

# Effects of turbidity, light level and prey concentration on feeding of juvenile weakfish *Cynoscion regalis*

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**ABSTRACT:** Highly turbid and dimly lit mid-Atlantic estuaries, such as Delaware Bay (USA), are important nursery areas of juvenile weakfish *Cynoscion regalis* where mysid shrimp *Neomysis americana* dominate their diet. Laboratory experiments were conducted to determine the effect of light, turbidity, and prey concentration on feeding by juvenile weakfish on mysid shrimp. Juveniles were fed 48 mysids daily at turbidities ranging from 0.95 to 11 nephelometric turbidity units (NTU) and light levels ranging from dark to  $0.70 \times 10^{14}$  quanta  $s^{-1} cm^{-2}$ . At all turbidities, they consumed virtually all prey in light as low as  $0.01 \times 10^{14}$  quanta  $s^{-1} cm^{-2}$ . However, complete darkness ( $<0.01 \times 10^{14}$  quanta  $s^{-1} cm^{-2}$ ) reduced feeding regardless of turbidity. Darkness reduced foraging efficiency to a similar degree among prey concentrations ranging from 0.5 to 4 times typical field densities, suggesting that feeding in the dark depends on prey concentration and is likely to depend on a less efficient, non-visual encounter rate. Therefore, under dark conditions adequate feeding may occur only when prey concentration is sufficiently high or when adequately dense patches of prey are encountered with sufficient frequency. Juvenile weakfish appear well-adapted for feeding under the highly turbid and frequently dark conditions of their estuarine nursery areas. Patterns of turbidity/light levels in conjunction with patterns of prey density are likely to control mysid availability to juvenile weakfish and influence patterns of feeding, growth, and survival.

**KEY WORDS:** Turbidity · Light · Fish · Feeding efficiency · Estuaries

## INTRODUCTION

Feeding success can affect growth in the early life of fishes and influence survival, year-class strength, and recruitment (Bannister et al. 1974, Cushing 1975, Folkvord & Hunter 1986, Houde 1987). Many fishes use turbid estuaries as nursery areas (Blaber & Blaber 1980, Boehlert & Morgan 1985) where finely divided suspended solids scatter and absorb light (Williams 1970). Turbidity is a ubiquitous feature of estuaries that can reduce visibility. It may negatively affect feeding success by decreasing reactive distance (Barrett et al. 1992, Gregory & Northcote 1993) and the volume of

water searched (Moore & Moore 1976, Gardner 1981) by reducing visual range (Vinyard & O'Brien 1976). Low light resulting from turbid conditions may also reduce foraging (Diehl 1988) and, coupled with turbidity, may reduce feeding by diminishing prey contrast and visibility (Miner & Stein 1993). Compared with larvae, this effect may be intensified for juveniles which search a larger volume (Boehlert & Morgan 1985, Chesney 1989) or feed on larger, more mobile prey capable of escaping the reduced visual field (Vinyard & O'Brien 1976, Hecht & van der Lingen 1992).

It has been suggested that reduced prey contrast associated with turbidity could reduce feeding success for larval fishes (Johnston & Wildish 1982, Dendrinos et al. 1984). However, in laboratory investigations of turbidity, feeding and growth of larval striped bass *Morone saxatilis* (Chesney 1989) and growth and survival of larval lake herring *Coregonus artedii* (Swenson &

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Matson 1976) were not reduced. For planktivorous fish, feeding ability was reduced under turbid conditions (Gardner 1981) while turbidity reduced growth rates in juvenile salmonids (Sigler et al. 1984). An inverse relationship between condition of esocids and water clarity was observed in the field (Craig & Babaluk 1989).

Delaware Bay (USA) in the mid-Atlantic bight is a nursery for juvenile weakfish *Cynoscion regalis* where mysid shrimp *Neomysis americana* taken by the juveniles near the bottom dominate their diet (Thomas 1971, Merriner 1975, Stickney et al. 1975, Chao & Musick 1977, Gre cay & Targett unpubl.). Juvenile weakfish occur in abundance throughout Delaware Bay, including the highly turbid regions near the head of the estuary (Thomas 1971, PSEGC 1984a), where reduced prey visibility could reduce feeding success. Juveniles from the turbid and poorly lit upper regions of Delaware Bay have a lower gut fullness, a lower proportion of mysids in their diet, and reduced condition and growth (Gre cay & Targett unpubl., R. Paperno, Targett & Gre cay unpubl.). The objectives of this study were to determine the effects of turbidity and light on feeding success and the influence of prey concentration on feeding in darkness.

