



Foraging by estuarine juveniles of two paralichthyid flounders: experimental analyses of the effects of light level, turbidity, and prey type

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ABSTRACT: Juvenile summer flounder *Paralichthys dentatus* and southern flounder *P. lethostigma* inhabit turbid salt marsh estuaries. Predation rates by juveniles (50–90 mm) were examined at 5 daytime light levels (6×10^{11} to 2×10^{14} quanta $s^{-1} cm^{-2}$) and in darkness and 4 turbidity levels (clear $[\leq 1]$, 11, 20, and 40 NTU) at an intermediate light level. Both species fed equally well on benthopelagic mysid shrimp and benthic spionid polychaetes at all daytime light levels tested. However, predation on mysids was significantly reduced in the dark. Consumption of polychaetes was not reduced in the dark by either species, illustrating the effectiveness of non-visual foraging methods on benthic prey. Turbidity levels tested did not affect predation on either prey type by either flounder species. Locomotor behavior was examined at the same turbidity levels. *P. lethostigma* spent more time swimming in the water column than *P. dentatus* in lower turbidity (clear–20 NTU), and both species reduced swimming at 40 NTU. It appears that both species primarily use a benthic-oriented ambush foraging strategy under high turbidity conditions. This is a particularly pronounced switch in foraging style for *P. lethostigma*. Estuarine turbidity is increasing due to the impacts of climate change. When turbidity is elevated enough to eliminate light sufficient for visual feeding on mysids (between darkness and the lowest light level tested), feeding on this motile prey is negatively impacted for both species. Turbidity can thus alter foraging modes and types of prey consumed, affecting nursery habitat quality and the prey base supporting these young fishes.

KEY WORDS: Paralichthyidae · *Paralichthys* · Juvenile · Early life history · Light · Turbidity · Predation · Feeding

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1. INTRODUCTION

Estuaries serve as nursery grounds for the juveniles of many fishes (Weinstein 1979, Hoss & Thayer 1993, Beck et al. 2001, Able & Fahay 2010). Abiotic conditions such as turbidity vary throughout an estuary and influence the distribution of fishes (Cyrus &

Blaber 1992, Hecht & van der Lingen 1992, Lunt & Sme e 2015). Turbidity is typically higher at the head of an estuary, as particles entrained in the freshwater inflow begin to flocculate at a salinity of ~4‰ (Markofsky et al. 1986). Reaching a maximum in oligohaline waters, turbidity generally decreases both upstream of the maximum and downstream toward the estuary

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mouth (Fisher et al. 1988, Park et al. 2008). Turbidity in estuaries is increasing worldwide due to anthropogenic influences such as erosion and sediment resuspension (Ruffin 1998, Lunt & Smee 2015).

Suspended particulates absorb light, causing a decrease in illumination, and scatter light, interfering with vision (Bruton 1985, Gre cay & Targett 1996, Minello & Benfield 2018). High levels of turbidity decrease reactive distance (the greatest distance at which prey are detected) and strike distance and can therefore affect the foraging ability of visual predators (Moore & Moore 1976, Vinyard & O'Brien 1976, Miner & Stein 1993, Minello & Benfield 2018, Bunnell et al. 2021). However, turbid water can offer protection from predators (Hecht & van der Lingen 1992, Maes et al. 1998, Bunnell et al. 2021), affording juvenile fishes a survival advantage during this critical early life stage (Cyrus & Blaber 1987b). Foraging in a turbid environment thus results in a tradeoff in which predation risk may be minimized but foraging rates may not be maximized (Werner et al. 1983). The impact of turbidity on both foraging ability and predation risk may thereby affect nursery habitat quality and, ultimately, year-class strength (Miller & Dunn 1980, Gre cay & Targett 1996, Bunnell et al. 2021).

The distributions of a number of fishes in estuaries have been shown to be dependent upon turbidity (Blaber & Blaber 1980, Cyrus & Blaber 1987a, 1992, Marchand 1993). Furthermore, Cyrus (1992) documented that several taxa common to South African and Australian estuaries are distributed within similar ranges of turbidity at each location. Jager et al. (1995) suggested that high turbidity may restrict feeding by juvenile plaice *Pleuronectes platessa* and flounder *Platichthys flesus* in nursery grounds in the Dutch Wadden Sea.

In the US South Atlantic Bight (SAB), larval summer flounder *Paralichthys dentatus* and southern flounder *Paralichthys lethostigma* move inshore from offshore spawning areas and settle on estuarine tidal flats (Howson & Targett 2020). There is considerable initial overlap in the distribution of post-settlement juveniles (Burke et al. 1991). Juvenile *P. dentatus* typically accumulate on flats in the lower estuary, but juvenile *P. lethostigma* continue to move farther up-estuary where they remain for months in highly turbid, oligohaline habitat (Powell & Schwartz 1977, Burke et al. 1991). With growth, juvenile *P. dentatus* spread into turbid tidal creeks in the lower estuary and also move into the middle reaches of the estuary (Burke et al. 1991). Both species encounter a range of turbidity conditions (0 to >40 nephelometric turbidity units, NTU) during their first few months in estuarine nursery areas.

During the early post-settlement period, both *P. dentatus* and *P. lethostigma* (≤ 20 mm standard length, SL) consume spionid polychaetes, spionid tentacles, and harpacticoid copepods (Burke 1995). However, their diets begin to differ with growth (20–60 mm SL) and differential distribution. Juvenile *P. dentatus* continue to feed mostly on benthos including spionid polychaetes and clam siphons, whereas the diet of juvenile *P. lethostigma* changes to primarily benthopelagic prey such as gammaridean amphipods and mysid shrimp active near or on the bottom (Burke 1995). This difference may be due to differential distribution of the prey (Powell & Schwartz 1979, Burke 1995) or to morphological or behavioral differences in foraging style between the species (Woolcott et al. 1968, Olla et al. 1972, Minello et al. 1987). *P. dentatus* have been reported to be primarily active foragers, whereas *P. lethostigma* are primarily ambush predators (Olla et al. 1972, Burke 1995, Minello & Benfield 2018).

Turbidity levels encountered in the field may impact the effectiveness of particular foraging methods differently (Lunt & Smee 2015, Bunnell et al. 2021). In the case of early juvenile *P. dentatus* and *P. lethostigma*, turbidity may differentially impact (1) foraging on benthopelagic prey such as mysids compared with less motile benthic prey such as polychaetes (e.g. have a different impact on each prey type) and/or (2) different foraging styles (e.g. have a different impact on each flounder species). In addition, potential impacts of turbidity levels on foraging efficiency could cause a change in foraging style (e.g. within flounder species). It has been shown that predation by *P. lethostigma* (130–150 mm total length, TL) on juvenile brown shrimp *Farfantepenaeus aztecus* (31–36 mm TL) decreases with increasing turbidity (Minello & Benfield 2018), although predation by smaller *P. lethostigma* (82–126 mm TL) on similarly sized *F. aztecus* was reported to increase with turbidity (Minello et al. 1987). No comparative information is available on the potential impact of turbidity and light levels on predation or locomotor activity of early juvenile *P. dentatus* and *P. lethostigma* (≤ 80 mm TL).

Because turbidity affects vision by decreasing illumination through light absorption and reducing visibility through light scattering, we used light level and turbidity treatments that allowed assessment of their independent effects on predation rates by early juvenile *P. dentatus* and *P. lethostigma*. Experiments compared potential foraging impacts when feeding on benthopelagic prey (mysid shrimp) vs. benthic prey (polychaetes). Comparisons of species with different foraging styles feeding on different prey types

will (1) help us understand the consequences and potential underlying adaptations associated with differential utilization of estuarine habitat by these flounders and (2) aid in the definition of optimal nursery habitat conditions for each species. The effect of turbidity on locomotor behavior was also compared between flounder species to examine potential differences in swimming responses to reduced visibility by fish with active vs. ambush predation styles.

2. MATERIALS AND METHODS

Three sets of experiments were conducted on juvenile *Paralichthys dentatus* and *P. lethostigma* to test (1) light level effects and (2) turbidity effects on predation rates as well as (3) turbidity effects on locomotor behavior.

2.1. Fish collection and maintenance

Juvenile *P. dentatus* and *P. lethostigma* (30–80 mm TL) were collected from the Newport and Pamlico Rivers, North Carolina, USA, using a beam trawl, haul seine, and otter trawl. Fish were maintained on an ad libitum ration consisting of approximately equal portions (by volume) of frozen mysid shrimp *Neomysis americana*, caught locally in Delaware Bay, and frozen commercial bloodworms (Diptera: Chironimidae). Immediately prior to experiments, fish were acclimated in clear water (≤ 1 NTU) for ≥ 14 d at 20°C, 15‰ salinity, a 12 h light:12 h dark light cycle, and a light level of $\geq 1 \times 10^{15}$ quanta $s^{-1} cm^{-2}$. All experiments were conducted at acclimation temperature, salinity, and light cycle, except for the dark treatment (0 h light:24 h dark).

2.2. Apparatus and general methodology for feeding experiments

Each treatment system consisted of a 243 × 64 cm light-colored tray containing four 60 × 60 × 20 cm clear plastic enclosures (modified from Greay 1989; our Fig. 1). Six 2.5 cm outflow ports were located near the top of each enclosure and covered with 1 mm mesh screening. Each treatment system contained 800 l of unfiltered recirculating seawater. The effective volume of each enclosure was ~60 l. There was one fish per enclosure, and the fish:water volume ratio for each treatment system did not exceed 1 g fish:35 l water. Enclosure bottoms consisted of 1 mm mesh screening to facilitate removal of un-

eaten prey. As flatfish maintained on screening developed irritations on their blind side (U. A. Howson pers. obs.), the screening was covered with a black polyethylene liner while fish were in the enclosure. Enclosures were positioned 5 cm above the tray bottom on a ledge that ran along both sides of the tray.

