Marine Biology 90, 1–8 (1985)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Zooplankton feeding ecology

A laboratory study of predation on fish eggs and larvae by the copepods *Anomalocera ornata* and *Centropages typicus*

Jefferson T. Turner *, Patricia A. Tester and William F. Hettler

National Marine Fisheries Service, NOAA, Southeast Fisheries Center, Beaufort Laboratory; Beaufort, North Carolina 28516, USA

Abstract

Hjort proposed that fishery year-class fluctuations are due mainly to variable larval mortality, and that most mortality is due to early starvation. Some larvae die because they do not find enough zooplankton to eat, but others may die because zooplankton eat them. We examined predation upon eggs, yolk-sac, and/or first-feeding larvae of Atlantic menhaden (*Brevoortia tyrannus*), gulf menhaden (*B. patronus*) and spot (*Leiostomus xanthurus*) by adults of larger (*Anomalocera ornata*) and smaller (*Centropages typicus*) copepods. *B. tyrannus* eggs were too large for either copepod to grasp or ingest. *A. ornata* could grasp and apparently kill, but not ingest, the smaller *L. xanthurus* eggs, but *C. typicus* could not. Both yolk-sac and first-feeding *B. tyrannus* larvae and first feeding *B. patronus* larvae were grasped and completely consumed in < 4 min by *A. ornata*. *C. typicus* ingested yolk-sac larvae of both fish, but not first-feeding larvae of either species. Ingestion rates by *A. ornata* were significantly related to prey density (ANOVA; $p < 0.001$). Ingestion rates by *C. typicus* (< 2 larvae copepod d^{-1}) were much lower than those of the larger *A. ornata* (up to 14 larvae copepod d^{-1}) at food concentrations of 10 to 50 larvae l^{-1}. However, expressed as % copepod body carbon ingested copepod d^{-1}, ration by the smaller copepod equalled or exceeded that of the larger. Since copepods and fish larvae can become concentrated together in surface windrows, copepod predation may represent a substantial source of mortality of fish larvae.

Introduction

Hjort (1914, 1926) proposed that fishery year-class fluctuations are due primarily to variable mortality of fish eggs and larvae. Two primary mechanisms were proposed: (1) transport by currents out of favorable areas ("larval drift"), and (2) starvation. Starvation was considered most important, and subsequent studies have confirmed the importance of sufficient amounts and types of food to larval survival (reviews by May, 1974; Hunter, 1981; Lasker, 1981; Blaxter and Hunter, 1982). Although many fish larvae undoubtedly die because they do not get enough to eat, others die because they are eaten.

Predation is a potentially high source of mortality of fish eggs and larvae. Since mortality of eggs and yolk-sac larvae can reach 95% per day (Hunter, 1981), and the presence of yolk insulates these stages against starvation, predation is an obvious candidate for much mortality. Although many fish eggs and larvae are eaten by other fishes (reviews by Hunter, 1981; Blaxter and Hunter, 1982), numerous observations of gut-content, rearing, and laboratory-feeding studies have revealed that a variety of planktonic invertebrates are also larval-fish predators (Table 1).

The calanoid copepod *Anomalocera ornata* (Family Pontellidae) is a patchy but abundant component of the winter neuston of the continental shelves of the northern Gulf of Mexico and western North Atlantic south of Cape Hatteras (see Turner and Collard, 1980 for a summary of records). During the same season in these waters, eggs and larvae of winter-spawning fishes such as Atlantic menhaden (*Brevoortia tyrannus*), gulf menhaden (*B. patronus*) and spot (*Leiostomus xanthurus*) are also present near the surface. Surface hydrographic discontinuities, such as windrows or fronts, appear to concentrate menhaden and spot larvae (Govoni *et al.*, 1983) as well as *A. ornata*. Although we know of no strictly quantitative data, nearly a decade of personal experience sampling *A. ornata* in the Gulf of Mexico and Atlantic has revealed that this copepod frequently becomes concentrated in surface windrows. Thus, due to temporal and spatial co-occurrence, the potential exists for predation interactions between *A. ornata* and spot and menhaden larvae.

We investigated the predation by adult male and female *Anomalocera ornata* on *Brevoortia tyrannus* and

* Present address: Biology Department, Southeastern Massachusetts University; North Dartmouth, Massachusetts 02747, USA

Table 1. Examples of marine zooplankters reported to prey upon fish larvae in gut-content, larval-fish-rearing, or laboratory-feeding studies

Predators	References
Copepods	Bailey (1984), Bailey and Yen (1983), Lillelund and Lasker (1971), Lebour (1925)
Euphausiids	Theilacker and Lasker (1974)
Hyperiid amphipods	Westernhagen and Rosenthal (1976), Westernhagen *et al.* (1979), Sheader and Evans (1975)
Decapod larvae	Lebour (1925)
Chaetognaths	Kuhlmann (1977), Coston-Clements (unpublished manuscript), Hettler (1981)
Ctenophores	Stevenson (1962), Lebour (1925)
Siphonophores	Purcell (1980; 1981 a, b)
Scyphomedusae	Bailey (1984), Bailey and Batty (1983), Fraser (1969), Möller (1980, 1984)
Hydromedusae	Arai and Hay (1982)

Leiostomus xanthurus eggs, *B. tyrannus* yolk-sac and first-feeding larvae, and *B. patronus* first-feeding larvae. To compare predation rates by the large (>4 mm total length) *A. ornata* with those of a smaller copepod, we also examined predation by adult female *Centropages typicus* (<2 mm total length) upon *B. tyrannus* and *L. xanthurus* eggs, yolk-sac, and first-feeding larvae. We sought to determine the effects of prey density and prey size on predation rate, and if these differed, with size of predator. In addition, we made microscopic observations of predation events to describe predation mechanisms and how these were affected by prey size or motion.