## MATERIALS AND METHODS

An adult male and female weakfish from Delaware Bay were strip spawned to produce fertilized eggs. Larvae were reared in 300 l cones filled with gently aerated seawater and fed rotifers *Brachionis plicatilis* and *Artemia* sp. nauplii through metamorphosis. Juveniles (ca 35 to 70 mm standard length, SL) were held in recirculated seawater (ca 32‰) and fed live mysids *Neomysis americana* from Delaware Bay.

**Turbidity/light level feeding experiment.** Daily ration of juvenile weakfish (number of mysids consumed daily) was measured and compared among 4 treatments of turbidity and 4 treatments of light in a crossed design. Turbidities were produced with bentonite, measured with a Seatech transmissometer (5 cm beam) and controlled by microcomputer (Gre cay 1989). Turbidity levels equivalent to beam attenuation coefficient values of 27.80, 14.20, 6.50, and 0.65 (11, 6.1, 3.1, and 0.95 nephelometric turbidity units, respectively) were maintained by the apparatus. These levels (henceforth referred to as high, medium, low, and clear) span the range typical of Delaware Bay (Gre cay & Targett unpubl.). Each turbid treatment level had 2 replicate enclosures 20 cm deep × 60 cm wide × 120 cm long (ca 12 l). Salinity, temperature, and photoperiod were maintained at 20‰, 20°C, and 14 h light:10 h dark, respectively. A single fish (ca 35 to 70 mm SL) was placed in each enclosure, held without food for 24 h, and then

weighed prior to each experiment. Live mysids *Neomysis americana* were used for all experiments.

The following schedule was maintained: Each day, within 1 h of lights off, 48 mysids were collectively weighed and placed in each of the eight 120 l containers to provide an initial prey concentration of 400 mysids  $m^{-3}$  — a density typical of Delaware Bay (PSEGC 1984b, Walker 1989). Fish were allowed to feed for the following 24 h. The next day, immediately after lights off, fish were caught in the dark and removed from the containers, and any uneaten mysids were removed from the enclosures. The fish were replaced in the enclosures, and 48 mysids were added. Uneaten shrimp were counted and weighed. This procedure tested all 4 turbidity levels at a single level of light and was repeated for 4 d.

The above protocol was repeated at 4 treatment levels of light. Light was measured with a Biospherical QSP irradiance meter and adjusted by wrapping fluorescent bulbs in concentric layers of screen mesh. Light levels were 0.70, 0.02, 0.01 ( $\times 10^{14}$ ) quanta  $s^{-1} cm^{-2}$  and darkness below the detection limits of the irradiance meter. These levels are henceforth referred to as high light, medium light, low light, and dark, respectively, and typify the range of those measured 1 m off the bottom in Delaware Bay (Gre cay & Targett unpubl.). Each time the experiment was repeated, juveniles were randomly distributed among the 8 replicate chambers. At the end of each experiment, fish were held without feeding for 24 h and reweighed.

Number of mysids consumed daily (daily ration) was the response compared among turbidity and light level treatments with 2-way analysis of variance (ANOVA) following confirmation of normality and homoscedasticity. Tukey's multiple comparison test ( $\alpha = 0.05$ ) was used to determine differences in daily ration among light and turbidity treatments. Within levels of turbidity, mean daily ration was compared among levels of light using 1-way ANOVA followed by Tukey's multiple comparison test ( $\alpha = 0.0125$ ). Similarly, within levels of light, mean daily ration was compared among levels of turbidity. Daily ration was used to calculate foraging efficiency, defined as the proportion of mysids consumed relative to the number initially available.

