

Fine-scale observations of the predatory behaviour of the carnivorous copepod *Paraeuchaeta norvegica* and the escape responses of their ichthyoplankton prey, Atlantic cod (*Gadus morhua*)

Howard I. Browman · Jeannette Yen ·
David M. Fields · Jean-François St-Pierre ·
Anne Berit Skiftesvik

Received: 26 April 2011 / Accepted: 19 July 2011 / Published online: 6 August 2011
© Springer-Verlag 2011

Abstract *Paraeuchaeta norvegica* (8.5 mm total length) and yolk-sac stage Atlantic cod larvae (4 mm total length) (*Gadus morhua*) larvae were observed in aquaria (3 l of water) using silhouette video photography. This allowed direct observations (and quantitative measurement) of predator–prey interactions between these two species in 3-dimensions. Tail beats, used by cod larvae to propel themselves through the viscous fluid environment, also generate signals detectable by mechanoreceptive copepod predators. When the prey is close enough for detection and successful capture (approximately half a body-length), the copepod launches an extremely rapid high Reynolds

number attack, grabbing the larva around its midsection. While capture itself takes place in milliseconds, minutes are required to subdue and completely ingest a cod larva. The behavioural observations are used to estimate the hydrodynamic signal strength of the cod larva's tail beats and the copepod's perceptive field for larval fish prey. Cod larvae are more sensitive to fluid velocity than *P. norvegica* and also appear capable of distinguishing between the signal generated by a swimming and an attacking copepod. However, the copepod can lunge at much faster velocities than a yolk-sac cod larva can escape, leading to the larva's capture. These observations can serve as input to the predator–prey component of ecosystem models intended to assess the impact of *P. norvegica* on cod larvae.

Communicated by U. Sommer.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-011-1763-y) contains supplementary material, which is available to authorized users.

H. I. Browman · J.-F. St-Pierre
Department of Fisheries and Oceans Canada, Maurice
Lamontagne Institute, Mont-Joli, QC G5H 3Z4, Canada

H. I. Browman (✉) · D. M. Fields · A. B. Skiftesvik
Institute of Marine Research, Austevoll Research Station,
5392 Storebø, Norway
e-mail: howard.browman@imr.no

Present Address:

H. I. Browman
Institute of Marine Research, Austevoll Research Station,
5392 Storebø, Norway

J. Yen
School of Biology, Georgia Institute of Technology,
310 Ferst Drive, Atlanta, GA 30332, USA

D. M. Fields
Bigelow Laboratory for Ocean Sciences,
West Boothbay Harbor, ME 04575, USA

Introduction

Traditional aquatic food webs place plankton at the base of the food chain, often with fish as the top predator. However, as larvae, fishes represent an important yet transient member of the plankton. At this small size, fish larvae are subject to predation by other members of the plankton, including copepods (Bailey and Houde 1989). For example, the calanoid copepods *Anomalocera ornata* and *Centropages typicus* feed on the yolk-sac stage larvae of Atlantic menhaden (*Brevoortia tyrannus*) and gulf menhaden (*B. patronus*) (Turner et al. 1985). Small (<7.5 mm) larvae of the Pacific sardine (*Sardinops sagax*) are eaten by the cyclopoid copepods *Corycaeus trickicus* and *C. japonicus* (García and Alejandre 1995). The calanoid copepod *Paraeuchaeta elongata* eats yolk-sac stage Pacific hake (*Merluccius productus*) larvae (Bailey and Yen 1983). *Paraeuchaeta norvegica* prey upon various copepods as well as the yolk-sac stages of flounder (*Platichthys flesus*),

plaice (*Pleuronectes platessa*), herring (*Clupea harengus*), turbot (*Scophthalmus maximus*) and Atlantic cod (*Gadus morhua*, henceforth, simply cod) (Bailey and Yen 1983; Bailey 1984; Yen 1987).

Although there have been both field and laboratory studies of the diet and predation rates of *Paraeuchaeta norvegica* feeding on copepods and fish larvae (Bailey and Yen 1983; Bailey 1984; Yen 1987; Tiselius et al. 1997; Olsen et al. 2000; Fleddum et al. 2001; Skarra and Kaartvedt 2003), no fine-scale observations of their predatory behaviour exist. Copepods use mechanoreception to detect fluid disturbances released by potential predators and prey (Fields and Yen 2002). Similarly, the lateral line system of juvenile and adult fish detect fluid motion to identify potential prey items, orient within a school and avoid predators (Montgomery et al. 1994; Rapo et al. 2009). In this study, we videotaped and quantitatively analysed the predator–prey interactions of *P. norvegica* feeding on yolk-sac stage cod larvae. Empirical observations, such as this, are essential for the accurate parameterization of ecosystem models that include copepods as predators on fish larvae.