Materials and methods

Fish eggs were produced by hormone injection of adult female fish. Larvae were reared from eggs according to Hettler (1981, 1983) and Hettler and Powell (1981). Larvae were transferred individually to experimental containers by pipetting. Copepods were collected by surface net tows in continental shelf waters within 10 km of Beaufort Inlet, North Carolina, USA, in February and March of 1983 and 1984, and returned to the laboratory within 1.5 h of capture. *Anomalocera ornata* adult males and females or *Centropages typicus* adult females were isolated by pipette. Experiments were initiated within 6 h of copepod collection by addition of copepods to containers with fish larvae.

Predation experiments were performed in uncovered large finger bowls (18 cm diameter) in one liter of 202-μm mesh-screened natural seawater from the Beaufort Channel. This provided the copepods with natural phytoplankton and microzooplankton in addition to fish larvae. In experiments using *Centropages typicus* females, five replicate bowls with five copepods each were used at each concentration of fish larvae (10, 20, 30, 40, 50 and 60 *Brevoortia tyrannus* yolk-sac larvae l^{-1}, and 10, 20, 30, 40 and 50 *Leiostomus xanthurus* yolk-sac larvae l^{-1}). The same regimes were used in experiments where *C. typicus* females were offered first-feeding larvae. In experiments using *Anomalocera ornata,* three replicates with three females each, and three replicates with three males each were performed at each concentration of fish larvae (10, 30, and 50 *B. tyrannus* yolk-sac larvae l^{-1}, and 10, 20, 30, 40, and 50 *B. tyrannus* first-feeding larvae l^{-1}). When *A. ornata* was provided first-feeding *B. patronus* larvae, six replicate bowls, each with three males or three females were used at each concentration of fish larvae (5, 10, and 15 larvae l^{-1}). A control bowl with no copepods was maintained for each experimental concentration of larvae.

Although we were able to examine predation of *Anomalocera ornata* on *Leiostomus xanthurus* eggs, we were unable to examine its predation on *L. xanthurus* larvae. Despite intensive sampling we were unable to obtain *A. ornata* when *L. xanthurus* larvae were available to be used as prey. This was because the last successful hatch of *L. xanthurus* eggs for the season was during the period when the seasonally ephemeral appearance of *A. ornata* off Beaufort had already passed (early March, 1984).

Experiments were performed with constant indoor lighting from 13.00 to 09.00 hrs the following day at approximately 22 °C, and were terminated by removal and counting of fish larvae. For first-feeding larvae this was accomplished by placing a bowl on a black background, removing larvae or parts of larvae by pipette, aided by a flashlight and magnifying lenses. Contents of each bowl were then screened through 20-μm-mesh netting to recover any overlooked larvae. Since yolk-sac larvae are much more difficult to see than first-feeding larvae, yolk-sac larvae were removed by triplicate screenings of the contents of each bowl through 20-μm-mesh netting.

Predation rates were equated with larvae missing from those introduced. Additionally, intact dead or partially eaten larvae were counted for determinations of larvae killed. However, these were not included in calculations of predation rates. We were unable to assess the extent of such copepod-induced mortality because mortality of larvae in control containers was variable, ranging from 0 to 95%. An average of 26.7% of the larvae died in the controls, but mortality was not density dependent. Rather, the between-experiment variability was greater than the within-experiment variability. This was a result of the variable viability of larvae from a given batch of eggs.

Copepod mortality during experiments was low. No *Centropages typicus* females died, but 8% of the *Anomalocera ornata* did ($n = 14$ of 174 copepods). Since *A. ornata* can leap out of the water and become stuck on the inner surface of a container above the water surface, all containers were checked each evening (usually 6 h after initiation of the experiment) to ensure that all three *A. ornata* in each bowl were alive and active. If a desiccated, dead copepod was discovered stuck to the inside of the bowl the next morning, its predation rate was calculated assuming that it had lived for half of the experimental period. The only *A.*

Table 2. Dry weight, carbon, and % carbon values of fish eggs and larvae and copepods used in experiments