Because measurements of daily ration and foraging efficiency depended on the reliability with which uneaten mysids were collected, retrieval efficiency was determined. This was done by placing 48 mysids in each enclosure with no fish present and collecting and counting the mysids after 24 h to determine percentage retrieved. This was repeated for 3 d ( $n = 24$ ). Retrieval efficiency was  $98\% \pm 0.014$  (95% confidence interval); therefore, the difference between number of mysids placed in the enclosures and number retrieved was assumed to reflect feeding.

**Prey concentration vs light/dark feeding experiment.** Foraging efficiency was compared among 4 prey concentrations in darkness and low light in the 120 l enclosures. The water was clear; temperature and salinity were as in the turbidity/light level experiments. Prey concentration treatments were 24, 48, 96, and 192 mysids per enclosure corresponding to densities 0.5, 1, 2, and 4 × those typical of Delaware Bay. Prior to the experiment, fish (ca 35 to 70 mm SL) were held without food for 24 h, weighed, and randomly distributed among levels of prey concentration. Each day, mysids were collectively weighed and introduced into the enclosures. Fish fed until lights out when uneaten mysids were removed, the fish were randomly redistributed, and the prey concentrations were restored. Uneaten mysids were weighed and counted to determine foraging efficiency. This was continued for 4 d. The experiment was conducted at low light (14 h light: 10 h dark) and repeated in constant darkness. At the end of the experiments, fish were held without feeding for 24 h and weighed. Foraging efficiency data among prey concentration/light level treatments were transformed by the arcsine-square root operator and analyzed by 2-way ANOVA followed by Tukey's multiple comparison test ( $\alpha = 0.05$ ).

## RESULTS

### Turbidity/light level feeding experiment

There was a slight but significant interaction between light and turbidity in controlling daily ration. However, only the main effect of light level was significant at  $\alpha = 0.05$  (Table 1). There were no differences in daily ration among turbidities within any level of light (Table 2). In all lighted treatments, the foraging efficiency did not differ from 1.00 (except for the medium turbidity/high light treatment which did not differ from

Table 1. *Cynoscion regalis*. ANOVA results using the number of mysids consumed at 4 light levels × 4 turbidity levels as the observation

Source of error	SS	df	F	p
<b>Main effects</b>				
Light	7874.61	3	61.77	0.000
Turbidity	50.55	3	0.40	0.756
<b>Interaction</b>				
Light/Turbidity	836.15	9	2.19	0.029

0.90). In darkness, daily ration was reduced at all levels of turbidity (Table 2). Daily ration did not differ among the high, medium, and low light treatments and virtually all available mysids were consumed. Mean daily ration was 45.6 mysids  $d^{-1}$  in lighted treatments and 26.4 mysids  $d^{-1}$  in darkness.

### Prey concentration vs light/dark feeding experiment

Only the main effect of light was significant in controlling foraging efficiency and there was no interaction between prey concentration and light level in this response (Table 3). At all prey concentrations, there was a significant reduction in foraging efficiency in darkness compared with low light but no differences among prey concentration levels. Across all prey concentrations tested, mean foraging efficiency was 0.71 in darkness and 0.93 in low light (Table 4).

## DISCUSSION

Our experiments show that when light is present, feeding by juvenile weakfish appears unaffected by turbidities and light conditions prevalent in their nursery areas in the upper reaches of the Delaware Bay

Table 2. *Cynoscion regalis*. Feeding by juvenile weakfish at 4 light and 4 turbidity treatment levels. Values are mean number of mysids eaten (No.), foraging efficiency, i.e. mean proportion consumed of the 48 mysids initially available ( $P$ ), and the number of fish per sample ( $N$ ) in parentheses. Within levels of turbidity, mean daily ration and foraging efficiency among treatments with the same superscript were not significantly different at  $\alpha = 0.0125$ . Row means (light) with the same superscript are not significantly different at  $\alpha = 0.05$ . No significant differences existed among column means (turbidity)