Two 2.4 m 60 W fluorescent light tubes suspended ~1 m above the water were used as the light source for each treatment system. Because the light spectrum is altered when the light level is reduced by a rheostat, lights were covered by wrapping black fiberglass screening until the desired level of illumination was reached. Illumination was measured as irradiance at the bottom of the enclosures using one of 2 light meters. Light levels ranging from 1×10^{13} to 2×10^{14} quanta $s^{-1} cm^{-2}$ were measured using a QSP 170B Irradiance Meter (Biospherical Instruments), and light levels of 6×10^{11} and 6×10^{12} quanta $s^{-1} cm^{-2}$ were measured with a more sensitive LI-250 Light Meter with quantum sensor (Li-Cor). The dark treatment had no light source and gave no measurable reading on the Li-Cor light meter. Treatment systems were each enclosed with black plastic to eliminate extraneous light.

Fish in the feeding experiments were fed the maintenance diet until the final 7 d of acclimation. At that point, fish were fed ad libitum on approximately equal portions (by volume) of live mysid shrimp *N. americana* and live polychaetes *Marenzelleria viridis* (Spionidae).

P. dentatus and *P. lethostigma* juveniles were tested concurrently for a given set of either light or turbidity treatment conditions. Food was withheld for 24 h prior to the start of each experiment to allow fish to clear their alimentary tracts, then initial weights (g) and lengths (mm) were recorded. Prey concentrations approximated field densities. Mysid shrimp (6–10 mm long) were presented at an initial density of 24 enclosure⁻¹ or 400 m⁻³, an average density in Delaware Bay (Walker 1989, Greay & Targett 1996). Polychaetes (10–20 mm long) were also supplied at a density of 24 enclosure⁻¹ or 67 m⁻². Field densities of *M. viridis* are highly variable and often site-dependent; field densities range from 0–2000 m⁻² (Ray 1990, U. A. Howson pers. obs.), so *M. viridis* density for these experiments was selected to equal mysid density. The experimental enclosures did not include sediment, although spionid polychaetes burrow in the natural environment. This setup allowed us to compare feeding on benthic vs. benthopelagic prey types without burial by *M. viridis* confounding their availability for foraging fish in these feeding experiments. Absolute feeding rates on *M. viridis* do not re-

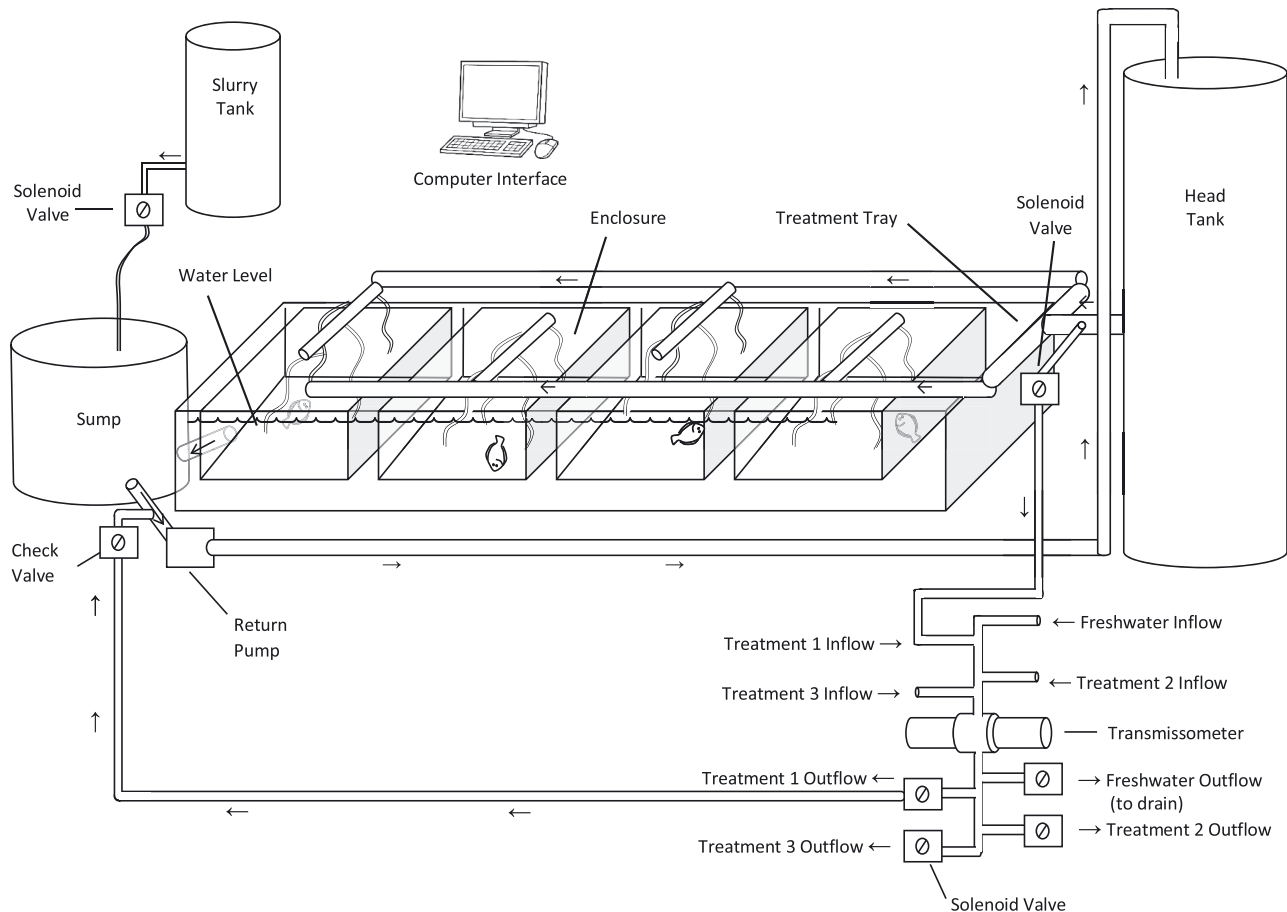


Fig. 1. Schematic of one treatment tray in the apparatus used to examine foraging impacts of light and turbidity levels on early juvenile *Paralichthys dentatus* and *P. lethostigma* preying on mysid shrimp (benthopelagic prey) vs. spionid polychaetes (benthic prey). Two 2.4 m 60 W fluorescent light tubes suspended ~1 m above the water provided light for each treatment tray. The computer interface was connected to solenoid valves associated with the transmissometer and its connected plumbing and with the slurry tank to control turbidity in the turbidity level experiments. Arrows denote direction of water flow. Modified from Greacy (1989)

present those on free-living (burrowing) individuals in nature, as that was not the purpose of this study.

Each day, 2 h prior to lights-on, fish were removed from each enclosure and housed in opaque containers. A hand-held light source with a 660 nm deep red Kodak R-68 filter was used to facilitate removal of fish in the dark. The polyethylene liners were then removed, enclosures lifted from the trays, and remaining prey items removed from the mesh screening and counted. Enclosures were returned to each tray, liners were reinstalled, and a new set of prey was introduced into each enclosure. Each fish was then assigned to another enclosure, as described below. Recovery efficiency of mysid shrimp and polychaetes from enclosures without fish was assessed prior to experiments to ensure >95% recovery of uneaten prey. Ammonium (NH_4^+), nitrite (NO_2^-), and nitrate (NO_3^-) levels were checked before and after each

experiment and never exceeded safe levels during experiments ($\text{NH}_4^+ < 0.1$ ppm, $\text{NO}_2^- < 0.2$ ppm, $\text{NO}_3^- < 20$ ppm; Aquarium Systems FasTest).

2.3. Feeding experiments—light level effects

The effects of light conditions and prey type on predation rates by *P. dentatus* and *P. lethostigma* were examined using 6 treatments: daytime darkness (light not detectable by light meter) and 5 daytime light levels (6×10^{11} , 6×10^{12} , 1×10^{13} , 1×10^{14} , and 2×10^{14} quanta $\text{s}^{-1} \text{cm}^{-2}$) in clear water (≤ 1 NTU). These 6 light conditions are referred to below, in order, as treatments 1–6. Light levels were based on those observed during daylight in the Newport River estuary, North Carolina, 0.3 m above the substrate (U. A. Howson unpubl. data). These levels

were also comparable to the daytime range measured near the bottom in Delaware Bay (Grecay & Targett 1996).

Each experiment included 2 light level treatments (one tray with 4 enclosures per treatment; Fig. 1) and lasted 8 d. An experiment was run using live mysid shrimp (benthopelagic prey) and then repeated with different fish, using live polychaetes (benthic prey). Thus, 6 total experiments were conducted: 3 trials, each with 2 light level treatments run concurrently, for each prey type. Trials (T) were designated by the 2 light level treatments used in the trial, as enumerated above. Trials included T14 (darkness and 1×10^{13} quanta $s^{-1} cm^{-2}$), T23 (6×10^{11} and 6×10^{12} quanta $s^{-1} cm^{-2}$), and T56 (1×10^{14} , and 2×10^{14} quanta $s^{-1} cm^{-2}$). Eight fish, 4 of each species (50–89 mm TL; 1.15–6.21 g) were used per experiment. Two enclosures per treatment tray each held one *P. dentatus* and 2 enclosures each held one *P. lethostigma*. Fish were reassigned to another enclosure every day such that no fish was in the same enclosure twice, and each fish spent 4 d in each light level treatment (1 d enclosure $^{-1}$). Predation rate (number of prey items consumed d^{-1}) of individual fish was measured as the response variable.