Organism	mg dry wt. individual^{-1} (means underlined, and ranges in parentheses)	mg carbon individual^{-1} (means underlined, and ranges in parentheses	% carbon (means underlined and ranges in parentheses)	n[a]
Brevoortia tyrannus egg (1.30–1.65 mm diameter)	0.053 (0.049–0.055)	0.021 (0.020–0.022)	40.5 (37.6–42.3)	8
Leiostomus xanthurus egg (0.72–0.87 mm diameter)	0.026 (0.024–0.031)	0.014 (0.013–0.017)	53.2 (52.9–53.4)	5
B. tyrannus yolk-sac larvae (3.2–3.6 mm length)	0.041 (0.032–0.056)	0.017 (0.015–0.021)	38.6 (26.8–47.5)	4
B. tyrannus first-feeding larvae (3.6–4.2 mm length)	0.055 (0.038–0.068)	0.015 (0.014–0.017)	28.3 (22.8–36.0)	4
L. xanthurus yolk-sac larvae (1.6–1.7 mm length)	0.019 (0.013–0.028)	0.008 (0.007–0.010)	47.2 (35.6–54.9)	3
L. xanthurus first-feeding larvae (2.3–2.7 mm length)	0.028 (0.022–0.033)	0.0068 (0.0067–0.0068)	25.7 (20.5–30.8)	2
B. patronus first-feeding larvae (3.0–3.9 mm length)	0.038 (0.036–0.040)	0.015 (0.014–0.015)[b]	38.6 (26.8–47.5)[b]	3
Centropages typicus female (1.6–2.0 mm length)[c]	0.038 (0.022–0.046)	0.013 (0.010–0.015)	35.5 (28.6–43.7)	4
Anomalocera ornata female (4.0–4.4 mm length)[d]	0.810 (0.791–0.846)	0.300 (0.294–0.311)	37.1 (34.8–39.3)	3
A. ornata male (4.2–4.3 mm length)[d]	0.630 (0.598–0.675)	0.237 (0.233–0.243)	37.5 (36.0–38.9)	3

[a] Refers to the number of replicates with 25–75 fish eggs or larvae each, 2–12 *A. ornata* each, or 25–50 *C. typicus* each that were used for dry weight and carbon measurements. Larval length and egg diameter ranges are from hundreds to thousands of measurements made by W. F. Hettler during rearing experiments

[b] No carbon determinations were made on *B. patronus* larvae. The mean carbon concentration of *B. tyrannus* first-feeding larvae (28.3%) was used for conversions

[c] Length range from Rose (1933)

[d] Length ranges from Sutcliffe (1949)

ornata that died during experiments were those stuck to the container above the surface of the water.

Carbon-specific predation rates were calculated using dry weight and carbon determination for all stages, sexes and species of copepods and fish eggs or larvae used. Live copepods or fish larvae were semi-narcotized by addition of distilled water to the dish of natural seawater in which they were swimming. Individuals were captured immediately with a forceps, dipped in three successive rinses of distilled water for salt elimination, and placed in tared aluminum boats. These were freeze-dried, weighed with a Cahn 25 Electrobalance[1], and carbon values were determined with a Carlo Erba Elemental Analyzer (Model 1106).

To elucidate the mechanisms of predation interactions, copepods and fish eggs and larvae were observed in petri dishes under a dissecting microscope.

Results

Observations

Anomalocera ornata males and females did not eat *Brevoortia tyrannus* eggs. Eggs were too large (1.30–1.65 mm diameter) for the copepods to grasp, and they simply bumped into them. *A. ornata* grasped the smaller *Leiostomus xanthurus* eggs (0.72–0.87 mm diameter) with their second maxillae, swam around holding the eggs for 4 to 6 min, and then they were discarded. These eggs were shriveled and immediately sank to the bottom of the petri dishes, in contrast to undamaged eggs which were smooth, rounded, and floated. Thus, *A. ornata* apparently can damage, but not ingest *L. xanthurus* eggs, although whether they can remove egg contents could not be determined.

Both *Brevoortia tyrannus* and *Leiostomus xanthurus* eggs were also too large for *Centropages typicus* females to grasp, and the eggs floated away when the copepods bumped into them.

Both *Anomalocera ornata* males and females ingested *Brevoortia tyrannus* yolk-sac larvae. Within one minute of being introduced to a petri dish, some *A. ornata* grabbed larvae by the head (using their second maxillae), and ingested the larvae, proceeding form head to tail. This took 3 to 4 min. Motion of prey did not always induce attack, since some *A. ornata* bumped into live and moving larvae as well as immobile, possibly dead larvae, but did not grasp them.

Anomalocera ornata males and females also ingested first-feeding *Brevoortia tyrannus* larvae. Within 5 min of

