaeta norvegica* on larvae of *Gadus morhua* at 15 larvae $\cdot$ l^{-1}.

Treatment	Response (number $\cdot$ predator^{-1} $\cdot$ day^{-1})
Live larvae	6.2 $\pm$ 3.7 fecal pellets egested
Heat-killed larvae	0.2 $\pm$ 0.6 fecal pellets egested
With antennae	10.75 $\pm$ 2.39 larvae ingested
Without antennae	1.80 $\pm$ 2.39 larvae ingested

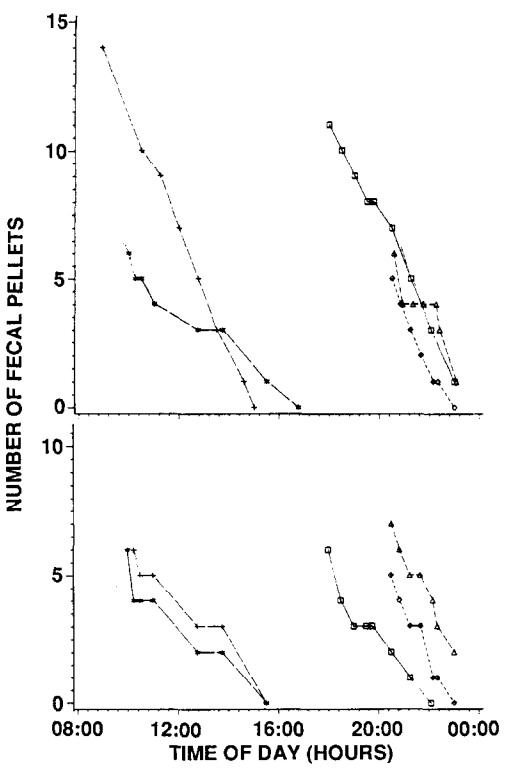

Fig. 5. Gut-evacuation curves at the specified time of day (x axis) of individual adult females of *Euchaeta norvegica* fed 2–4-day-old yolk-sac larvae of *Gadus morhua* where initial values are the total number of fecal pellets egested. To minimize overlap the data have been plotted on two separate graphs.

TABLE II

Predation rates (amount ingested · predator^{-1} · day^{-1}) of *Euchaeta norvegica* in single, compared with mixed-prey experiments (± 95% CI): the prey consisted of *Gadus morhua* larvae and adult females of three copepod species, *Temora longicornis* O.F. Müller (TEM), *Acartia clausii* Giesbrecht (ACA) and *Pseudocalanus* sp. (PSE): the concentration of each prey in both the single-species and mixed-prey experiments was 10 · l^{-1} in 4-l experimental jars.

Species	Length (μm)	Number of prey ingested		Dry weight (DW; μg)	DW ingested		Mixed/single
		Single	Mixed		Single	Mixed	
TEM	767	3.25	2.06 ± 1.31	12.5	40.6	25.8	0.64
ACA	1003	4.00	3.17 ± 3.19	8.7	34.8	27.6	0.79
PSE	982	8.75	5.54 ± 1.40	17.8	155.7	98.6	0.63
Cod	3692	8.25	3.34 ± 1.43	50.0	412.5	167.0	0.42
						Sum = 319.0	

TABLE III

Size (± coefficient of variation) of fecal pellets of three developmental stages of *Euchaeta norvegica* fed 2–4-day-old larvae of *Gadus morhua*.