There was a significant difference in initial weights of fish among the 3 light level trials (linear model, $p < 0.0001$) but less effect of fish species ($p = 0.09$), prey type ($p = 0.04$), and the trial \times prey type interaction ($p = 0.017$). Accordingly, effects of light level variation on prey consumption were determined for each trial separately.

2.4. Feeding experiments—turbidity level effects

The light-scattering effects of turbidity on predation rates by *P. dentatus* and *P. lethostigma* feeding on both prey types were examined using 4 treatments: 3 levels of turbidity (11, 20, and 40 NTU; means: 180, 234, and 314 mg l^{-1} bentonite, respectively) and a clear treatment (≤ 1 NTU) which served as a control. Treatment levels corresponded to turbidity levels observed in the spring in the Newport River estuary (U. A. Howson unpubl. data), and spanned the range of turbidity typical of SAB and Mid-Atlantic Bight (MAB) estuaries (Able et al. 2010, Whipple et al. 2018). Turbidity (NTU), in the laboratory and *in situ*, was measured with a HF Scientific Model DRT 15 turbidimeter.

To eliminate the light-absorbing effects of turbidity (reduction in illumination), light level from the fluo-

rescent light tubes was adjusted, as described above, so that illumination at the bottom of enclosures was equal (6×10^{12} quanta $s^{-1} cm^{-2}$) across all treatments. Turbidity levels were monitored by a 5 cm beam transmissometer (SeaTech/Western Environmental Technology Laboratories) and controlled by computer in a modified version of the system described in Grecay (1989) (Fig. 1). Computer control was facilitated through a program written in LabView software (v. 5.0.1; National Instruments). The transmissometer measured percentage light transmission through the water, which was converted to a beam attenuation coefficient (α) by $\alpha = 20 \ln(100/T) m^{-1}$, where T is percent transmission. Treatment levels of 11, 20, and 40 NTU corresponded to α values of 27, 38, and 66. Solenoid valves at the outlet of each treatment head tank shunted water sequentially to the transmissometer. After being filled and flushed twice with treatment water, the transmissometer was filled again and a reading was taken and recorded by the computer. If the turbidity was above the level set for that treatment, no adjustment was made. If the reading was below the expected value, the solenoid valve associated with a tank containing a slurry of bentonite and water was opened (for a time proportional to the difference between the reading and the expected level), and slurry was shunted to the sump for that particular treatment tray. After any adjustments were made, the transmissometer was emptied, flushed twice with freshwater, and the cycle was repeated for the next treatment tray. In this manner, each turbidity level was checked and adjusted every 15–20 min. The daily prey removal process re-suspended some bentonite that had settled out over the prior 24 h, causing a short-term (< 1 h) increase in the α value. Each day, computer control was briefly suspended (~ 15 min) to clean the transmissometer optical surfaces.

Two experiments were conducted, one using each prey type. Each experiment consisted of the 4 turbidity treatments run concurrently, with one treatment tray (4 enclosures; Fig. 1) per treatment. A total of 16 fish, 8 per species (62–90 mm TL; 2.01–6.09 g), were used in each 8 d experiment. Two enclosures per treatment tray each held one *P. dentatus* and 2 enclosures held one *P. lethostigma*. Fish were reassigned to another enclosure every day, such that no fish was in the same enclosure twice, and each fish spent 2 d in each treatment. Predation rate (number of prey items consumed d^{-1}) of individual fish was measured as the response variable. Initial fish weights did not differ between fish species or prey types (2-way linear model, $p > 0.05$).

2.5. Locomotor activity experiments — turbidity level effects

The effect of turbidity on activity was examined by observing both flounder species' locomotor behavior in 3 turbidity levels and a clear treatment control. Fish were fed ad libitum on approximately equal portions (by volume) of frozen mysid shrimp *N. americana* and frozen commercial bloodworms (Diptera: Chironimidae) until 1 d prior to a trial. Food was removed immediately prior to the onset of the dark period, and experiments began the following morning within 1 h of lights-on.

Fish were placed individually in 11.4 l circular clear plastic tanks (bottom diameter: 25 cm). Circular containers were used to minimize fish entrapment in corners. Containers were filled with water (salinity: 15‰) to a depth of 20 cm at one of the same 4 treatment levels used in the turbidity level feeding experiments (clear, 11, 20, or 40 NTU). Containers were placed on a clear plastic table, and lighting was provided by a 40 W incandescent bulb suspended above the table. Each container was wrapped in black plastic to eliminate extraneous light and prevent fish from receiving movement cues from fish in neighboring containers. Light levels in containers were adjusted by layering black fiberglass screening over the clear container lid until light at the bottom of each container was 6×10^{12} quanta $s^{-1} m^{-2}$, the light level used in the turbidity level feeding experiments. Aeration was provided by a single air stone centered 5 cm above the bottom, which kept the bentonite in suspension for longer than 4 h. A black blind surrounded the entire experimental apparatus. Trials were videotaped using a CCD camera (Model EO-6500, Exxiss) mounted below the table and connected to a monitor and VCR located outside the room.

A trial began when 4 fish (60–90 mm TL) were placed individually into containers at the 4 treatment levels and the blind was drawn. Preliminary observations indicated that it took up to 2 h for a flounder to initiate movement when placed into a container. A 2 h delay was therefore established before recording began and behavior was then recorded for 30 consecutive minutes. Trials were repeated 5 times for each species, using different fish for each trial. Containers were rinsed with fresh water and allowed to air-dry between trials. Two *P. dentatus* and one *P. lethostigma* jumped from their containers during trials and had to be eliminated from the analyses.

Fish in the containers exhibited behavior typical of fish held in culture tanks. Movements were counted and timed. Bottom movements were characterized by

motion on or closely associated with the substrate, while water column movements were any discrete motion into the water column from a position on the bottom. If a fish changed location in one movement (e.g. traveled on the bottom some distance, then rose into the water column), movement for each location was treated separately. Time spent swimming can vary due to changes in either the number or duration of individual movement bouts, or both, so we examined these subcomponents of water column and bottom activity. Response variables for individual fish during each 30 min trial included total time spent swimming in the water column, moving on the bottom, and inactive on the bottom; number of movements in the water column vs. movements on bottom; and duration of individual movements in the water column vs. movements on bottom.

2.6. Statistical analyses

2.6.1. Prey consumption and light level

The number of prey items eaten per day by individual fish was recorded during each 8 d experiment. Because each fish was measured on a subset of days and treatment levels, random effects associated with day and subject (individual fish) were present but could not be fully accommodated with mixed models. Thus, we used the proportion of prey items consumed by each fish at a given light level over the course of a trial as a measure of consumption. To estimate the effects of light level, fish species, and prey type on prey consumption, we calculated the difference between proportion of prey consumed by individual fish at the 2 light levels run concurrently in a given trial (proportion of prey consumed at higher light level minus the proportion consumed at lower light level). The same individual fish were tested at both light levels in a given trial. The effects of fish species, prey type, and trial were examined using a balanced 3-way replicated linear model, with log transformation of the response variable as suggested by Box Cox analysis, using the R package 'car' (Fox & Weisberg 2011; R v.4.2.1, R Core Team, 2021).

2.6.2. Prey consumption and turbidity

We used the proportion of prey items eaten by each fish as a measure of consumption. For each species, a 2-way unreplicated generalized linear model (GLM) with quasibinomial link function was used to examine the effect of turbidity on prey consumption.

2.6.3. Locomotor activity

Effects of turbidity level and fish species on the proportion of total time spent actively moving, swimming in the water column, plus moving on the bottom were analyzed by linear models. Turbidity level and fish species effects on the number and median duration of individual movement bouts that occurred in the water column and on the bottom were analyzed using linear models for unbalanced designs (Type III sums of squares) using log or square root transformation of the response variable if suggested by Box Cox analysis as implemented in the R package 'car'.

3. RESULTS

3.1. Effects of light level on predation

Predation rates (mean proportion of available prey consumed $\text{d}^{-1} \text{fish}^{-1}$ in a given light level treatment) by *Paralichthys dentatus* ranged from 0.12–0.88 on mysids and 0.21–0.93 on polychaetes (Fig. 2). Rates for *P. lethostigma* were 0.12–0.86 on mysids and 0.48–0.88

on polychaetes. Prey consumption was significantly affected by light conditions (trials), prey type, and their interaction, with no difference between the 2 flounder species (Table 1). Mysid consumption was lower in the dark than in the 5 lighted levels for both species (Fig. 2). In contrast, no such reduction in predation on polychaetes was evident by either flounder species across the range from darkness through the 5 lighted treatment levels (Fig. 2). Light levels, ranging from 2×10^{14} to 6×10^{11} quanta $\text{s}^{-1} \text{cm}^{-2}$ (the lowest lighted level tested), had no effect on mysid or polychaete consumption by either species (Fig. 2), indicating that the light threshold for visual feeding, on motile prey like mysids is between darkness and 6×10^{11} quanta $\text{s}^{-1} \text{cm}^{-2}$. The significant interaction between prey type and trial, but no interaction between prey type and fish species (Table 1), show that predation by both flounder species was similarly affected by prey type in the trial that included the dark treatment.

Although fish weight differed between trials, a substantial decrease in predation on mysids in the dark treatment was exhibited by fish of intermediate weight within the size range of experimental fish (Fig. A1 in the Appendix).