[1] Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA

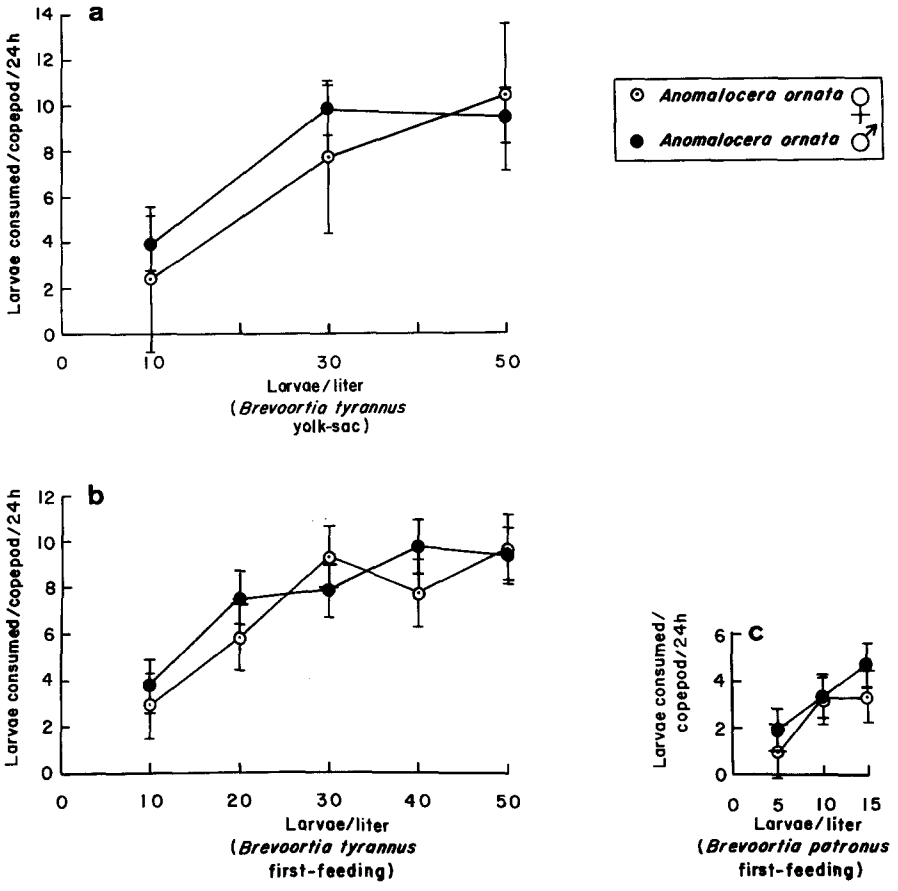

Fig. 1. *Anomalocera ornata.* Rates of consumption of fish larvae versus concentrations of fish larvae offered, when larvae were (a) *Brevoortia tyrannus* yolk-sac larvae, (b) *B. tyrannus* first-feeding larvae, or (c) *B. patronus* first-feeding larvae. Data points are means of 3 (a and b) or 6 (c) replicates, and error bars are ±95% CI

being introduced, copepods started to attack larvae. Five predation events were observed within 10 min. Attacks occurred so rapidly that we could not see exactly how they happened. Rather, we observed copepods swimming around the dish holding struggling fish larvae. In four of these observations, copepods grabbed larvae by the tail, and in one by the head. In all cases, the struggling larvae gradually disappeared into the copepod's mouth within 2 to 3 min. Copepods held larvae with their second maxillae, and although the larvae continued to struggle violently, once grasped, none escaped. As with predation on yolk-sac larvae, it did not appear that motion of the larvae caused the attack. Many moving larvae swam into copepods without being attacked. Indeed, during these "bump and run" encounters, both the copepods and the fish larvae simultaneously exhibited avoidance of each other.

Centropages typicus ingested both live and dead *Brevoortia tyrannus* yolk-sac larvae, grabbing them by either the head or the tail, and completely consuming them within less than 3 min. In other cases, larvae were only partially consumed (approximately 1/3 eaten) before copepods dropped them. In some cases, larvae caught by the head broke loose after a short struggle and swam away. However, their heads were opaque (rather than clear as in undamaged larvae), and these larvae appeared to die within a minute of release. *C. typicus* females did not appear to pursue larvae that had escaped their grasp. In some cases, copepods grabbed moving larvae in mid-body behind the yolk sac, but the larvae wiggled loose and swam away. *C. typicus* appeared impervious to many swimming larvae. In several instances when copepods and larvae collided, both exhibited simultaneous avoidance. Some copepods did not appear attracted to larvae, even when in close proximity. Thus, random encounter appeared to initiate attack.

Predation by *Centropages typicus* on *Leiostomus xanthurus* yolk-sac larvae generally followed the same pattern as predation on *Brevoortia tyrannus* larvae. However, additional observations of *C. typicus* predation upon *L. xanthurus* larvae that were in the process of emerging from eggs revealed that copepods can cause mortality of fish larvae in excess of that caused by ingestion of entire larvae. As larvae emerge from the egg, they do so tail first (a process that usually takes about 30 min). Copepods were observed to nibble upon wiggling tails of larvae emerging from eggs. Within 1.5 to 3.5 min, the copepods ate entire tails (up to approximately 1/4 of the length of the larva), and then disengaged. Eggs that were about to hatch moved due to flexing of the tail of the larvae about to emerge. In some cases, *C. typicus* appeared to hover near such moving eggs and wait for the tail to emerge. They then bit off the tails as they emerged. Larvae that had been so wounded turned opaque and died within 10 to 15 min. First-feeding larvae of both fish species were too large (Table 2) for *C. typicus* to catch or ingest.

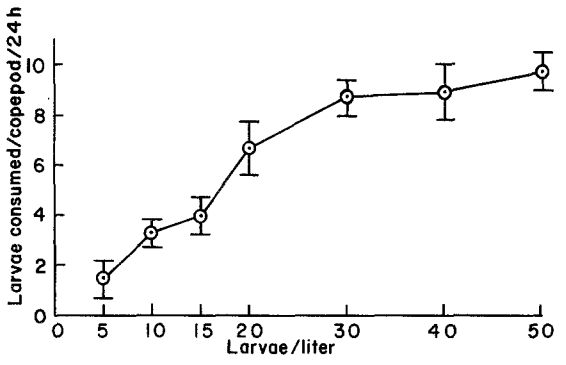

Fig. 2. *Anomalocera ornata.* Rates of consumption of fish larvae versus concentrations of fish larvae offered (combined for all species and stages of larvae and both sexes of copepods). Data points are means of 6 or 12 replicates (total $n=47$), and error bars are ±95% CI