E. norvegica stage	Prosome length (μm)	Fecal pellet size (μm)		Volume × 10^{-6} μm^3 ($\pi r^2 h$)
		Length (h)	Width ($2r$)	
CVI female	5668.5 ± 1.7%	546.7 ± 21.4%	148.1 ± 15.8%	9.4
CV	4200.0 ± 3.7%	441.4 ± 20.4%	106.7 ± 16.8%	3.9
CIV	3010.0 ± 8.2%	287.1 ± 24.0%	69.8 ± 30.0%	1.1

ESTIMATION OF PREDATION RATES BASED ON FECAL PELLET PRODUCTION

Euchaeta norvegica can defecate a maximum of 14 fecal pellets, although on average 6.58 ± 1.92 ($n = 12$) pellets are produced (Fig. 5). If one pellet has a volume of 9.4×10^{-6} μm^3 (Table III), then 14 fecal pellets occupy a gut volume of 131.6×10^{-6} μm^3. The fecal pellets were very black with melanin pigments which are found in the skin and eyes of cod larvae. There was no significant difference in the size of fecal pellets produced by the adult female copepod fed different stages of larvae. Some fecal pellets, analyzed microscopically, contained larval otoliths. No lenses were found. On several occasions, specimens of *E. norvegica* were found in the fjord with dark guts, indicating natural consumption of darkly pigmented prey, possibly including fish larvae. In the laboratory, the last three developmental copepodid (C) stages of *E. norvegica*, CIV, CV, and CVI, could eat cod larvae, evident by the presence of black pigment in the gut seen through their translucent exoskeleton and the production of black fecal pellets (Table III). Assuming fecal pellets to be cylindrical, fecal pellet volumes for adult copepods were 8.5 times larger than CIV pellets and 2.4 times larger than CV pellets.

The number of larvae ingested · fecal pellet egested^{-1} remained a constant with larval stage: 0.564 ± 0.37 cod ingested · fecal pellet egested^{-1} ($n = 29$). Therefore, an average copepod that evacuates 6.5 fecal pellets has ingested 3.7 larvae to fill its gut. The instantaneous gut-evacuation rate was 0.429 ± 0.110 (Table IV) where the r values of

TABLE IV

In situ rates and fecal pellet production by adult females of *Euchaeta norvegica* fed 2–4-day-old larvae of *Gadus morhua*: the 95% CI values are given.

Number of fecal pellets	6–7
Conversion factor (larvae ingested · pellet egested)	0.56 ± 0.37
Instantaneous gut evacuation rate (h^{-1})	0.429 ± 0.110
Ingestion rate (larvae · h^{-1})	1.56
Max. ingestion rate in laboratory (larvae · predator^{-1} · day^{-1})	6.3 ± 1.2
Feeding interval (h)	4

the exponential decline in gut contents over time (see gut-evacuation curves in Fig. 5) averaged 0.942 ± 0.032. The ingestion rate can be computed as the product of the number of pellets times the conversion factor (larvae · pellet^{-1}) and the evacuation time, assuming the rate of ingestion equals the rate of egestion. The resulting ingestion rate was 1.56 larvae · h^{-1}. Therefore, to achieve the maximum feeding rate of 6.3 larvae · predator^{-1} · day^{-1}, each predator must feed for 4 h.

DISCUSSION

Euchaeta norvegica is numerous within the center of the cod-spawning area of Skrova in the Lofoten Islands off northern Norway (Wiborg, 1954). It is one of several potential invertebrate predators of fish larvae, including euphausiids, amphipods, ctenophores, and medusae (B. Ellertsen, pers. comm.). Because the last three developmental stages of *E. norvegica* can actively ingest yolk-sac larvae of *Gadus morhua*, this carnivorous copepod may represent an important source of mortality on cod larvae, thus affecting recruitment in this fish population.

Typically, *Euchaeta norvegica* ingests copepods (Lowndes, 1935), preferring those having prosome lengths of 900 μm (Yen, in prep.), which is $\approx 70\%$ the length of the second basipodal segment of the predatory copepod's maxillipedal feeding appendage. Copepod prey are clasped parallel to the basipod (Yen, 1985). When offered cod larvae which are nearly the same length as the copepod, this predatory copepod will actively ingest them. *E. norvegica* is able to grasp the larva perpendicular to its basipod whose length is similar to the width of the larva. When *E. norvegica* are offered both cod larvae and copepods, feeding rates on cod were reduced. *E. norvegica* can digest cod faster than copepods because its gut-evacuation rate when fed cod was twice as fast as when fed copepods (Yen, in prep.). Fish larvae are easier to digest because they lack a cuticular skeleton.