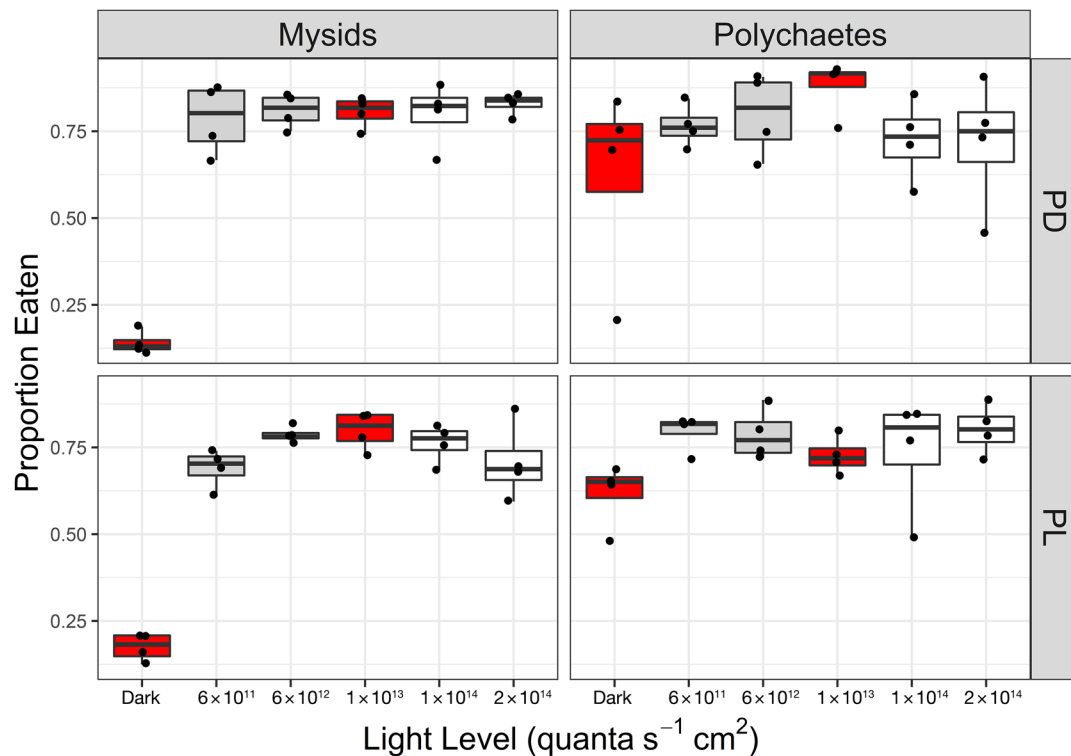


Fig. 2. Predation rates (proportion of available prey consumed) by individual early juvenile *Paralichthys dentatus* (PD) and *P. lethostigma* (PL) feeding on 2 prey types: mysid shrimp (benthopelagic prey) vs. spionid polychaetes (benthic prey) in 6 light level treatments during 8 d experiments. Analysis examined the difference between consumption at the higher and lower concurrently run light level in each of 3 trials. Concurrently run light levels are indicated by different colors. Plots show medians as horizontal lines within boxes, which enclose the middle 50% of the data (25th to 75th percentile); dots are data points for individual fish

Table 1. Results of a 3-way replicated linear model showing the effects of light levels on predation rates of individual early juvenile *Paralichthys dentatus* and *P. lethostigma* feeding on 2 prey types: mysid shrimp (benthopelagic prey) vs. spionid polychaetes (benthic prey) during 8 d experiments. The analysis examined the difference between total consumption at the higher and lower concurrently run light level in each trial, as $\log(\text{difference} + 1.2)$. Trial T14 tested light levels 1 vs. 4, T23 tested light levels 2 vs. 3, and T56 tested light levels 5 vs. 6; where numbers 1–6 refer to light levels in increasing order from (1) dark (light not detectable by light meter) through (2) 6×10^{11} , (3) 6×10^{12} , (4) 1×10^{13} , (5) 1×10^{14} , and (6) 2×10^{14} quanta $s^{-1} cm^{-2}$. **Bold** indicates significance at $p < 0.05$

	Sum Sq	df	F	Pr(>F)
Prey type	0.1223	1	13.5445	<0.0001
Fish species	0.0032	1	0.3519	0.5567
Trial	0.7630	2	42.2438	<0.0001
Prey type × fish species	0.0004	1	0.0452	0.8328
Prey type × trial	0.2410	2	13.3442	<0.0001
Fish species × trial	0.0111	2	0.6145	0.5465
Prey type × fish species × trial	0.0295	2	1.6356	0.2090
Residuals	0.3251	36		

3.2. Effects of turbidity level on predation

Predation rates (mean proportion of available prey consumed $d^{-1} fish^{-1}$ in a given turbidity treatment) by *P. dentatus* ranged from 0.62–0.98 on mysids and 0.62–1.0 on polychaetes. Rates for *P. lethostigma* were 0.54–0.98 on mysids and 0.65–0.98 on polychaetes (Fig. 3). Prey consumption was unaffected by turbidity treatments ranging from clear water to 40 NTU for either flounder species (Fig. 3), and no significant effects of turbidity were detected in any fish species/prey type combination (GLM likelihood ratio χ^2 : *P. dentatus*, mysids = 2.425, $p = 0.521$; polychaetes = 4.194, $p = 0.286$; *P. lethostigma*, mysids = 3.839, $p = 0.247$; polychaetes = 4.002, $p = 0.243$).

3.3. Effects of turbidity on locomotor activity

Overall activity level (time spent swimming in the water column plus moving on the bottom) was significantly affected by turbidity, flounder species, and their interaction (Table 2). *P. lethostigma* spent much

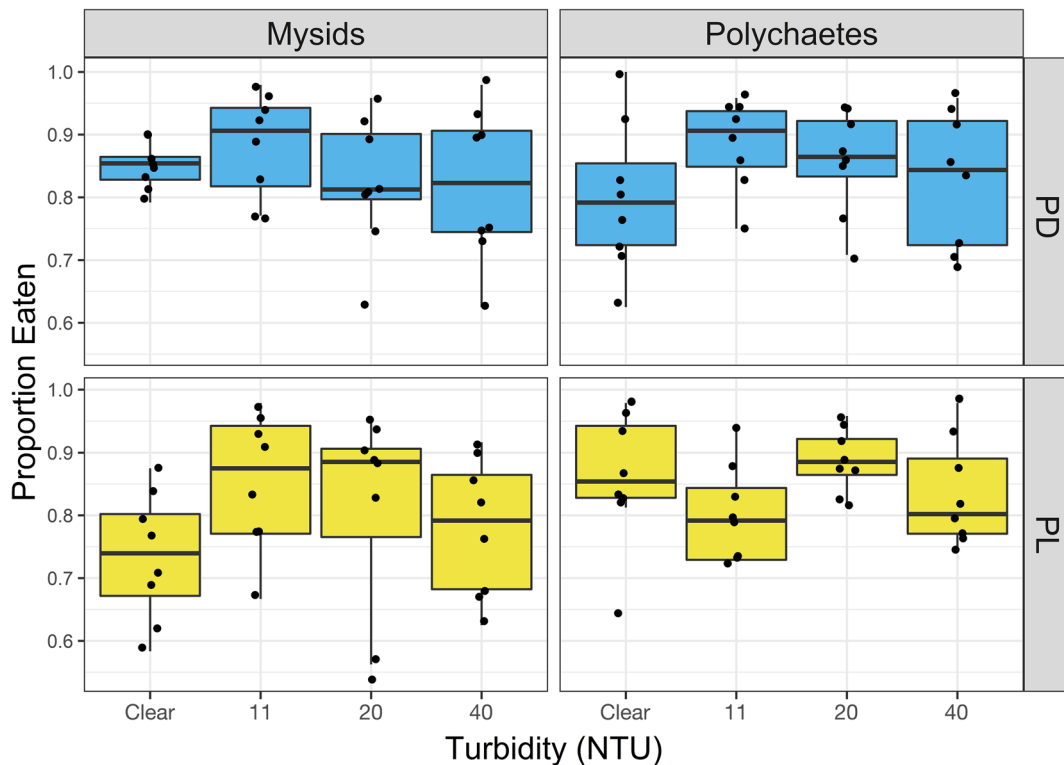


Fig. 3. Predation rates (proportion of available prey consumed) by individual early juvenile *Paralichthys dentatus* (PD) and *P. lethostigma* (PL) feeding on 2 prey types: mysid shrimp (benthopelagic prey) vs. spionid polychaetes (benthic prey) across 4 turbidity treatments during 8 d experiments. Plots show medians as horizontal lines within boxes, which enclose the middle 50% of the data (25th to 75th percentile); dots are data points for individual fish

Table 2. Effects of turbidity levels (≤ 1 , 11, 20, 40 NTU) on the proportion of total time spent actively moving (swimming in the water column plus moving on the bottom) by early juvenile *Paralichthys dentatus* and *P. lethostigma* during 30 min observation periods. Response variable transformed to $1/\sqrt{\text{proportion of time actively moving} + 0.1}$. **Bold** indicates significance at $p < 0.05$

	Sum Sq	df	F	Pr(>F)
Turbidity	10.724	3	33.5877	<0.0001
Fish species	4.065	1	38.1942	<0.0001
Turbidity \times fish species	1.654	3	5.1819	0.0055
Residuals	3.086	29		

more time swimming in the water column than moving on the bottom in clear water and intermediate turbidity levels and also more time swimming in the water column than *P. dentatus* did (Figs. 4 & 5). Both species were relatively inactive at 40 NTU, the high-

est turbidity tested (Fig. 5). *P. dentatus* spent a majority of time inactive on the bottom, regardless of turbidity level (Fig. 4). Activity in the water column varied with turbidity in a non-linear way, as both species appeared to exhibit increased activity at intermediate turbidity level(s) (Fig. 5).