Light level	Turbidity level												Row means		
	Clear			Low			Medium			High			No.	P	N
	No.	P	N	No.	P	N	No.	P	N	No.	P	N			
Dark	30.9	0.64	(7) <sup>a</sup>	23.7	0.49	(7) <sup>a</sup>	27.6	0.57	(7) <sup>a</sup>	23.6	0.49	(7) <sup>a</sup>	26.43	0.55	(28) <sup>a</sup>
Low	43.9	0.91	(7) <sup>b</sup>	47.3	0.99	(7) <sup>b</sup>	47.6	0.99	(7) <sup>b</sup>	47.4	0.99	(7) <sup>b</sup>	46.54	0.97	(28) <sup>b</sup>
Medium	43.3	0.90	(7) <sup>b</sup>	47.9	1.00	(7) <sup>b</sup>	47.3	0.99	(7) <sup>b</sup>	47.3	0.99	(7) <sup>b</sup>	46.43	0.97	(28) <sup>b</sup>
High	46.5	0.97	(8) <sup>b</sup>	43.3	0.90	(8) <sup>b</sup>	37.8	0.79	(8) <sup>b</sup>	47.6	0.99	(8) <sup>b</sup>	43.78	0.91	(32) <sup>b</sup>
Column means	41.3	0.86	(29)	40.6	0.85	(29)	40.0	0.83	(29)	41.7	0.87	(29)			

Table 3. *Cynoscion regalis*. ANOVA results of foraging efficiencies at 4 prey concentration levels  $\times$  2 light levels (light/dark)

Source of error	SS	df	F	p
<b>Main effects</b>				
Prey concentration	0.06	3	0.93	0.432
Light	0.63	1	32.20	0.000
<b>Interaction</b>				
Prey conc. $\times$ Light	0.03	3	0.56	0.641

Table 4. *Cynoscion regalis*. Foraging efficiency (mean proportion consumed of the number of mysids initially available) of juvenile weakfish at 4 prey concentration levels and 2 (light/dark) light levels. Different superscripts indicate that differences in row means (light vs dark) are significant ( $\alpha = 0.05$ ). No differences existed among column means (prey concentrations)

Light level	No. of mysids per 120 l enclosure				Row means
	24	48	96	192	
Low	0.98	0.96	0.94	0.84	0.93 <sup>a</sup>
Dark	0.68	0.73	0.75	0.68	0.71 <sup>b</sup>
Column means	0.82	0.84	0.84	0.75	

estuary. In light as low as  $0.01 \times 10^{14}$  quanta  $s^{-1} cm^{-2}$  they feed with a foraging efficiency of 0.98 (this was reduced to 0.84 or 35% of the juveniles' wet weight in the highest prey concentration and possibly represents feeding to satiation). This high efficiency among all levels of turbidity in lighted treatments may be a consequence of the fish having sufficient time to encounter all available prey in the test enclosures. It is possible that differences in foraging efficiency among turbidities may become evident if foraging time is limited. In darkness daily ration was substantially reduced. However, among all tested prey concentrations the daily ration decreased by a comparable proportion of the initial feeding level suggesting that prey capture depends on a less efficient, nonvisual encounter rate between predator and prey.

Previous investigations of fish larvae have yielded results ranging from no effect of turbidity on feeding (Breitburg 1988, Chesney 1989) or growth (Swenson & Matson 1976) to an enhancement of feeding (Boehlert & Morgan 1985). Because predaceous juvenile fishes are larger and visually search a larger volume of water, their feeding may be more affected by turbidity (Boehlert & Morgan 1985, Chesney 1989). In turbid water, juvenile flounder *Platichthys flesus* >6 cm fed less than their smaller cohorts (Moore & Moore 1976). Turbid water reduced reactive distance in small bluegills *Lepomis macrochirus* (Vinyard & O'Brien

1976, Gardner 1981), restricted vision of juvenile salmonids to 2–5 cm (Sigler et al. 1984) and reduced feeding in adult Atlantic croaker *Micropogonias undulatus* and pinfish *Lagodon rhomboides* (Minello et al. 1987). Larger fishes may be more adversely affected by the reduced visual range resulting from turbidity (Gregory 1994). However, feeding by juvenile weakfish is unaffected by turbidities typically found in nursery areas such as Delaware Bay.