Materials and methods

Larval fish culture and copepod collection

Cod larvae were reared from eggs spawned from broodstock at the Department of Fisheries and Oceans Canada's Maurice Lamontagne Institute in Mont-Joli, Québec. Larvae 4 days post hatch (dph)—~4 mm total length—were used in the experiments. Observations were restricted to this size and developmental stage because *Paraeuchaeta norvegica* consume yolk-sac stage cod larvae but do not eat eggs or older larvae (Bailey and Yen 1983; Bailey 1984; Yen 1987).

Adult female *Paraeuchaeta norvegica*—~8 mm body length—were captured at station RIKI01 (48°40.00N 68°35.00W, at a depth of 340 m) using a 1-m vertical net with a 333- μ m mesh. The net was hauled from a depth of 350 m to the surface at a speed of 0.5 m s⁻¹ or less. The net's cod end was partially blocked to minimize damage to the animals. The contents of the cod end was gently poured into 4-l jars filled with filtered sea water and maintained at 4°C and 28 PSU. Upon arrival in the laboratory, animals were sorted and kept at 6°C until the experiments. *P. norvegica* were fed on brine shrimp and small copepods until 24 h before the experiments.

Behavioural observations

Behavioural observations were made in glass aquaria (15 × 15 × 15 cm) surrounded by black contact paper (except for 10 cm openings that allowed viewing from the

sides) using a 3-dimensional silhouette imaging system (described in detail by Browman et al. 2003). Cod larvae ($n = 50$) and adult females of *Paraeuchaeta norvegica* ($n = 20$) were placed into experimental vessels in 3 l of filtered seawater (the same water in which the copepods and the cod larvae were maintained and at the same temperature). Interactions between free-swimming larvae and either free-swimming copepods or tethered predatory copepods were recorded on S-VHS videotape. The synchronously recorded orthogonal views allow exact determination of the 3-dimensional positions of targets (copepods and cod larvae), which appear in both fields of view simultaneously.

In the geographic region of this study, eggs and yolk-sac larvae of cod are typically distributed in the upper 100 m of the water column (Ouellet 1997). A significant but variable percentage of adult female *Paraeuchaeta norvegica* undertake diel vertical migrations, swimming into the upper 100 m of the water column at night to feed (Yen 1985; Vestheim et al. 2005; Tønnesson et al. 2006). Since yolk-sac stage cod and *P. norvegica* will most commonly overlap spatiotemporally at night, all observations were made in the dark (the light source used to generate the silhouette images was a far-red LED run at an intensity far below the sensitivity threshold of yolk-sac cod or *P. norvegica*). In any case, the feeding rate of *P. norvegica* is unaffected by light (Olsen et al. 2000).

Quantitative kinematic analyses

Every 1/30th of a second, the 3-dimensional positions were determined by tracking the 2-D positions (X–Z and Y–Z) of plankton movement in paired orthogonal 2-D projections of the same individual using TRAKFISH software. From the 3-dimensional positional information, distances, velocities and angles were then calculated using ANAPATHS software (see Browman et al. 2003 for software details). An encounter was defined as any interaction that resulted in a behavioural response in either the predator (*Paraeuchaeta norvegica*) or the prey (cod larvae). These encounters were further characterized as follows: Detection of *P. norvegica* by cod larvae was defined (a posteriori) as the instant when the larva exhibited an escape reaction in response to *P. norvegica*. Detection of cod larvae by *P. norvegica* was defined (a posteriori) as the instant when the copepod either changed its orientation towards the potential prey item or stopped moving its cephalic appendages in close proximity of a cod larva. Although this most likely underestimates the true physiological detection distance, it nonetheless provides a conservative measure of the behavioural threshold for detection. Signal strength was estimated as a direct translation of animal movement to water movement. A $1/r^3$ decline in water flow speed was used to estimate signal strength at the

location of the detector (Kalmijn 1988). The escape speeds of cod larvae in response to a swimming predator and an attacking predator were compared using a two-tailed *t* test. Characteristics of the prey escape response were analysed by linear regression using Sigmapstat 3.5. An alpha level of 0.05 was used to determine significance in all statistical tests.

Results

Behaviour

Swimming movements of *Paraeuchaeta norvegica*

Adult females of the subarctic carnivorous copepod, *Paraeuchaeta norvegica*, had total lengths of ~ 8.5 mm ($n = 6$). At 6°C , *P. norvegica* swam at an average speed of 13.6 mm s^{-1} ($\text{SD} = 5.9$, $n = 42$) often following a spiral trajectory (Fig. 1; see supplemental video A). During an attack or an escape response, *P. norvegica* accelerated to speeds up to 48.9 mm s^{-1} (average = 34.4 , $\text{SD} = 17.4$, $n = 16$) and reached Reynolds numbers ($\text{Re}\#$) of ~ 352 [see supplemental videos B (attack) and C (escape)].

Swimming movements of cod larvae

Yolk-sac larvae (4 dph) of cod were about 4 mm in length and 1 mm in width. Although they were stationary most of

the time, cod larvae beat their tails intermittently generating swimming bursts that transported them over short distances. When disturbed, cod larvae swam at a maximum speed of 15.7 mm s^{-1} ($\text{SD} = 7.9$, $n = 52$).