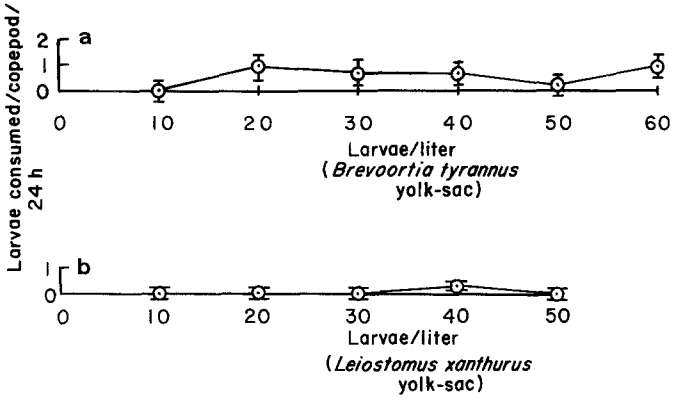

Fig. 3. *Centropages typicus.* Rates of consumption of fish larvae by copepods versus concentration of fish larvae offered, when prey were (a) *Brevoortia tyrannus* yolk-sac larvae or (b) *Leiostomus xanthurus* yolk-sac larvae. Data points are means of 3 replicates and error bars are ± 95% CI

Predation rates

Both male and female *Anomalocera ornata* completely consumed *Brevoortia tyrannus* yolk-sac (Fig. 1a) and first-feeding (Fig. 1b) larvae, and *B. patronus* first-feeding larvae (Fig. 1c). At a given larval concentration, analysis of variance revealed no significant difference ($p<0.01$) in the number of larvae consumed, by either sex of copepod, species of fish, or stage of fish larvae. However, there was a highly significant ($p<0.001$) relation between number of larvae consumed and number offered (Fig. 2). *Centropages typicus* females consumed low numbers of yolk-sac larvae of *B. tyrannus* (Fig. 3a) and *Leiostomus xanthurus* (Fig. 3b).

Carbon and dry weight determinations (Table 2) were used to convert predation rates to a carbon ration basis (% copepod body carbon ingested vs larval fish carbon offered). These conversions revealed that carbon ration was dependent on carbon offered up to approximately 0.3 mgC l^{-1} for *Anomalocera ornata* predation on both yolk-sac and first-feeding larvae of *Brevoortia tyrannus* and on first-feeding larvae of *B. patronus* (Fig. 4). From approximately 0.3 to 0.825 mgC l^{-1}, these copepods ingested means of 29 to 67% of their body carbon per day ($\bar{x}=51.4\%$). The mean carbon ration values of *Centropages typicus* females feeding upon *Leiostomus xanthurus* yolk-sac larvae (9–127% of body carbon ingested) were highly variable (Fig. 4). Even though predation on fish larvae by *C. typicus* was low (Fig. 3) in terms of percent of copepod body carbon ingested, these rates were equivalent to, or greater than, those of the larger *A. ornata.*

Discussion

Copepods, particularly large ones such as *Anomalocera ornata,* are capable of inflicting mortality on larval fish. Since

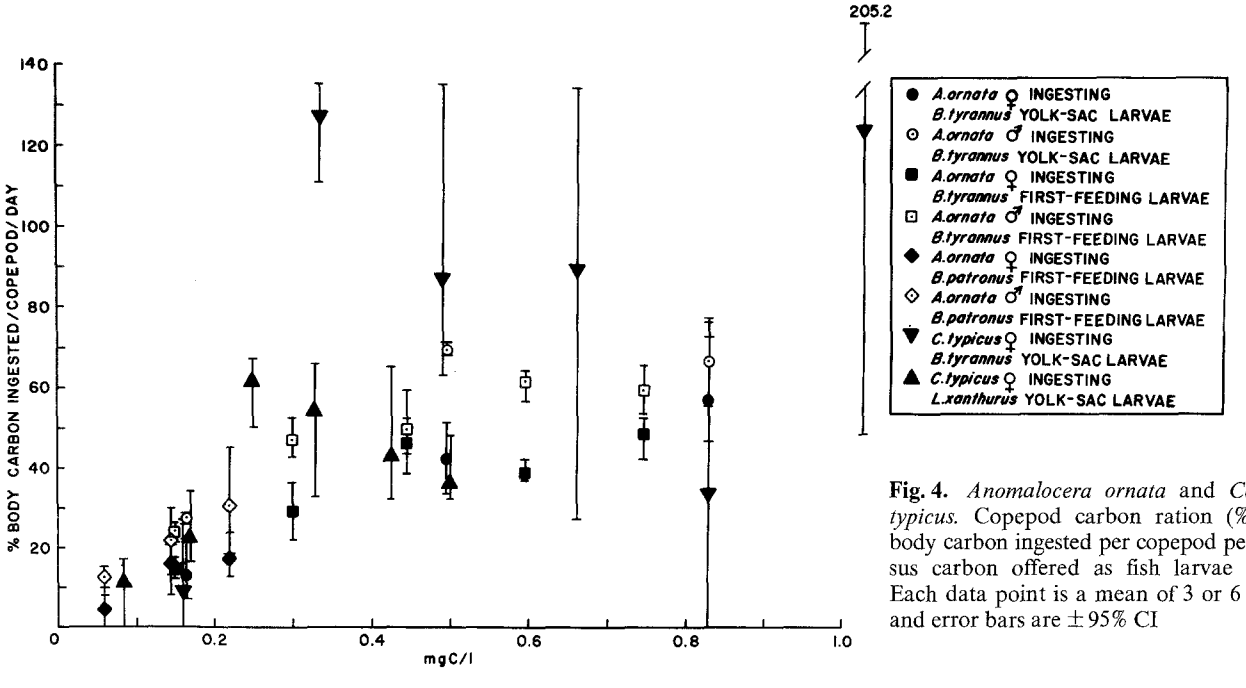

Fig. 4. *Anomalocera ornata* and *Centropages typicus.* Copepod carbon ration (% copepod body carbon ingested per copepod per day) versus carbon offered as fish larvae (mgC l^{-1}). Each data point is a mean of 3 or 6 replicates, and error bars are ± 95% CI