Increased light has been reported to improve feeding, growth and survival of larvae by improving prey visibility (Blaxter 1965, Hunter 1967, Barahona-Fernandes 1979, Hinshaw 1985, Chesney 1989). Feeding may be reduced when turbidity reduces light level and prey contrast (Johnston & Wildish 1982, Sigler et al. 1984, Chesney 1989) particularly when prey densities are low (Breitburg 1988). However, in our experiments, juvenile weakfish were efficient predators in highly turbid, dimly lit conditions with continuously declining prey concentrations, and were capable of capturing virtually all available prey within 24 h provided that some light was available.

Fishes vary in their ability to feed in darkness; capture efficiency is not affected by darkness in bream *Abramis brama* and roach *Rutilus rutilus* but is markedly reduced for perch *Perca fluviatilis* (Diehl 1988). Juvenile weakfish are described as visual feeders (Chao & Musick 1977) while other sciaenids (such as larval *Leiostomus xanthurus* and *Micropogonias undulatus*) are known to feed in darkness (Govoni et al. 1983). Our results show that juvenile weakfish can also feed in darkness, albeit at much reduced rates. In the prey concentration/light experiment darkness reduced feeding by 24% at the prey concentrations tested while in the turbidity/light experiment there was a 42% reduction. This difference may be due to the suspended solids interfering with other modes of perception such as olfaction or mechanoreception. While indicative of significant reduction in foraging efficiency, these figures reflect the number of prey available and cannot be applied directly to the field where concentrations would not be expected to change as fish fed (i.e. there would be constant replacement of eaten prey) Despite this, the fact that there are no differences in foraging efficiency among prey concentrations in darkness suggests that feeding in darkness depends on encounter rate for juvenile weakfish.

In this investigation, feeding depended on light as well as prey density. In estuarine regions where light is extinguished by high turbidity, prey density could become inordinately important in influencing feeding success, growth, and survival. Although mysids are ubiquitous throughout Delaware Bay (PSEGC 1984b, Walker 1989), darkness in turbid areas may cause juvenile weakfish to switch from highly efficient visual feeding to less effi-

cient encounter rate feeding. Under such circumstances, feeding could become directly dependent on prey concentration. Such a decrease in efficiency and discrimination in feeding behavior could result in a broadening of the diet and the reduced feeding and condition found among juveniles from these turbid areas (Gre cay & Targett unpubl.). Because juveniles can consume 42% of available mysids in total darkness, a prey concentration of 386 mysids in the 120 l enclosure should enable them to feed maximally, suggesting that a daily initial prey concentration of 3216 mysids  $m^{-3}$  would be necessary to sustain maximal feeding in darkness in the field. However, this density is rarely reached in upper Delaware Bay (PSEGC 1984b, Walker 1989).

It is likely that turbid environments are beneficial to some young fishes. Despite reduced feeding, turbid and dark conditions may confer an advantage in survival by reducing risk of predation by larger predators, as has been speculated for other fishes (Ritchie 1972, Blaber & Blaber 1980, Boehlert & Morgan 1985, Miller et al. 1985). In addition, turbidity may increase encounter rate with prey when fishes increase their foraging activity and/or when schooling behavior of prey increases their dispersal and availability (Vandenbyllaardt et al. 1991). Also, negative effects of turbidity on feeding may be obviated by adopting foraging strategies that expand the diet to include a greater variety of prey (Hecht & van der Lingen 1992). The turbid upper reaches of the estuary may also provide a refuge from marine predators. Using the head of the estuary as part of their nursery area, juveniles may become spatially separated from adult weakfish and summer flounder *Paralichthys dentatus* (Taylor 1988), found in greatest abundance in the lower and middle bay where significant predation by these species occurs (Daiber & Smith 1971).

These experiments underscore the important role of light in feeding by juvenile weakfish, which appear to be unaffected by turbidity; they demonstrate that a less efficient, non-visual encounter rate dependent on prey concentration determines feeding rates in darkness. Therefore, where nursery areas are devoid of light, such as in the turbid upper reaches of Delaware Bay, obtaining sufficient nutrition may depend on mysid densities. Refuge from predators provided by dark and turbid conditions may constitute a survival advantage which obviates the negative effects of reduced feeding and growth rates.

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