Encounters between *Paraeuchaeta norvegica* and cod larvae

Encounters occurred over a wide range of lateral and dorsal/ventral angles relative to the body axis of *Paraeuchaeta norvegica*. (Fig. 2). Most of the encounters ($n = 71$) triggered an escape response by cod larvae ($n = 54$). *P. norvegica* detected ($n = 15$) and attacked ($n = 9$) numerous prey during these encounters. Overall, the encounter angles showed no obvious left/right bias. Most of the encounters occurred anterior of the copepods. Approximately 90% of all encounters occurred within $\pm 90^\circ$ of the head of the copepod. Dorsal/ventral trajectories (Fig. 2) indicated that encounters were more frequent ventrally than dorsally. The highest number of attacks and escapes occurred within a relatively narrow (up to 30°) ventral area of *P. norvegica*'s body axis.

Predatory behaviour of *Paraeuchaeta norvegica*

Adult female *Paraeuchaeta norvegica* captured and ingested cod larvae. Attacks only occurred in response to a tail beat by a cod larva—immobile larvae elicited no

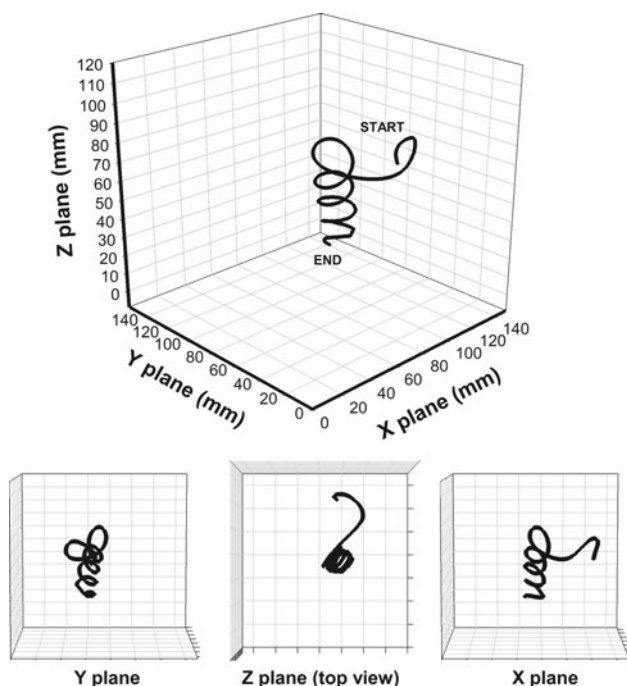


Fig. 1 Example of a spiral swimming trajectory of adult female *Paraeuchaeta norvegica* (also see Supplemental material, video A)

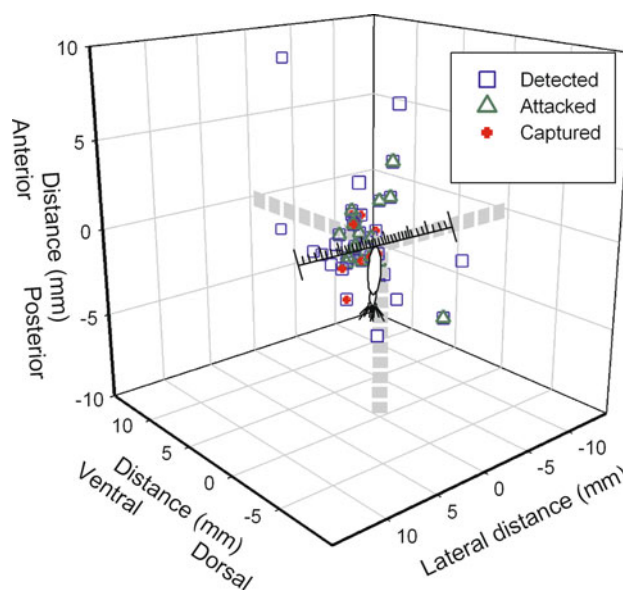


Fig. 2 Perceptual field of adult female *Paraeuchaeta norvegica* showing the locations of yolk-sac (4 dph) larvae of Atlantic cod (*Gadus morhua*) that elicited a predatory response (detection followed by attack). The grey square hash marks represent the predator's orientation. The tick marks on the copepod's antennae represent the sensory setae

response of any kind. During an attack, the antennules of *P. norvegica* were retracted posteriorly along the side of the body, and at the same time, the urosome flexed anteriorly. These opposing appendage movements are necessary to maintain position in a low Re fluid regime. To propel the predatory copepod towards its prey, the swimming legs are deployed posteriorly in a rapid metachronal sequence, and at the same time, the urosome is flexed posteriorly constraining the accelerated fluid into a narrow and focused jet. The thrust generated by the jet that is formed by the simultaneous posteriorly directed movements of all these appendages moves the predator rapidly forward along a slightly ventral trajectory, propelling the predator to maximum speeds of 48.9 mm s^{-1} (average speeds of 34.4 mm s^{-1} $SD = 17.4$, $n = 16$) and average distances of 3.0 mm ($SD = 1.1$, $n = 11$). As the predatory copepod lunged forward, the maxillipeds opened and extended forward to grasp the prey. The speed of the lunge accompanied by maxilliped extension at $Re > 300$ thins the boundary layer so that capture is possible. All of the attacks observed were successfully completed in approximately 30–40 ms. Typically, the copepod grabbed the cod larva at its midsection, manoeuvred the head into its mandibles and periodically adjusted the grip of its maxillipeds. The process of larval consumption took approximately 8.5 min (measured as the time from the instant that a larva was captured until no part of it could be observed in the copepod's mouth parts).