we know of no quantitative data for the abundance of *A. ornata*, we cannot extrapolate the impact of its predation on natural populations of fish larvae. Nonetheless, since *A. ornata* and fish larvae can likely become concentrated together in surface windrows, the impact of predation may be substantial, albeit intermittent. Our predation rate data are only for larvae completely consumed, and do not include partially-eaten or killed but unconsumed larvae. Thus, our predation rates undoubtedly are conservative estimates of total mortality rates. Lillelund and Lasker (1971) and Bailey and Yen (1983) also noted that other copepods can kill fish larvae without consuming them.

As in other studies (Bailey, 1984; Lillelund and Lasker, 1971; Westernhagen *et al.*, 1979), we found that predation rates were affected by sizes of prey relative to those of predators. For instance, the smaller copepod *Centropages typicus* could ingest yolk-sac larvae of both *Brevoortia tyrannus* and *Leiostomus xanthurus*, but could not ingest the larger first-feeding larvae of either fish species. Conversely, the large copepod *Anomalocera ornata* ingested both larval sizes of both fish species at approximately equal rates for a given prey concentration (Fig. 1). Thus, Hunter's (1981) suggestion that only yolk-sac fish larvae are subject to zooplankton predation does not apply to large motile predators such as *A. ornata*. In addition, *A. ornata* ingested higher numbers of fish larvae (up to 14 d^{-1}) than did the smaller *C. typicus* (< 2 d^{-1}), but in terms of carbon ration, rates for both copepods were generally equivalent (Fig. 4).

We found that eggs were not consumed, an observation also made by Bailey and Yen (1983) and Kuhlmann (1977). Again, this was partly related to prey size. *Brevoortia tyrannus* eggs were too large (1.3–1.6 mm diameter) for either copepod to grasp, and even the smaller eggs of *Leiostomus xanthurus* (0.7–0.9 mm diameter) were too large for *Centropages typicus* to grasp. *Anomalocera ornata* did grasp *L. xanthurus* eggs, but they were too large to be ingested. In addition to their large size, many fish eggs apparently are difficult for copepods to grasp because they float. For this reason, Theilacker and Lasker (1974) concluded that euphausiid predation on floating anchovy eggs was slight.

Analysis of variance indicated that predation rates by *Anomalocera ornata* were related to prey density (Fig. 2). This was not evident for *Centropages typicus* (Fig. 3). Density-dependent predation upon fish larvae by copepods, amphipods, and scyphomedusae has also been demonstrated in other studies (Lillelund and Lasker, 1971; Westernhagen and Rosenthal, 1976; Bailey and Batty, 1983; Bailey and Yen, 1983).

Several studies of predation on fish larvae by copepods and chaetognaths (Lillelund and Lasker, 1971; Kuhlmann, 1977; Bailey and Yen, 1983; Bailey, 1984) have indicated that prey motion is important in eliciting predation strikes. However, our microscopic observations are in contrast to this. We found that both species of copepods attacked moving as well as immobile larvae. Conversely, there were many cases where both a copepod and a fish larva exhibited simultaneous avoidance reactions after a collision. Thus, our limited observations suggest that *Anomalocera ornata* and *Centropages typicus*, like the amphipods in the study of Westernhagen and Rosenthal (1976), attack fish larvae by random encounter. However, it did appear that *C. typicus* females were attracted to, hovered near, and waited for the tails of *Leiostomus xanthurus* larvae that were in the process of emerging from eggs.

Our rates of predation of larval fish by copepods are high, but not because alternative prey were absent. All experiments were conducted in 202-μm-screened estuarine water. Thus, the copepods had available as food high natural concentrations of phytoplankton and microzooplankton, in addition to the added fish larvae. Both *Anomalocera ornata* and *Centropages typicus* are broadly omnivorous (Turner, 1978, 1984, in press, unpublished data).

In view of the significant relationships between predation rates and prey densities, however, it is likely that the predation rates presented here are artificially high, because experimental densities of larval fish were higher than those usually found in nature. Although estuarine fish larvae may occasionally reach field densities of 0.1 to 0.34 larvae l^{-1} during seasonal abundance maxima (Pearcy, 1962; Olney, 1983; Bourne and Govoni, in preparation), these values are still one to two orders of magnitude lower than our experimental prey concentrations (5–60 larvae l^{-1}). Our predator densities (3–5 copepods l^{-1}) were also quite high. This suggests that predation rates as high as those reported here could only occur in nature if copepods and fish larvae became simultaneously concentrated by physical and/or behavioral mechanisms.

Both zooplankton and crustacean micronekton have been repeatedly found in concentrations of 100 to more than 1 000 times higher than average background densities (Omori and Hamner, 1982). In perhaps the most extreme example of this, Alldredge *et al.* (1984) found aggregations of copepods of up to 26 000 individuals l^{-1} in waters where background densities were less than 0.5 individuals l^{-1}. Although this aggregation was apparently behaviorally-induced, there have been other reports of physically-induced aggregations.