Number of swimming bouts into the water column was influenced primarily by turbidity, with a less significant difference between fish species and no significant interaction (Table 3A, Fig. 6). The turbidity effect appears largely due to both species undertaking fewer bouts into the water column at the highest turbidity level (Fig. 6). Median number of water column bouts during 30 min observation periods for *P. lethostigma* ranged from 14–26 in the clear, 11, and 20 NTU water treatments and declined to 3 in the 40 NTU treatment; the decline by *P. dentatus* was from 4–19 in the clear, 11, and 20 NTU treatments to 0 in the 40 NTU treatment (Fig. 6). Number of move-

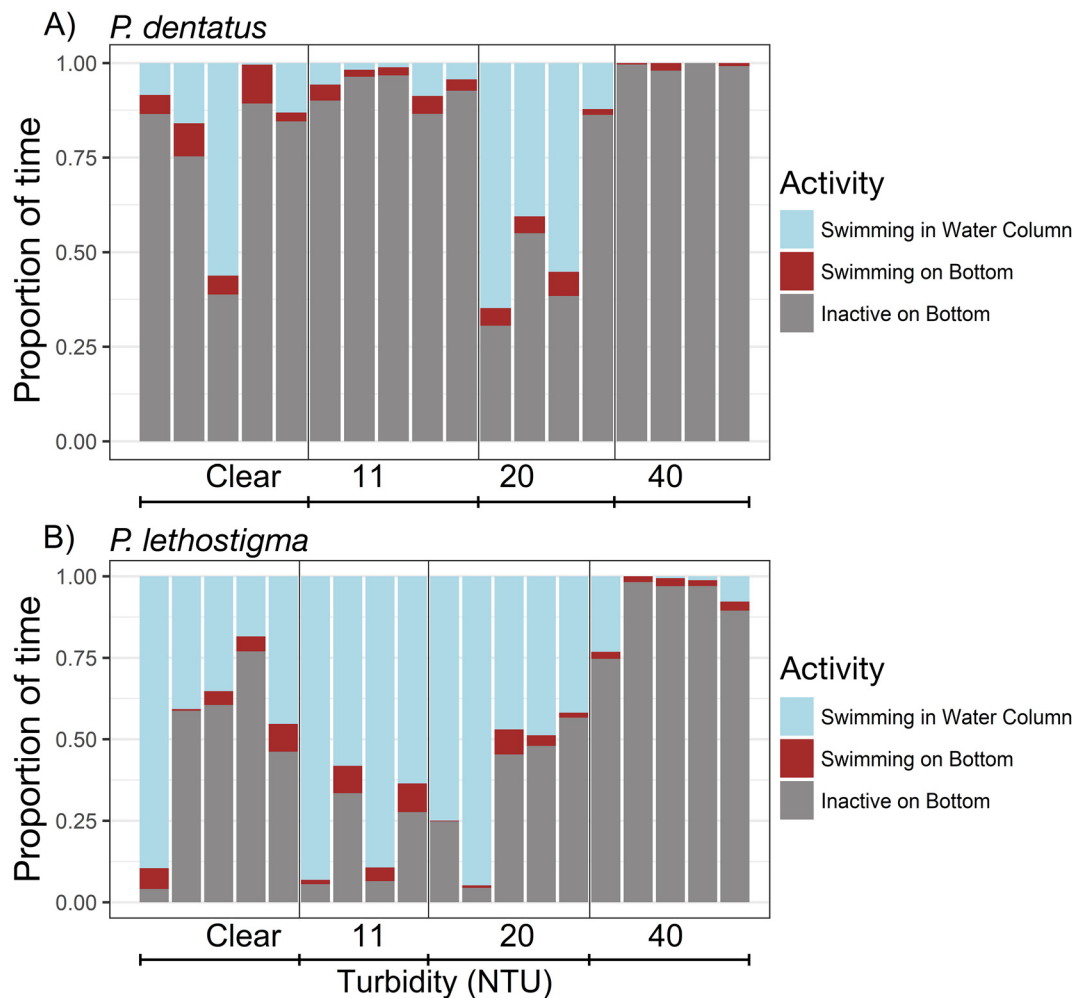


Fig. 4. Proportion of time spent swimming in the water column, swimming on the bottom, and inactive on the bottom across 4 turbidity treatments by individual early juvenile (A) *Paralichthys dentatus* and (B) *P. lethostigma* during 30 min observation periods. Each column depicts activity for an individual fish. Vertical lines separate turbidity treatment levels

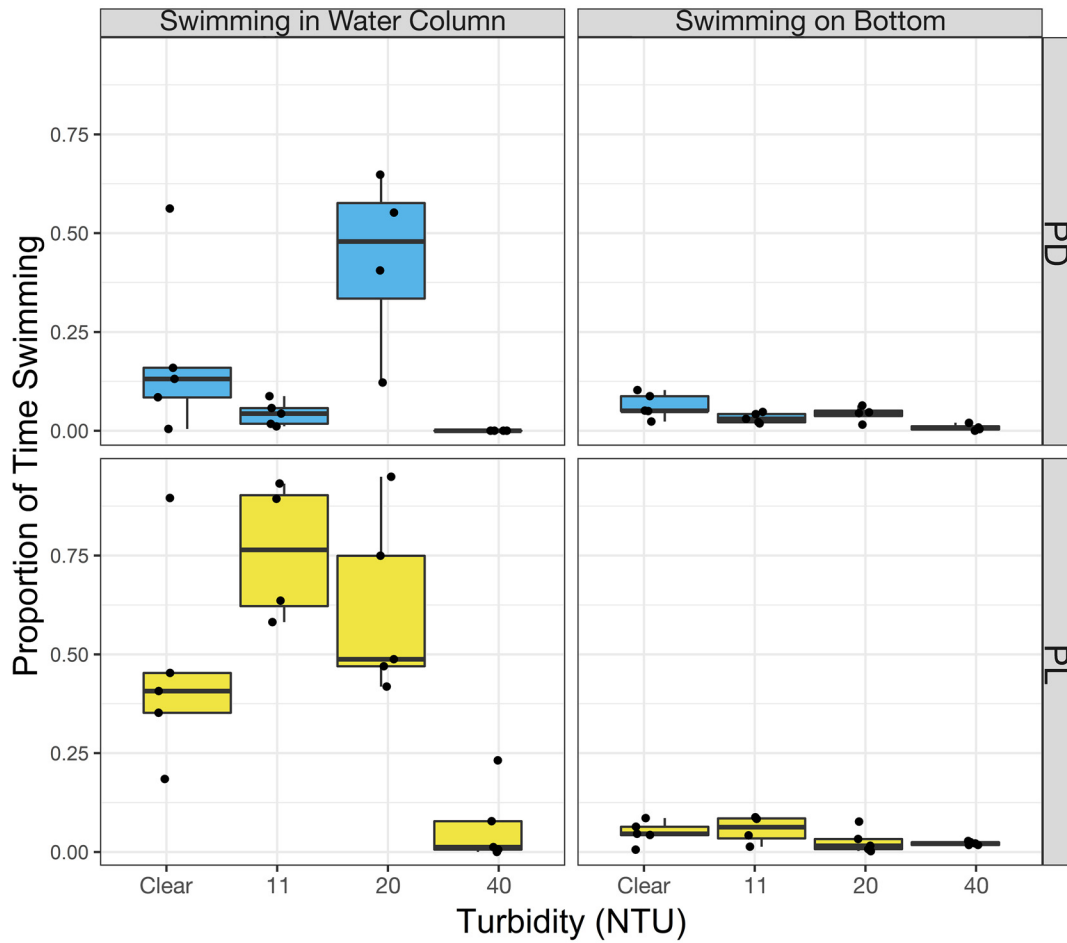


Fig. 5. Proportion of total time spent swimming in the water column vs. swimming on the bottom across 4 turbidity treatments by individual early juvenile *Paralichthys dentatus* (PD) and *P. lethostigma* (PL) during 30 min observation periods. Total time refers to the combined time swimming in the water column, swimming on the bottom, and inactive on the bottom. Plots show medians as horizontal lines within boxes, which enclose the middle 50% of the data (25th to 75th percentile); dots are data points for individual fish

Table 3. Effects of turbidity levels ($\leq 1, 11, 20, 40$ NTU) on the number of individual movement bouts that occurred (A) in the water column and (B) on the bottom by early juvenile *Paralichthys dentatus* and *P. lethostigma* during 30 min observation periods. Response variable transformations: for (A): $\log(\text{number of bouts in the water column} + 2)$; for (B): $\sqrt{\text{number of bouts on the bottom} + 0.1}$. **Bold** indicates significance at $p < 0.05$

	Sum Sq	df	F	Pr(>F)
(A) Number of movement bouts in the water column				
Turbidity	18.846	3	12.8652	<0.0001
Fish species	2.600	1	5.3257	0.0283
Turbidity × fish species	3.174	3	2.1665	0.1135
Residuals	14.160	29		
(B) Number of movement bouts on the bottom				
Turbidity	23.94	3	2.7480	0.0608
Fish species	0.49	1	0.1677	0.6851
Turbidity × fish species	15.51	3	1.7798	0.1730
Residuals	84.23	29		

ment bouts on the bottom was not significantly affected by either turbidity or species (Table 3B). However, *P. dentatus* made more movements on the bottom than into the water column across all turbidity treatments (Fig. 6).