Perceptual fields

3-D perceptual field of Paraeuchaeta norvegica to cod larvae

The maximum detection distance for *Paraeuchaeta norvegica* feeding on cod larvae was 16.6 mm (Table 1) with an average distance of 4.2 mm ($SD = 3.2$, $n = 35$; Fig. 2). An attack only occurred in response to the larval fish initiating an escape reaction. Of the 35 detection events observed, 69% resulted in an attack response. The maximum attack distance was 6.0 mm with an average distance of 3.2 mm ($SD = 1.2$, $n = 24$). Only 10% of the attacks (6% of detected prey) resulted in a successful capture. The maximum capture distance was 3.8 mm with an average distance of 2.6 mm ($SD = 1.3$, $n = 2$). The size and geometry of the perception volume was estimated from the maximum distances found for *P. norvegica*'s detections, attacks and captures of cod larvae (Table 1; Fig. 3). There were no obvious bilateral asymmetries (Fig. 3a). The maximum distance associated with each behaviour occurred anterior (Fig. 3a) and ventral (Fig. 3b) to the animal's forward-directed longitudinal body axis. The dorso-ventral asymmetry in the detection volume is clearly seen in lateral

Table 1 Dimensions of the perceptual field of adult female *Paraeuchaeta norvegica* feeding on yolk-sac (4 dph) larvae of Atlantic cod (*Gadus morhua*)

	Maximum distance (mm)
Detection	
3-dimensional distance	16.6
Ventral	<i>14.1</i>
Dorsal	<i>4.9</i>
Lateral	<i>4.5</i>
Anterior	<i>8.2</i>
Posterior	<i>5.6</i>
Attack	
3-dimensional distance	6.0
Ventral	<i>3.5</i>
Dorsal	<i>4.9</i>
Lateral	<i>3.1</i>
Anterior	<i>4.8</i>
Posterior	<i>3.1</i>
Capture	
3-dimensional distance	3.8
Ventral	<i>2.7</i>
Dorsal	<i>1.1</i>
Lateral	<i>2.4</i>
Anterior	<i>0.5</i>
Posterior	<i>1.2</i>

Distances in bold are the maximum observed distances in three-dimensional space. Values in italics are maximum distances in each component dimension

view (Fig. 3b): *P. norvegica* detected prey over 300% further in the ventral direction relative to the dorsal. This difference becomes progressively smaller when the animal initiates an attack response (Table 1). *P. norvegica* detect moving yolk-sac stage cod larvae within a volume 1.4 ml . Attack and capture volumes were considerably smaller, 0.2 and 0.1 ml , respectively. By multiplying the surface area of the ellipsoid associated with each behaviour (Fig. 3c) by the average swimming speed (13.6 mm s^{-1}), we calculated the flux rate of fluid through each of the detection, attack and capture volumes (Table 2). *P. norvegica* is able to scan 1.9 ml s^{-1} (6.6 l h^{-1}) of fluid and passes 0.5 ml s^{-1} (2.0 l h^{-1}) and 0.2 ml s^{-1} (0.7 l h^{-1}) through the attack and capture volume, respectively (Table 2). Depending on the abundance and distribution of cod larvae in the water column, encounter rates can be significant. If an encounter occurs more than every 10 min, the copepod will be able to capture and have time to ingest it despite the long handling time. Also, there were instances when the copepod was ingesting one larva into its mandibles using its maxillae and capturing a second larva with its maxillipeds. Having 6 pairs of cephalic appendages can be