Surface windrows induced by Langmuir circulation have long been known to concentrate plankton and other particulates (see Pollard, 1977 and Barstow, 1983 for reviews). Although there have apparently been no reports of windrow concentration of fish larvae to densities as high as our prey concentrations, Alldredge (1982) found concentrations of the appendicularian *Oikopleura longicauda* of up to 3 565 individuals l^{-1} in surface windrows. Surface densities between windrows were only 0.2 to 1.2 individuals l^{-1}. Thus, if appendicularians can become concentrated in windrows by a factor of 17 825 times, it appears at least possible that physical mechanisms could concentrate fish larvae by factors of at least 10 to 100 times above reported abundance maxima necessary to approach our experimental prey densities. Indeed, Shanks (1983) found concentrations of fish larvae by factors of 13 to 36 times in surface slicks associated with tidally forced internal waves,

although he presented his data as larvae per unit of towing time rather than as larvae per volume filtered.

In conclusion, our results suggest that if windrows, slicks, or behavioral aggregations simultaneously concentrate large numbers of copepods along with high numbers of larval fish or eggs ready to hatch, copepod predation could inflict substantial mortality on larval fish patches. Since marine fish larvae have been found in coincident high abundance with their zooplankton prey (Fortier and Leggett, 1984; Govoni *et al.*, 1985), it appears likely that there can also be coaggregation of fish larvae and their zooplankton predators.

Acknowledgements. We thank D. Willis, Captain of the R/V "Onslow Bay" for sampling assistance, M. LaCroix for dry weight and carbon analyses, and H. Gordy for photographing the figures. G. Thayer and J. Govoni provided helpful criticism of the manuscript. This research was supported by a contract from the Ocean Assessment Division, National Ocean Service, NOAA, to the Southeast Fisheries Center's Beaufort Laboratory, NMFS.

Literature cited

Alldredge, A. L.: Aggregation of spawning appendicularians in surface windrows. Bull. mar. Sci. *32,* 250–254 (1982)

Alldredge, A. L., B. H. Robinson, A. Fleminger, J. J. Torres, J. M. King and W. M. Hamner: Direct sampling and *in-situ* observation of a persistent copepod aggregation in the mesopelagic zone of the Santa Barbara Basin. Mar. Biol. *80,* 75–81 (1984)

Arai, M. N. and D. E. Hay: Predation by medusae on Pacific herring (*Clupea harengus pallasi*) larvae. Can. J. Fish. aquat. Sci. *39,* 1537–1540 (1982)

Bailey, K. M.: 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 (1984)

Bailey, K. M. and R. S. Batty: A laboratory study of predation by *Aurelia aurita* on larval herring (*Clupea harengus*): experimental observations compared with model predictions. Mar. Biol. *72,* 295–301 (1983)

Bailey, K. M. and J. Yen: Predation by a carnivorous marine copepod, *Euchaeta elongata* Esterly, on eggs and larvae of the Pacific hake, *Merluccius productus.* J. Plankt. Res. *5,* 71–82 (1983)

Barstow, S. F.: The ecology of Langmuir circulation: a review. Mar. environ. Res. *9,* 211–236 (1983)

Blaxter, J. H. S. and J. R. Hunter: The biology of clupeoid fishes. Adv. mar. Biol. *20,* 1–223 (1982)

Bourne, D. W. and J. J. Govoni: Distribution of fish eggs and larvae in Narragansett Bay (Rhode Island and Massachusetts). (In preparation)

Coston-Clements, L.: Predation of chaetognaths on larval fish. (unpublished manuscript)

Fortier, L. and W. C. Leggett: Small-scale covariability in the abundance of fish larvae and their prey. Can. J. Fish. aquat. Sci. *41,* 502–512 (1984)

Fraser, J. H.: Experimental feeding of some medusae and Chaetognatha. J. Fish. Res. Bd Can. *26,* 1743–1762 (1969)

Govoni, J. J., D. E. Hoss and P. B. Ortner: The interaction of larval gulf menhaden, *Brevoortia patronus,* and spot, *Leiostomus xanthurus,* with the Mississippi River plume. Eos *64* (52), 1022 (1983)

Govoni, J. J., A. J. Chester, D. E. Hoss and P. B. Ortner: An observation of episodic feeding and growth of larval *Leiostomus xanthurus* in the northern Gulf of Mexico. J. Plankt. Res. *7,* 137–146 (1985)

Hettler, W. F.: Spawning and rearing Atlantic menhaden. Prog. Fish-Cult. *43,* 80–84 (1981)

Hettler, W. F.: Transporting adult and larval gulf menhaden and techniques for spawning in the laboratory. Prog. Fish-Cult. *45,* 45–48 (1983)

Hettler, W. F. and A. B. Powell: Egg and larval fish production at the NMFS Beaufort Laboratory, Beaufort, N. C., USA. Rapp. P.-V. Reun. Const. int. Explor. Mer *178,* 501–503 (1981)

Hjort, J.: Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun. Cons. int. Explor. Mer *20,* 1–228 (1914)

Hjort, J.: Fluctuations in the year classes of important food fishes. J. Cons. int. Explor. Mer *1,* 5–38 (1926)