Median duration of individual swimming bouts into the water column was significantly affected by turbidity and fish species, with no significant interaction (Table 4A, Fig. 7). Median duration of bouts into the water column by *P. lethostigma* was longer than those by *P. dentatus* across all turbidity treatments and declined at the highest turbidity level in both species (Fig. 7). Median duration of water column bouts during 30 min observation periods (shown as log-transformed values in Fig. 7) ranged from 32–42 s (in the clear, 11, and 20 NTU water treatments), declining to 11 s in the 40 NTU treatment by *P. lethostigma*; and from 11–20 s to no

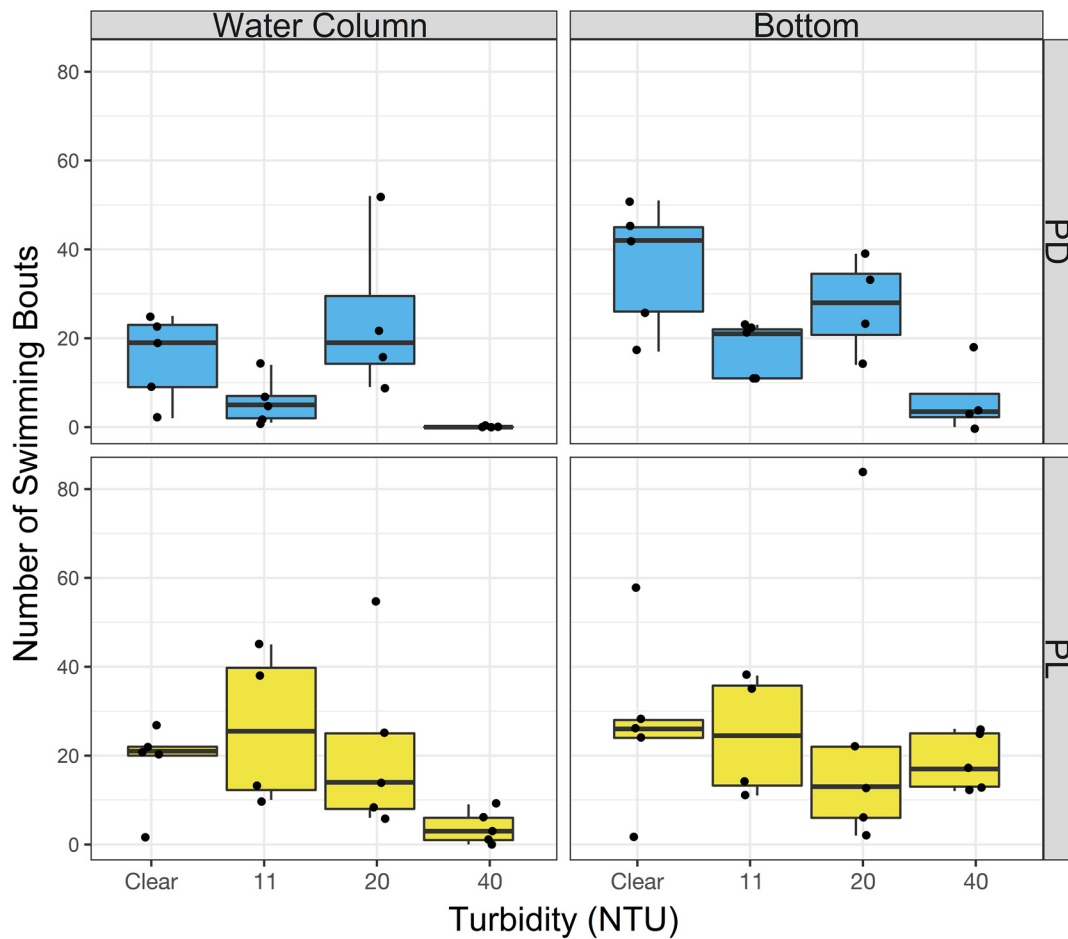


Fig. 6. Number of movement bouts that occurred in the water column vs. on the bottom across 4 turbidity treatments by individual early juvenile *Paralichthys dentatus* (PD) and *P. lethostigma* (PL) during 30 min observation periods. Plots show medians as horizontal lines within boxes, which enclose the middle 50% of the data (25th to 75th percentile); dots are data points for individual fish

Table 4. Effects of turbidity levels ($\leq 1, 11, 20, 40$ NTU) on the median duration of individual movement bouts (A) in the water column and (B) on the bottom by early juvenile *Paralichthys dentatus* and *P. lethostigma* during 30 min observation periods. Response variable transformations: for (A): $\log(\text{median duration of bouts in the water column} + 1)$; for (B): $\text{median duration of bouts on the bottom} + 1$. **Bold** indicates significance at $p < 0.05$

	Sum Sq	df	F	Pr(>F)
(A) Median duration of individual movement bouts in the water column				
Turbidity	31.768	3	10.5011	<0.0001
Fish species	16.758	1	16.6182	0.0003
Turbidity \times fish species	2.641	3	0.8729	0.4664
Residuals	29.244	29		
(B) Median duration of individual movement bouts on the bottom				
Turbidity	5.34	3	3.0205	0.0457
Fish species	0.37	1	0.6202	0.4374
Turbidity \times fish species	0.99	3	0.5583	0.6468
Residuals	17.10	29		

bouts in the same treatments for *P. dentatus*. Median duration of individual movement bouts on the bottom was much less than for those in the water column (except for *P. dentatus* at 40 NTU) and was only slightly affected by turbidity (Fig. 7, Table 4B). Although not visible in the log-transformed Fig. 7 plot, it appears the marginally significant turbidity effect ($p = 0.04$) is due to a relatively small decline in bout duration across treatment levels, particularly by *P. lethostigma*. The range of bout durations for *P. lethostigma* declined from 2–5 s in clear water to 2–4 s, to all 2 s, to 1–2 seconds in the 11, 20, and 40 NTU treatments, respectively.

Taken together, these locomotor activity results show that *P. lethostigma* was the more active of the 2 species and spent much more time swimming in the water column than moving on the bottom in clear water and intermediate turbidity levels. *P. dentatus* spent a majority of time inactive on the bottom,

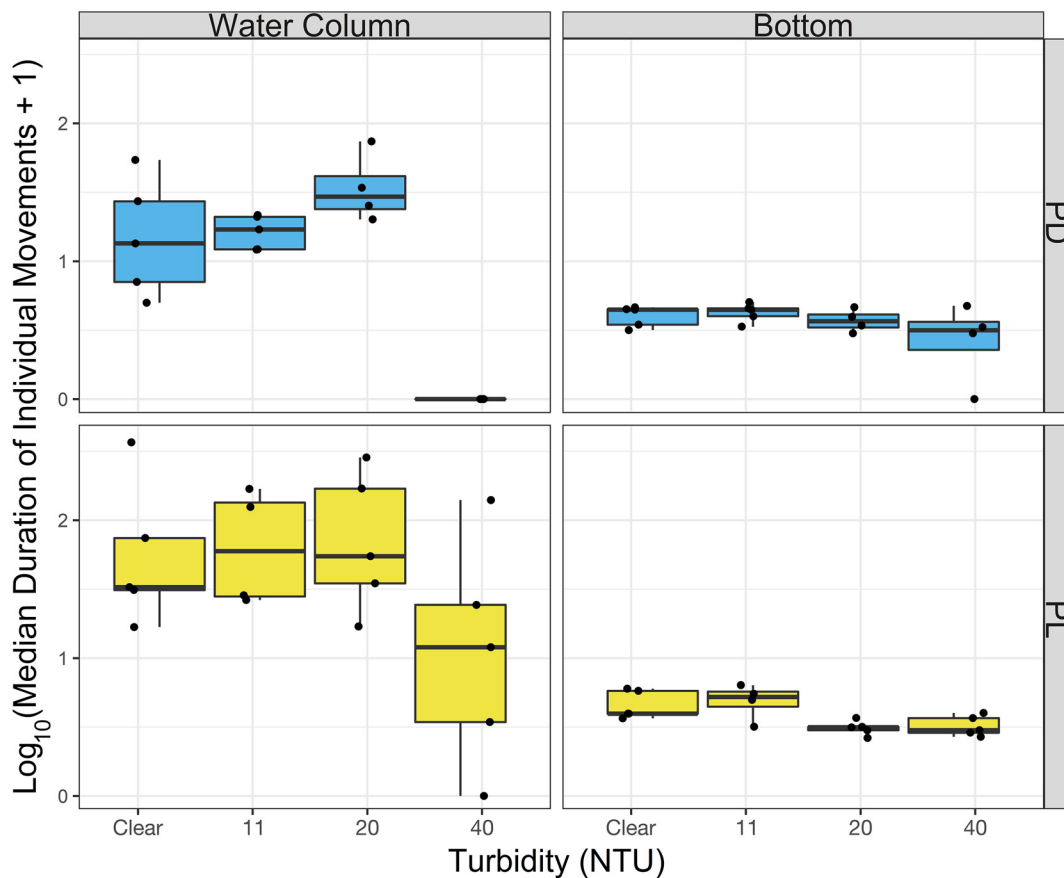


Fig. 7. Median duration of individual movement bouts in the water column vs. on the bottom across 4 turbidity treatments by individual early juvenile *Paralichthys dentatus* (PD) and *P. lethostigma* (PL) during 30 min observation periods. Duration of bouts is plotted as $\log_{10}(\text{median duration} + 1)$ for visualization. Plots show medians as horizontal lines within boxes, which enclose the middle 50% of the data (25th to 75th percentile); dots are data points (medians for individual fish)

regardless of turbidity level. Time swimming in the water column declined significantly for both species at 40 NTU, the highest turbidity tested. The turbidity effect was due to both species undertaking fewer individual bouts into the water column and bouts of shorter duration at the highest turbidity level. This effect was particularly strong for *P. dentatus*. Number and duration of movement bouts on the bottom were relatively unaffected by turbidity; *P. dentatus* made more movements on the bottom than into the water column across all turbidity treatments.