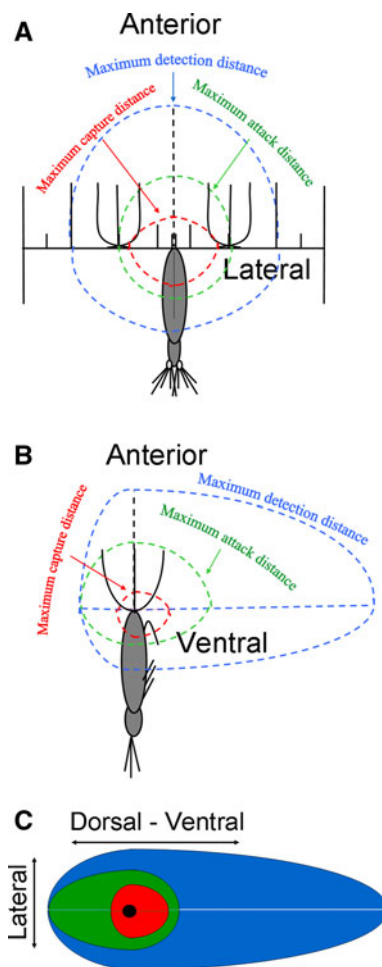


Fig. 3 Schematic representation of the geometry of the detection field (blue), attack area (green) and capture area (red) of adult female *Paraeuchaeta norvegica* preying on Atlantic cod (*Gadus morhua*) larvae from the **a** Dorsal view, **b** Lateral view and **c** Anterior ‘birds-eye’ view looking down on *P. norvegica*. The black dot in the centre of panel c represents the head of the *P. norvegica*. Distances used to depict the geometry of each behavioural region are drawn from Table 1 (color figure online)

Table 2 Surface area, volume and flux rate through the detection, attack and capture regions of adult female *Paraeuchaeta norvegica* feeding on yolk-sac (4 dph) larvae of Atlantic cod (*Gadus morhua*)

	Surface area top view (cm ²)	Maximum volume (ml)	Maximum flux (ml s ⁻¹)	Maximum flux (l h ⁻¹)
Detection	1.4	1.4	1.8	6.6
Attack	0.4	0.2	0.5	2.0
Capture	0.1	0.0	0.2	0.7

Flux rates are calculated from the flow rate produced by the swimming speed (13.6 mm s⁻¹) passing through the surface area associated with each region

quite useful, especially where only one pair (the antennules) is used for remote detection, while the other 5 pairs can be used to handle multiple prey.

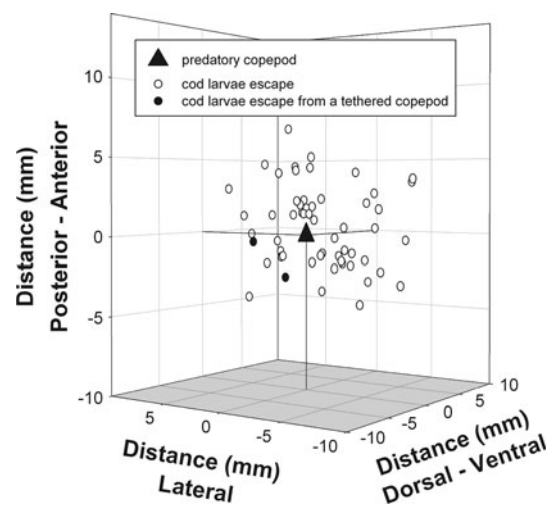


Fig. 4 Locations from which yolk-sac (4 dph) larvae of Atlantic cod (*Gadus morhua*) initiated escape responses to a tethered (closed circles) or a free swimming (open circles) adult female *Paraeuchaeta norvegica*. The black lines are approximately the length of an adult female copepod

3-D perceptual field of cod larvae to *Paraeuchaeta norvegica*

Cod larvae initiated an escape reaction in response to the fluid disturbance created by a swimming or attacking *Paraeuchaeta norvegica*. When the predator was swimming at an average speed of 13.6 mm s⁻¹, cod larvae detected them at a maximum distance of 9.2 mm and an average distance of 4.6 mm (SD = 1.9 mm, n = 54; Figs. 4, 5). Escape responses by cod larvae were uniformly distributed around the copepod (Fig. 4). If the cod larva exhibited an escape reaction prior to being attacked, they escaped at speeds of 15.5 mm s⁻¹ (SD = 7.9, n = 52). There was no relationship between the velocity of escape reactions undertaken by cod larvae and the distance from the predator at which escapes were initiated (p = 0.79; Fig. 5a). Nor was there a relationship between the distance from the predator at which cod larvae initiated an escape reaction and the swimming speed of the predatory copepod (p = 0.95; Fig. 5b). Cod larvae detected attacking copepods at an average distance of 4.2 mm (SD = 3.2, n = 35). These results suggest that the speed and timing of the escape reaction is not determined by vision. However, when *P. norvegica* approaches a cod larva at its normal mean speed of 13.6 mm s⁻¹ (SD = 5.9, n = 42), the cod larva escapes at a speed of 15.5 mm s⁻¹ (SD = 7.9, n = 52) (t = 3.68; p < 0.01). When *P. norvegica* is moving at a stronger mean speed of 34 mm s⁻¹ (SD = 17.4 mm s⁻¹, n = 16), the cod larva escapes at a mean speed of 28.2 mm s⁻¹ (SD = 8.5, n = 8). The larval escape speed was significantly higher in response to the