Hunter, J. R.: Feeding ecology and predation of marine fish larvae. *In:* Marine fish larvae, pp 33–77. Ed. by R. Lasker. Seattle: Univ. Washington Press 1981

Kuhlmann, D.: Laboratory studies on the feeding behaviour of the chaetognaths *Sagitta setosa* J. Müller and *S. elegans* Verril with special reference to fish eggs and larvae as food organisms. Meeresforschung *25,* 163–171 (1977)

Lasker, R.: The role of a stable ocean in larval fish survival and subsequent recruitment. *In:* Marine fish larvae, pp 80–87. Ed. by R. Lasker. Seattle: Univ. Washington Press 1981

Lebour, M. V.: Young anglers in captivity and some of their enemies. A study in a plunger jar. J. mar. biol. Ass. UK. *13,* 721–734 (1925)

Lillelund, K. and R. Lasker: Laboratory studies of predation by marine copepods on fish larvae. Fish. Bull. U.S. *69,* 655–667 (1971)

May, R. C.: Larval mortality in marine fishes and the critical period concept. *In:* The early life history of fish, pp 3–19. Ed. by J. H. S. Blaxter. Berlin: Springer-Verlag 1974

Möller, H.: Scyphomedusae as predators and food competitors of larval fish. Meeresforschung *28,* 90–100 (1980)

Möller, H.: Reduction of a larval herring population by jellyfish predator. Science, N.Y. *224,* 621–622 (1984)

Olney, J. E.: Eggs and early larvae of the bay anchovy, *Anchoa mitchilli,* and the weakfish, *Cynoscion regalis,* in lower Chesapeake Bay with notes on associated ichthyoplankton. Estuaries *6,* 20–35 (1983)

Omori, M. and W. M. Hamner: Patchy distribution of zooplankton: behavior, population assessment and sampling problems. Mar. Biol. *72,* 193–200 (1982)

Pearcy, W. G.: Ecology of an estuarine population of winter flounder, *Pseudopleuronectes americanus* (Walbaum). II. Distribution and dynamics of larvae. Bull. Bingham Oceanogr. Coll. *18,* 16–38 (1962)

Pollard, R. T.: Observations and theories of Langmuir circulations and their roles in near surface mixing. *In:* A voyage of discovery. George Deacon 70th anniversary volume, pp 235–251. Ed. by M. Angel. Oxford: Pergamon Press 1977

Purcell, J. E.: Influence of siphonophore behavior upon their natural diets: evidence for aggressive mimicry. Science, N.Y. *209,* 1045–1047 (1980)

Purcell, J. E.: Feeding ecology of *Rhizophysa eysenhardti,* a siphonophore predator of fish larvae. Limnol. Oceanogr. *26,* 424–432 (1981 a)

Purcell, J. E.: Dietary composition and diel feeding patterns of epipelagic siphonophores. Mar. Biol. *65,* 83–90 (1981 b)

Rose, M.: Copépodes pélagiques. Faune Fr. *26,* 1–374 (1933)

Shanks, A. L.: Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. *13,* 311–315 (1983)

Sheader, M. and F. Evans: Feeding and gut structure of *Parathemisto guadichaudi* (Buerin) (Amphipoda, Hyperiidae). J. mar. biol. Ass. U.K. *55,* 641–656 (1975)

Stevenson, J. C.: Distribution and survival of herring larvae (*Clupea pallasi* Valenciennes) in British Columbia waters. J. Fish. Res. Bd Can. *19,* 735–809 (1962)

Sutcliffe, W. H.: A new species of calanoid copepod from North Carolina. J. Elisha Mitchell Sci. Soc. *65,* 273–275 (1949)

Theilacker, G. H. and R. Lasker: Laboratory studies of predation by euphausiid shrimps on fish larvae. *In:* The early life history of fish, pp 287–299. Ed. by J. H. S. Blaxter. Berlin: Springer-Verlag 1974

Turner, J. T.: Scanning electron microscope investigations of feeding habits and mouthpart structures of three species of copepods of the Family Pontellidae. Bull. mar. Sci. *28,* 487–500 (1978)

Turner, J. T.: The feeding ecology of some zooplankters that are important prey items of larval fish. NOAA Techn. Rep. NMFS *7,* 1–28 (1984)

Turner, J. T.: Zooplankton feeding ecology: contents of fecal pellets of the copepod *Anomalocera ornata* from continental shelf and slope waters of the Gulf of Mexico. P. S. Z. N. I. Mar. Ecol. (In press)

Turner, J. T. and S. B. Collard: Winter distribution of pontellid copepods in the neuston of the eastern Gulf of Mexico continental shelf. Bull. mar. Sci. *30,* 526–529 (1980)

Westernhagen, H. V. and H. Rosenthal: Predator-prey relationship between Pacific herring *Clupea harengus palassi,* larvae and a predatory hyperiid amphipod, *Hyperoche medusarum.* Fish. Bull. U.S. *74,* 669–674 (1976)

Westernhagen, H. V., H. Rosenthal, S. Kerr and G. Furstenberg: Factors influencing predation of *Hyperoche medusarum* (Hyperiida: Amphipoda) on larvae of the Pacific herring *Clupea harengus pallasi.* Mar. Biol. *51,* 195–201 (1979)

Date of final manuscript acceptance: July 16, 1985.
Communicated by J. M. Shick, Orono