4. DISCUSSION

4.1. Effects of decreased light level on predation

Predation rates have generally been shown to decrease with a reduction in available light (Vinyard & O'Brien 1976, Hinshaw 1985, Utne 1997, Hurst et

al. 2007, Bunnell et al. 2021). In the present study, both *Paralichthys dentatus* and *P. lethostigma* fed equally well on benthic prey and more active benthopelagic prey over the range of light levels tested (6×10^{11} to 2×10^{14} quanta $\text{s}^{-1} \text{cm}^{-2}$). The lowest light levels were lower than in comparable studies that have shown a reduction in feeding with decreased light levels; e.g. 6.0×10^{13} quanta $\text{s}^{-1} \text{cm}^{-2}$ (Vandenbyllaardt et al. 1991) and 6×10^{12} to 4.8×10^{15} quanta $\text{s}^{-1} \text{cm}^{-2}$ (Utne 1997).

There was no reduction in consumption of polychaetes in the dark. The light threshold for visual feeding on motile prey like mysids by these flounder species appears to be between darkness and 6×10^{11} quanta $\text{s}^{-1} \text{cm}^{-2}$. Reduction in available light can result in a decrease in the detection distance between predator and prey and an increase in the incidence of non-visual foraging methods (Higham et al. 2015). Predation on polychaetes in the dark by early juvenile *P. dentatus* and *P. lethostigma* illustrates the

effectiveness of non-visual foraging methods such as prey detection by mechanoreception via the acoustico-lateralis system (inner ear and lateral line) or chemoreception. The fish in this study could potentially consume polychaetes in darkness by chance encounters. However, the magnitude of predation by both flounder species on benthic spionid polychaetes in the dark in the present study is apparently due to a switch in feeding mode to foraging using non-visual cues when visual feeding is not possible. The effectiveness of this feeding mode on benthic prey is evident, as feeding on polychaetes continued in the dark even as density declined during each daily feeding period. The result was no apparent reduction in overall feeding rate compared with feeding in the light.

Other flatfishes have also been shown to employ non-visual foraging mechanisms. Juvenile European plaice *Pleuronectes platessa* primarily use vision for feeding, whereas juvenile sole *Solea solea* rely mainly on mechanoreception and chemoreception, but both species opportunistically consume dead prey items when only chemosensory mechanisms are functional (Batty & Hoyt 1995). Mattila & Bonsdorff (1998) showed that juvenile European flounder *Platichthys flesus* ate more sedentary benthic prey (bivalves) than active epibenthic amphipods in the dark. Predation on both prey types was significantly lower in the dark than in light.

Mysids are negatively phototactic, so their potential use of the entire volume of the experimental enclosures would increase in darkness. Reduced predation on mysids in the dark by both flounder species suggests that they do not forage as effectively on prey dispersed in the water column in the dark, and/or that the fish remain associated with the bottom in the absence of light. Results for the flounder species in the present study are similar to those found for juvenile weakfish preying on live mysids, where predation was unaffected by low light levels (light range from 1.0×10^{12} to 7.0×10^{13} quanta $s^{-1} cm^{-2}$) but was significantly reduced in darkness (Grecay & Targett 1996). This finding is in contrast to predation by several juvenile flatfish species on the macrozooplankton *Artemia* sp. in complete darkness, albeit at low predation rates (Hurst et al. 2007).

At very low light levels, prey may be difficult to detect visually due to a reduction in contrast, and foraging rates can be compromised (Lythgoe 1979, Diehl 1988, Miner & Stein 1993, Bunnell et al. 2021). Mysids are nearly transparent and present less contrast than polychaetes. However, the present results show that predation on mysids by juvenile flounder does not diminish significantly with a decrease in

light to 6×10^{11} quanta $s^{-1} cm^{-2}$. Gulf killifish *Fundulus grandis* fed on grass shrimp *Palaemonetes pugio* in clear water (<2 NTU) equally well at light levels ranging from $14\text{--}20 \mu E m^{-2} s^{-1}$ (8.4×10^{14} to 1.2×10^{15} quanta $s^{-1} cm^{-2}$) (Benfield & Minello 1996). Thetmeyer & Kils (1995) showed that as long as herring *Clupea harengus* were positioned below mysids *Praunus flexuosus* within a $30\text{--}90^\circ$ range, prey contrast was high, and the mysids were visible to the herring. Conversely, visibility of the herring to the mysid prey was low. At other viewing angles, prey contrast was extremely low. Juvenile *P. dentatus* and *P. lethostigma* may utilize a similar strategy to prey on mysids in low light, considering the benthic nature and camouflage ability of these species

4.2. Effects of turbidity on predation

Juveniles of both *P. dentatus* and *P. lethostigma* fed equally well across a range of turbidity levels typical of SAB and MAB estuaries (at 6×10^{12} quanta $s^{-1} cm^{-2}$ light). These results are similar to those of Grecay & Targett (1996), who found that juvenile weakfish fed equally well on live mysids at turbidity levels from 1–11 NTU, at low light levels similar to the present study. However, predation by juvenile sablefish decreased with turbidity up to 10 NTU (De Robertis et al. 2003), while juvenile *P. lethostigma* feeding rate increased with turbidity (30–54 NTU) (Minello et al. 1987). Increased turbidity may have resulted in an interaction between decreasing reactive distance of the predator and an increase in prey activity, which could increase encounter rates and therefore predation rates (Minello & Benfield 2018).

Foraging ability in turbid water is species-specific but can change with ontogeny (Utne-Palm 2002). Prey behavior and abiotic environmental conditions may affect foraging ability (Higham et al. 2015, Bunnell et al. 2021) and potential differences in relative behavioral reactions of predator and prey to turbidity and associated light level (Minello et al. 1987, Benfield & Minello 1996, Reid et al. 1999). Miner & Stein (1993) reported that feeding rates by larval bluegill *Lepomis macrochirus* increased with turbidity (10–31 NTU) at high light levels >460 lx ($\sim 9 \mu mol s^{-1} m^{-2}$ or 5.4×10^{14} quanta $s^{-1} cm^{-2}$) but decreased with turbidity (11–64 NTU) at low light levels <460 lx. They suggested that at low light levels and high levels of turbidity, light intensity is reduced below the threshold required to maximize predation rates, while at high light levels, prey contrast may increase with turbidity. In the present study, predation rates of both

flounder species did not decrease with increasing turbidity, even at the very low light used (6.0×10^{12} quanta $s^{-1} cm^{-2}$ or $0.1 \mu mol s^{-1} m^{-2}$). This suggests that any interaction of turbidity with light intensity at this level was not sufficient to negatively impact visual feeding on either benthopelagic mysids or benthic polychaetes.

Visual adaptations that increase sensitivity to available light and broaden spectral sensitivity, or the ability to see particularly well at certain wavelengths of light (Nicol 1989, Hárosi 1996), could provide a selective advantage to fishes foraging in a turbid environment, where environmental conditions result in reduced light and a limited range of transmitted wavelengths due to particulates in the water. More sensitive vision, offset by reduced acuity, and broader spectral sensitivity occur in benthic sciaenids (Horodysky et al. 2008) and *P. dentatus* (Horodysky et al. 2010), and are likely to be found in *P. lethostigma*. Reactive distance decreases with increasing turbidity in a variety of fishes (Vinyard & O'Brien 1976, Confer et al. 1978, Utne 1997, Lunt and Smee 2015, Bunnell et al. 2021). However, predation rates in the present study did not decrease significantly at any level of turbidity tested on either prey type for either species.

Foraging on spionid polychaetes such as *Marenzelleria viridis*, which have limited visual capabilities (Land & Nilsson 2012), should be largely or entirely a function of reactive distance of predator to prey. Foraging on mysid shrimp, in contrast, is presumably a function of the relative reactive distance of both predator and prey, as mysids have complex eyes with which to see and attempt to evade predators. Increased predation by adult *P. lethostigma* on brown shrimp with increasing turbidity could be mediated, in part, by lower visual acuity of the invertebrate compound eye compared with the vertebrate eye (Land & Nilsson 2012) as well as the lack of reaction of the shrimp to immobile ambush predators (Minello et al. 1987). As there were no significant effects of turbidity on foraging by either flounder species across the turbidity levels tested in the present study, any potential decrease in visual acuity of mysids apparently did not increase their vulnerability to predation.

4.3. Locomotor activity

Although *P. dentatus* and *P. lethostigma* have been previously reported to be active foragers and ambush predators, respectively (Olla et al. 1972, Burke 1995, Minello & Benfield 2018), the present results show that early juvenile *P. lethostigma* are actually the

more active swimmers, particularly at lower turbidity, and *P. dentatus* behave more like ambush predators. Turbidity-related movement in the present study was considered to be hunger-induced exploration related to foraging activity, perhaps altered by perceived predation risk at a particular level of turbidity. Studies have shown that activity in fishes can be affected by turbidity through a tradeoff between its relative effect on foraging success and predation risk (Pangle et al. 2012, Bunnell et al. 2021). Satiated juvenile *P. dentatus* and *P. lethostigma* were far less active than unfed individuals, often remaining mostly inactive on the bottom for hours and exhibiting fewer bouts of movement into the water column (U. A. Howson pers. obs.).

Swimming activity of flounder can also be affected by abiotic environmental conditions whereby the fish seeks more tolerable, or preferred, conditions (Miller et al. 1985). However, thermohaline stress was minimized in the present study by using acclimation and experimental temperature and salinity levels that are not physiologically stressful (Howson & Targett 2020). Elevated turbidity levels may also cause physiological stress in fishes (Newcombe & MacDonald 1991), but threshold levels are typically above naturally occurring turbidity (see Gregory & Northcote 1993).