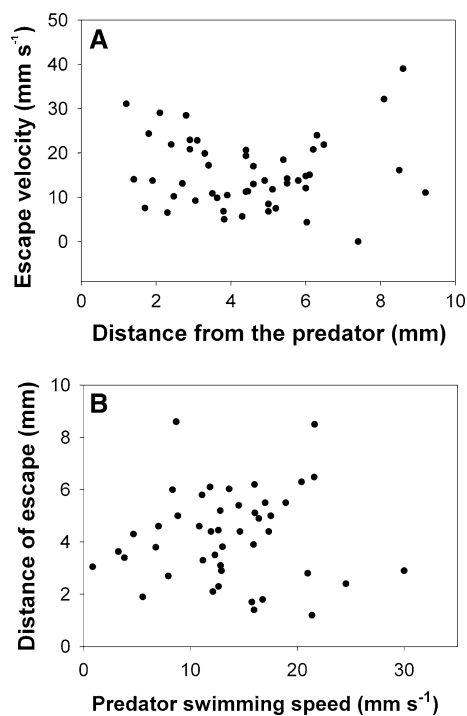


Fig. 5 Characteristics of the escape response of yolk-sac (4 dph) larvae of Atlantic cod (*Gadus morhua*) in response to fluid signals created by *Paraeuchaeta norvegica*. **a** The prey escape speed as a function of the distance from the predator when it initiates the escape response. **b** The distance at which cod larvae initiate an escape reaction as a function of the swimming speed of the predator. Relationships are not statistically significant

rapidly attacking copepod predatory copepod. These results suggest that the fluid signal plays a prominent role in the magnitude of the cod larvae escape response.

Discussion

Sensory ecology of predatory copepod interactions with fish larvae

Both cod larvae and *Paraeuchaeta norvegica* rely on various water-borne signals to obtain information about their biotic and abiotic environments. However, during the early larval period, cod larvae are clearly outmatched by the predatory abilities of *P. norvegica*. Early stage cod larvae have limited mobility and poorly developed sensory modalities and escape responses (Fuiman and Magurran 1994; Yin and Blaxter 1986) making them particularly susceptible to predation by the mechanoreceptive predators such as *P. norvegica*. In general, cod larvae exhibit sporadic swimming activity, remaining motionless in the water column much of the time. When *P. norvegica* swam near a cod larva, the larva detected the predator and initiated an escape reaction. Assuming that cod larvae were responding

to the fluid velocity created by the swimming copepod, the threshold water speed causing the escape reaction can be calculated. The swimming speed of *P. norvegica* is 13.6 mm s^{-1} (SD = 5.9, $n = 45$) creating a wake that attenuates with distance. The average detection distance at which the fish initiated an escape reaction was 4.6 mm. Since the fluid signal generated is attenuated by fluid viscosity, causing a decrease in fluid velocity as a function of the distance cubed (Kalmijn 1988), we can calculate a threshold fluid velocity for the larval cod of $140 \mu\text{m s}^{-1}$.

During the escape response, cod larvae propelled themselves by beating their tails at frequencies up to 35 beats s^{-1} (Yin and Blaxter 1986). The tail beats of swimming fish larvae generate localized fluid motions that provide mechanical signals that can be detected by rheotactic copepods, including *Paraeuchaeta norvegica* (Yen 1987; Tiselius et al. 1997; Olsen et al. 2000; Fields and Yen 2002). During the escape reaction, cod larvae reach an average speed of 15.7 mm/s. Using this average escape speed, *P. norvegica*'s mean detection distance of 4.2 mm and a $1/r^3$ decline in fluid velocity, the average threshold velocity for detection by *P. norvegica* is $212 \mu\text{m s}^{-1}$. Thus, the predator is 33% less sensitive than their prey to fluid mechanical disturbances, explaining why the cod larvae perceived the approaching predator before the predator perceives the larva. This difference in sensitivity enables the prey to initiate an escape before the predator detects it. However, the escape reaction of the prey provides additional information to the predator that permits an accurate directed attack.

The instant the larva initiated an escape response by beating its tail, *Paraeuchaeta norvegica* lunged towards it. Attacks by *P. norvegica* on cod larvae were initiated at an average separation distance of 3.2 mm resulting in a calculated threshold for an attack response of $480 \mu\text{m s}^{-1}$. The attack volume was similar in size and geometry to that reported for *Euchaeta rimana* (Doall et al. 2002). At the speeds achieved by *P. norvegica* during an attack (34 mm s^{-1}), the copepod covers the 3.2-mm separation distance in $\sim 90 \text{ ms}$. This is over twice the escape speed of 4-mm cod larvae, explaining why they could catch them even while they were trying to escape. However, cod larvae only slightly older than those used here had average swim speeds of $\sim 70 \text{ mm s}^{-1}$ (Williams et al. 1996), a speed substantially faster than *P. norvegica*'s attack speed. This is consistent with earlier observations describing a rapid reduction in predation rate by *P. norvegica* on larger cod (Bailey 1984; Yen 1987). The rapidity of the attack by *P. norvegica* is also noteworthy, since such transient events, which occur on small scales, can only be observed using the methods and approach reported upon here.