E. norvegica exhibited density-dependent predation rates on cod larvae. Rates were saturated at a low prey density of 5 larvae $\cdot l^{-1}$. This predator achieves the same maximum ration on cod larvae as on copepods (Yen, in prep.), which is 10% of its body weight $\cdot$ day^{-1}. A temperate congener, *E. elongata*, also consumed a maximum of 10% of its body weight $\cdot$ day^{-1} of hake larvae (Bailey & Yen, 1983). At the observed hourly feeding rate of *E. norvegica*, derived from laboratory measured gut-evacuation rates, this larger congener could achieve its maximum daily ration on cod within 4 h.

Tactile nonvisual predators, like *E. norvegica*, respond to the size and movement of its prey, two important factors influencing predation by invertebrates on fish larvae (Bailey, 1984; Bailey & Batty, 1984). Larval fish movements vary depending on the amount of time spent beating their tails and resting and, as the larvae mature, the behavior changes to beating and gliding (Hunter, 1981). This tail-beat attracts the attention of the cruising *E. norvegica* which actively grasps its prey and ingests it tail first, often leaving the head portion behind. The first antennae, the location of mechanoreceptors, were needed for detecting prey movement. The lack of predation on eggs and dead larvae is due to the lack of movement detectable by the predatory copepod. At high concentrations of larval cod, E_I and ingestion rate declined, possibly due to confusion of the predator by the presence of too many prey. There was very little change in feeding rates on yolk-sac larvae older than 2 days. Therefore, for the 9 days that cod spend as yolk-sac larvae, each stage is equally vulnerable to the nonselective predation by *E. norvegica*. A slight increase in feeding rates may be noted at ≈ 2–3 days. At this point, the eyes of the larvae become functional leading to increased activity which make the larvae more easily detected by the predator.

The nonselective feeding pattern of *E. norvegica* on yolk-sac cod larvae is in contrast with the behavior of the temperate congener, *E. elongata*. *E. elongata* showed a marked stage-specific selective feeding pressure on the middle yolk-sac larvae of *Merluccius productus* (Bailey & Yen, 1983). Unlike cod, hake larvae undergo a substantial change in activity and escape ability as they progress through the larval stages, resulting in this variable response. Another predatory copepod, *Labidocera trispinosa*, shows a linear decline in feeding rate with the age of its larval anchovy prey (Lillelund & Lasker, 1971). This is related to the exponential increase in avoidance capabilities as anchovy larvae age and grow in length (P. W. Webb, quoted in Hunter, 1981). Another way for a larval fish to avoid capture by small invertebrate predators is to become large, as evolved in the genus *Sebastes*, which bear live young that are large and mobile. The larvae were very capable of evading capture by *Euchaeta norvegica*. These differences in swimming behavior and escape ability as a function of size and maturation state of various species of larval fish elicited distinct patterns of predation by several nonvisual tactile crustacean predators. To understand the causes of larval mortality better, a thorough understanding of their early-life history is needed.

Copepods that have ingested cod larvae have darkly pigmented gut contents, distinct through the translucent exoskeleton. *E. norvegica* with black-pigmented material in the gut have been collected from the sea. The melanin, which is derived from pigments in the skin and eyes of the larval cod, may be a possible tracer of fish remains in the gut of invertebrate predators which macerate their prey because melanin was found in the fecal pellets. Larval otoliths also have been found in these fecal pellets. The fecal pellet method outlined here may be useful for assessing predation rates in nature. Sediment traps could be employed to monitor larval consumption by invertebrate predators excreting negatively buoyant fecal pellets. A method, however, is needed to relate the amount of melanin in fish larvae to that found in the fecal pellets of invertebrates.

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