Movement of flatfish into the water column increases with hunger (Creutzberg et al. 1978), presumably due to an increase in foraging effort. In this study, food had been withheld for ~12 h prior to the beginning of the experiment. Both species spent more time swimming in the water column and on the bottom at lower turbidity (clear–20 NTU), with swimming time diminished by at least an order of magnitude at 40 NTU. Feeding rates in the predation experiments, however, did not change for either flounder species preying on either prey type over this turbidity range. This indicates that the juveniles of both flounder species primarily use an ambush foraging strategy at the highest turbidity tested, possibly a result of increased perceived risk of predation or to exploit changes in prey behavior. Increased predation by adult *P. lethostigma* with turbidity when feeding on brown shrimp was consistent with the ambush feeding style exhibited by adult *P. lethostigma*, coupled with an increase in shrimp activity which increased encounter rates with flounder (Minello et al. 1987). The absence of a decline in feeding rates with increasing turbidity in the present study may also be an indication that experimental turbidity levels did not diminish reactive distance enough to significantly impact feeding rate. Minello & Benfield (2018) proposed that feeding rate would not be impacted by

increasing turbidity until the reactive zone decreased to less than the size of the strike zone (e.g. of an ambush predator).

Predation risk to a camouflaged flounder from visual predators is relatively low regardless of turbidity, as long as the flounder is motionless. However, foraging activity increases predation risk (Lima & Dill 1990). Since reactive distance decreases with increasing turbidity (Vinyard & O'Brien 1976, Moore & Moore 1976, Bunnell et al. 2021), predation risk for a foraging flounder may increase with turbidity as the ability of the flounder to effectively detect predators decreases. Adult *P. dentatus* in the water column exhibit an alarm reaction to movement by immediately dropping to the substrate and remaining still to avoid potential predation (Olla et al. 1972), indicating the importance of vision in predator detection. In the present study, fish movement was limited at high turbidity in both species, suggesting that innate reaction to potential predation risk resulted in behavior consistent with predator avoidance at high turbidity. However, flounder feeding rate did not decrease on either prey type over the turbidity range tested. It appears likely that juveniles of both species primarily use an ambush foraging strategy under high turbidity conditions, and prey on both motile benthopelagic and more sedentary benthic prey as effectively as when more actively foraging under lower turbidity (clear–20 NTU) conditions. This behavior represents a particularly pronounced shift in foraging style for *P. lethostigma*.

Increased hunger over time may motivate fish to increase swimming movements to some degree with time (and thereby increase predation risk) in order to feed more actively (Milinski 1986, Vandenbyllaardt et al. 1991). In the locomotor activity trials, flounder were observed for 30 min (after a 2 h acclimation period), whereas predation rates in the turbidity experiments were assessed every 24 h in 8 d experiments. It is possible that augmentation with more active feeding occurs (as long as light is above feeding threshold levels) when these flounders encounter high turbidity levels for extended periods of time. It should be noted that increases in turbidity to levels ≥ 40 NTU in shallow SAB and MAB estuaries are generally due to storms and associated wind and wave effects occurring over storm-event time scales (Able et al. 2010, Whipple et al. 2018, National Estuarine Research Reserve System 2021). Further research may clarify the temporal stability of the behavioral response to high turbidity (40 NTU) seen by juvenile *P. dentatus* and *P. lethostigma* in the present study.

4.4. Summary

The turbidity levels investigated in this study (clear [≤ 1], 11, 20, and 40 NTU) spanned the range of turbidity typical of SAB and MAB estuaries. Spionid polychaetes (benthic prey) and mysid shrimp (benthopelagic prey) were used as prey in separate trials to test for effects of prey type on the impacts of light and turbidity levels on predation. *P. dentatus* and *P. lethostigma* fed equally well on mysids and polychaetes at all 5 light levels tested (6×10^{11} to 2×10^{14} quanta $s^{-1} cm^{-2}$). However, although predation on polychaetes was not reduced in the dark, feeding by both flounder species on mysids was significantly reduced. The light threshold for visual feeding on motile prey like mysids by these flounder species appears to be between darkness and 6×10^{11} quanta $s^{-1} cm^{-2}$.

Predation rates by both species were not constrained by the highest turbidity level tested (40 NTU) when preying on either prey type, even in low light (6×10^{12} quanta $s^{-1} cm^{-2}$). Turbidity may have an indirect effect on feeding when high turbidity blocks light and visual feeding is eliminated. Absence of a reduction in consumption of polychaetes in the dark by either species illustrates the effectiveness of non-visual cues such as mechanoreception (via the acoustico-lateralis system) or chemoreception when preying on benthic prey. Reduced predation rates on benthopelagic prey by both flounder species in darkness illustrate that although predation continues on more active prey in darkness, foraging efficiency using non-visual cues is reduced.

Although juvenile and adult *P. dentatus* have been reported to be primarily active foragers and *P. lethostigma* primarily ambush predators (Olla et al. 1972, Burke 1995, Minello & Benfield 2018), the present study demonstrates that early juvenile *P. lethostigma* is the more active swimmer of the 2 species, particularly at lower turbidity, and *P. dentatus* spends a majority of time inactive on the bottom regardless of turbidity level. These results suggest that early juvenile *P. lethostigma* are actually the more active foragers and *P. dentatus* behaves more like an ambush predator. However, both species respond similarly in terms of foraging success on each prey type over a range of light and turbidity levels. They also respond similarly in terms of changes in swimming activity over a range of turbidity levels. Under high turbidity conditions, both species—but particularly the more active *P. lethostigma*—substantially reduce water column swimming activity, potentially due to elevation in perceived predation risk, and apparently

adopt an ambush foraging strategy. The observed turbidity effect was due to both species undertaking fewer and shorter individual bouts into the water column at the highest turbidity level; this effect was particularly strong for *P. dentatus*.

Turbidity in estuaries is increasing worldwide due to anthropogenic influences such as erosion and sediment resuspension (Ruffin 1998, Lunt & Smee 2015), and a variety of other processes resulting from climate change and the associated increase in frequency and severity of storms (Rabalais et al. 2009, Robins et al. 2016, Chen et al. 2018, Colombano et al. 2021). Whereas turbidity and low light interact to reduce visibility, constraints on these juvenile paralichthyid flounders are low as long as light is available and turbidity levels are moderate. Locomotory behavior in unfed fish was reduced for both species at 40 NTU, perhaps due to a trade-off between foraging effort and perceived predation risk. However, elevated turbidity can eliminate light sufficient for visual feeding, and the results reported here show the negative impact of darkness on mysid predation by *P. dentatus* and *P. lethostigma*. Also, by reducing swimming in the water column, elevated turbidity can induce a change in feeding mode for both species, which could significantly impact foraging efficiency if food resources are limited or patchily distributed. Turbidity levels can thus alter foraging modes and the types of prey consumed, thereby impacting nursery habitat quality and the prey base supporting these young fishes.

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Appendix.

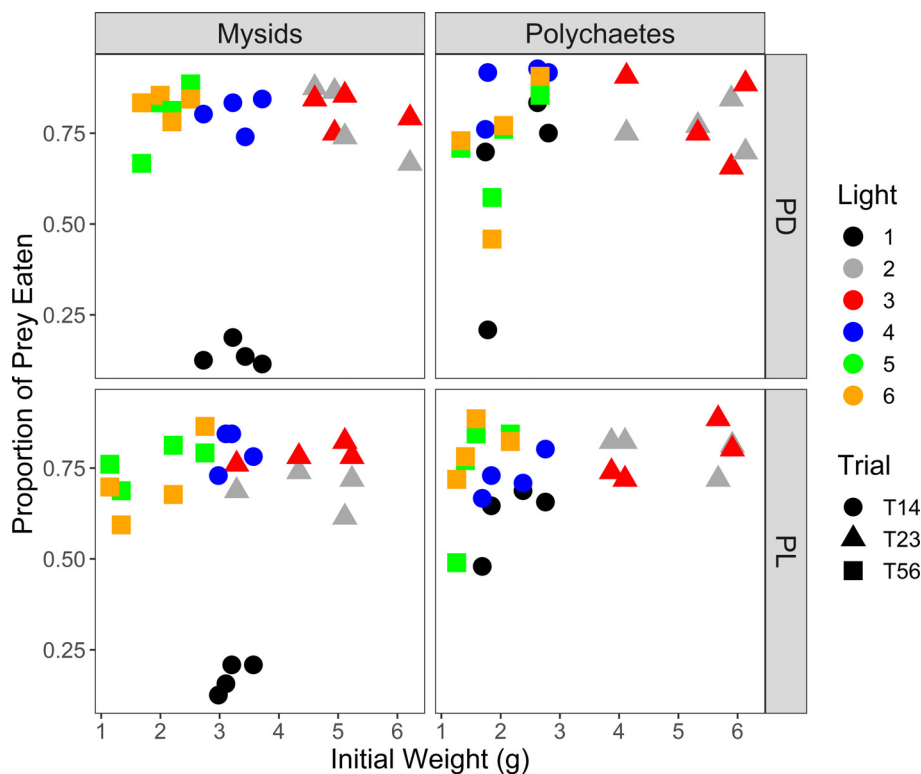


Fig. A1. Effect of initial fish weight on prey consumption (proportion of available prey consumed) by individual early juvenile *Paralichthys dentatus* (PD) and *P. lethostigma* (PL) feeding on 2 prey types: mysid shrimp (benthopelagic prey) vs. spionid polychaetes (benthic prey) in 6 light level treatments during 8 d experiments. For each species–prey combination, each trial consists of $n = 4$ fish at 2 light levels. In each panel, the 2 light levels tested in each trial are separated using color, and the 3 trials are separated by shape. Trial T14 tested light levels 1 vs. 4, T23 tested light levels 2 vs. 3, and T56 tested light levels 5 vs. 6; where numbers 1–6 refer to light levels in increasing order from (1) dark (light not detectable by light meter) through (2) 6×10^{11} , (3) 6×10^{12} , (4) 1×10^{13} , (5) 1×10^{14} , and (6) 2×10^{14} quanta $s^{-1} cm^{-2}$