The threshold values of *Paraeuchaeta norvegica* are much lower than those found for the smaller (2.5 mm)

congener *Euchaeta rimana* attacking an artificial fluid disturbance ($\approx 20 \text{ mm s}^{-1}$, Fields and Yen 2002). Part of the discrepancy may be due to the longer sensory hairs on *P. norvegica* (Yen and Nicoll 1990 (Table 1); which would provide higher sensitivity to the low-frequency stimuli produced by the swimming fish (Fields and Weissburg 2005). Perceptual volumes are the product of the sensory abilities of the predator and the species-specific signals created by their prey (e.g., Doall et al. 2002). When swimming, the predatory copepod creates a feeding current that entrains potential prey, such as fish larvae, bringing them closer to the copepod mouthparts. Cod larvae escape in any location within the copepod feeding current (Fig. 4), while attacks launched by the predator are aimed primarily into the region ahead and above the copepod (Fig. 3). Primary sensory hairs of the antennules project up and forward of the copepod. The swimming legs also propel the copepod up and forward. Hence, the most likely location of successful prey capture within the sensory field is in this region. Thus, the geometry of the detection and attack volumes reflect the swimming speed of the prey and the sensitivity of the predator. The capture volume is the balance between the strength of the predator's attack response and the prey's ability to escape. Therefore, different prey organisms are detected and consumed at very different rates, independent of their size. As cod larvae mature and increase their swimming speed, they will likely be detected at a great distance by *P. norvegica*. However, as cod larvae increase their escape speed, the capture volume of *P. norvegica* will likely decrease. This probably explains why *P. norvegica* does not eat larger fish larvae.

Ecological context

Predation and starvation are two key factors that can cause high mortality in larval stages of aquatic organisms such as fish (e.g., Lasker et al. 1978; Bailey and Houde 1989). During the early stages of development, most larval fish possess a yolk sac that mitigates or alleviates their need to feed, at least for a short time. For fish species such as cod that hatch with large yolk sacs, starvation is not the dominant governor of mortality during the first few days after hatching. In this study, we characterized how a predatory copepod detects, successfully attacks and ingests yolk-sac stage cod larvae.

Paraeuchaeta norvegica consume an average of between 2.2 and 6.3 yolk-sac stage cod larvae day^{-1} , depending upon the abundance of larvae in the experiment (Bailey 1984; Yen 1987). *Paraeuchaeta norvegica* required approximately 8.5 min to consume a single cod larva. Atlantic and gulf menhaden larvae were captured and consumed in less than 4 min by *Anomalocera ornata* (Turner et al. 1985). Feeding rates of *A. ornata* on yolk-sac

larvae of these species were up to 14 larvae copepod $^{-1}$ day^{-1} but only 2 larvae copepod $^{-1}$ day^{-1} for *Centropages typicus*. The calanoid copepod *Paraeuchaeta elongata* eats yolk-sac stage Pacific hake (*Merluccius productus*) larvae at a rate of approximately 4 day^{-1} (Bailey and Yen 1983).

The vertically integrated abundance of adult female *Paraeuchaeta norvegica* in the Norwegian Sea is approximately 130 m^{-2} (Fleddum et al. 2001). At this density, the potential impact of *P. norvegica* on cod larvae is between 186 and 819 larvae $\text{day}^{-1} \text{ m}^{-2}$, with maximum rates as high as $1,430 \text{ day}^{-1} \text{ m}^{-2}$ (based upon a feeding rate of 11 prey copepod $^{-1} \text{ day}^{-1}$ drawn from Yen (1987)). Predation on fish larvae by juvenile *P. norvegica* is also possible but has never been estimated. Thus, under some circumstances, *P. norvegica* can be a very significant source of mortality on the early life stages of cod (at least prior to first-feeding). As the larvae get larger, predation rates decline rapidly (Bailey 1984; Yen 1987). In this study, we made direct 3-dimensional observations of interactions between free-swimming and/or tethered *P. norvegica* in order to describe and characterize the fine-scale interactions between this predaceous copepod and cod larvae.

Accurately parameterizing trophic interaction models requires an understanding and characterization of the predator–prey relationship between different members of the plankton at different life stages (e.g., North et al. 2009). For zooplankton–ichthyoplankton interactions, that can only be achieved through direct fine-scale observations such as those presented here.

Acknowledgments Thanks to Marise Bélanger for her assistance in extracting the behavioural data from the videotapes. This research was supported by the Department of Fisheries and Oceans Canada and by the Norwegian Institute of Marine Research (Fine-scale interactions in the plankton project to HIB). JY was partially supported by National Science Foundation grant CBET 0625898.

References

- Bailey KM (1984) Comparison of laboratory rates of predation on five species of marine fish larvae by three planktonic invertebrates: effects of larval size on vulnerability. *Mar Biol* 79:303–309
- Bailey KM, Houde ED (1989) Predation on eggs and larvae of marine fishes and the recruitment problem. *Adv Mar Biol* 25:1–83
- Bailey KM, Yen J (1983) Predation by a carnivorous marine copepod, *Euchaeta elongata* Esterly, on eggs and larvae of the Pacific Hake, *Merluccius productus*. *J Plankton Res* 5:71–82
- Browman HI, St-Pierre J-F, Skiftesvik AB, Racca R (2003) Behaviour of Atlantic cod (*Gadus morhua*) larvae: an attempt to link maternal condition with larval quality. In: Browman HI, Skiftesvik AB (eds) *The big fish bang*. Institute of Marine Research, Bergen, pp 71–95
- Doall MH, Strickler JR, Fields DM, Yen J (2002) Mapping the free-swimming attack volume of a planktonic copepod, *Euchaeta rimana*. *Mar Biol* 140:871–879

- Fields DM, Weissburg MJ (2005) Evolutionary and ecological significance of mechanosensor morphology: copepods as a model system. *Mar Ecol Prog Ser* 287:269–274
- Fields DM, Yen J (2002) Fluid mechanosensory stimulation of behaviour from a planktonic marine copepod *Euchaeta rimana* Bradford. *J Plankton Res* 24:747–755
- Fleddum A, Kaartvedt S, Ellertsen B (2001) Distribution and feeding of the carnivorous copepod *Paraeuchaeta norvegica* in habitats of shallow prey assemblages and midnight sun. *Mar Biol* 139:719–726
- Fuiman LA, Magurran AE (1994) Development of predator defenses in fishes. *Rev Fish Biol Fisher* 4:145–183
- García RP, Alejandre RV (1995) Predation upon larvae of the Pacific sardine *Sardinops sagax* by cyclopoid copepods. *J Crust Biol* 15:196–201
- Kalmijn AJ (1988) Hydrodynamic and acoustic field detection. Sensory biology of aquatic animals. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds) Sensory biology of aquatic animals. Springer, New York, pp 83–130
- Lasker R, Parsons TR, Jansson BO, Longhurst AR, Saetersdal G (1978) The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. *Rapp P V Reun Cons Int Explor Mer* 173:212–230
- Montgomery J, Coombs S, Janssen J (1994) Form and function relationships in lateral-line systems—comparative data from 6 species of Antarctic Notothenioid fish. *Brain Behav Evol* 44:299–306
- North EW, Gallego A, Petitgas P (eds) (2009) Manual of recommended practices for modelling physical–biological interactions during fish early life. *ICES Coop Res Rep* 295
- Olsen EM, Jørstad T, Kaartvedt S (2000) The feeding strategies of two large marine copepods. *J Plankton Res* 22:1513–1528
- Ouellet P (1997) Characteristics and vertical distribution of Atlantic cod (*Gadus morhua*) eggs in the northern Gulf of St. Lawrence, and the possible effect of cold water temperature on recruitment. *Can J Fish Aquat Sci* 54:211–233
- Rapo MA, Jiang H, Grosenbaugh MA, Coombs S (2009) Using computational fluid dynamics to calculate the stimulus to the lateral line of a fish in still water. *J Exp Biol* 212:1494–1505
- Skarra H, Kaartvedt S (2003) Vertical distribution and feeding of the carnivorous copepod *Paraeuchaeta norvegica*. *Mar Ecol Prog Ser* 249:215–222
- Tiselius P, Jonsson PR, Kaartvedt S, Olsen EM, Jørstad T (1997) Effects of copepod foraging behaviour on predation risk: an experimental study of the predatory copepod *Paraeuchaeta norvegica* feeding on *Acartia clausi* and *A. tonsa* (Copepoda). *Limnol Oceanogr* 42:164–170
- Tønnesson K, Nielsen TG, Tiselius P (2006) Feeding and production of the carnivorous copepod *Paraeuchaeta norvegica* in the Skagerak. *Mar Ecol Prog Ser* 314:213–225
- Turner JT, Tester PA, Hettler WF (1985) Zooplankton feeding ecology. A laboratory study of predation on fish eggs and larvae by the copepods *Anomalocera ornata* and *Centropages typicus*. *Mar Biol* 90:1–8
- Vestheim H, Kaartvedt S, Edvardsen B (2005) State-dependent vertical distribution of the carnivore copepod *Paraeuchaeta norvegica*. *J Plankton Res* 27:19–26
- Williams PJ, Brown JA, Gotceitas V, Pepn P (1996) Developmental changes in escape response performance of five species of marine larval fish. *Can J Fish Aquat Sci* 53:1246–1253
- Yen J (1985) Vertical distribution and migratory activity of three species of *Euchaeta*, a carnivorous marine copepod. *Bull Mar Sci* 37:781–782
- Yen J (1987) Predation by a carnivorous marine copepod, *Euchaeta norvegica* Boeck, on eggs and larvae of the North Atlantic cod *Gadus morhua* L. *J Exp Mar Biol Ecol* 112:283–296
- Yen J, Nicoll NT (1990) Setal array on the first antennae of a carnivorous marine copepod, *Euchaeta norvegica*. *J Crust Biol* 10:218–224
- Yin MC, Blaxter JHS (1986) Morphological changes during growth and starvation of larval cod (*Gadus morhua* L.) and flounder (*Platichthys flesus* L.). *J Exp Mar Biol Ecol* 104:215–228