Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish

Alex De Robertis, Clifford H. Ryer, Adriana Veloza, and Richard D. Brodeur

Abstract: Contrast degradation theory predicts that increased turbidity decreases the visibility of objects that are visible at longer distances more than that of objects that are visible at short distances. Consequently, turbidity should disproportionately decrease feeding rates by piscivorous fish, which feed on larger and more visible prey than particle-feeding planktivorous fish. We tested this prediction in a series of laboratory feeding experiments, the results of which indicated that prey consumption by two species of planktivorous fish (juvenile chum salmon (*Oncorhynchus keta*) and walleye pollock (*Theragra chalcogramma*)) is much less sensitive to elevated turbidity than piscivorous feeding by sablefish (*Anoplopoma fimbria*). Planktivorous feeding in the turbidity range tested (0–40 nephelometric turbidity units (NTU)) was reduced at high light intensity, but not at low light intensity. Comparatively low (5–10 NTU) turbidity decreased both the rate at which sablefish pursued prey and the probability of successful prey capture. These results suggest that turbid environments may be advantageous for planktivorous fish because they will be less vulnerable to predation by piscivores, but will not experience a substantial decrease in their ability to capture zooplankton prey.

Résumé : La théorie de la dégradation des contrastes prédit qu'une turbidité accrue décroît plus la visibilité d'objets qui sont visibles à de plus grandes distances que celle d'objets visibles à de courtes distances. En conséquence, la turbidité devrait faire décroître de façon disproportionnée les taux d'alimentation des poissons piscivores qui se nourrissent de proies plus grandes et plus visibles par comparaison aux taux d'alimentation des poissons planctonophages qui se nourrissent de particules. Une série d'expériences d'alimentation en laboratoire nous a permis de vérifier cette prédiction : la consommation de proies de deux espèces de poissons planctonophages, de jeunes saumons kéta (*Oncorhynchus keta*) et des goberges de l'Alaska (*Theragra chalcogramma*), est beaucoup moins affectée par une augmentation de la turbidité que la consommation de poissons par des morues charbonnières (*Anoplopoma fimbria*). Dans la gamme des turbidités étudiées (0–40 unités néphélométriques de turbidité, NTU), l'alimentation des planctonophages est réduite aux fortes intensités de lumière, mais non aux intensités faibles. Des turbidités relativement faibles (5–10 NTU) entraînent une réduction du taux de poursuite ainsi que de la probabilité de capture des proies chez la morue charbonnière. Ces résultats semblent démontrer qu'un environnement turbide peut être avantageux pour les poissons planctonophages parce qu'ils y sont moins vulnérables à la prédation par les poissons piscivores, sans que leur capacité à capturer des proies zooplanctoniques ne soit substantiellement réduite.

[Traduit par la Rédaction]

Introduction

Scattering and absorption of light by suspended materials in turbid waters limits visibility in aquatic environments through two primary mechanisms. Under elevated turbidity, light attenuation increases (Kirk 1985), decreasing light penetration, which impairs vision. This process is of particular importance to organisms occupying deeper waters because small turbidity-induced changes in light extinction coefficients have large cumulative effects at depth (Eiane et al. 1999). In addition to reducing ambient light intensity, turbidity can impair visibility by degrading apparent contrast (Lythgoe 1979). Scattering of light by suspended materials reduces the apparent difference in brightness between an object and its background, which decreases the visibility of the object. For an object to be visible, its apparent contrast must exceed a physiological threshold value known as the contrast threshold. The contrast threshold of fish depends on factors such as object size and light intensity (Anthony 1981) but should remain constant for a given prey and illumination. In water, the scattering of light due to suspended particles influences contrast as follows (Duntley 1962):

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$$C_a = C_0 e^{-\alpha r} \tag{1}$$

where C_a is apparent contrast, C_0 is inherent contrast of the object, α is the beam attenuation coefficient for visible light (a measure of water clarity and the sum of the absorption (a) and scattering (b) coefficients for visible light), and r is the distance between the object and the eye. The degree of contrast degradation thus depends on the optical properties of the water and increases exponentially with the distance between the object and the eye. Thus, for a given increase in turbidity (α), contrast degradation will reduce the visibility of large prey such as fish that can be seen at great distances (i.e., large r), much more than the visibility of small prey that can only be seen at short distances (i.e., small r). Likewise, contrast degradation is likely to be an important factor in near-surface waters during the day when light intensity is relatively high and prey-sighting distances are long and likely to be less important when light intensity is relatively low and prey-sighting distances are short.

Fishes are the primary visual predators in many aquatic systems and are often functionally divided into piscivores and planktivores, based on their primary prey. The ability of visually foraging fish to detect prey depends on light intensity, water clarity, and prey characteristics such as size, pigmentation, and motion (Confer et al. 1978; O'Brien 1987; Aksnes and Utne 1997). Piscivorous and planktivorous fish consume prey of different sizes, and changes in water clarity are likely to affect them in different ways. Piscivores feed on large conspicuous fish, whereas planktivorous fish feed on small, comparatively inconspicuous zooplankton. Under high light intensity in clear water, piscivores are able to detect fish prey at distances much larger than those at which planktivorous fish are able to detect zooplankton prey (Breck 1993). Thus, for a given increase in turbidity, contrast degradation should disproportionately impair prey detection by piscivores relative to planktivores. All other things being equal, moderately turbid waters may be advantageous habitats for planktivorous fish because their encounter rates with piscivorous predators are reduced more than their encounter rates with planktonic prey.

In this study, we examine the effect of turbidity-induced light scatter on feeding rates in a series of laboratory experiments using two species of fish that are planktivorous as juveniles, chum salmon (*Oncorhynchus keta*) and walleye pollock (*Theragra chalcogramma*), and a piscivore, sablefish (*Anaplopoma fimbria*). We test the prediction that increased turbidity depresses the feeding rates of piscivores more than those of planktivores. In addition, we test the hypothesis that feeding by planktivorous fish is more likely to be impaired by increases in turbidity at high light levels when zooplankton prey are visible at longer distances.

Materials and methods

Fish collection and maintenance

Chum salmon were raised from eggs collected from wild adults returning to Whiskey Creek, Tillamook County, Oregon, in November 2001. When the chum had completely absorbed their yolk sac, they were transferred to seawater. Juvenile walleye pollock (45–60 mm) were captured in May 2002 from Puget Sound near Port Townsend, Washington, by dip-netting them as they aggregated around a light. Fish were transported to the laboratory and held in 720-L tanks provided with a continuous flow of seawater. Pollock were held in the laboratory for 4–6 weeks before experimentation, and chum were held for 6 months before beginning experiments. Sablefish used as predators in the piscivory experiments were collected as ~50-mm juveniles 32 km off the coast of Newport, Oregon, in May 2001 and were held in the laboratory for 13 months. All species were primarily fed formulated foods at rations sufficient to promote growth, but they readily consumed live prey.

Planktivory experiments

Feeding rates of juvenile chum and pollock were measured under varying levels of turbidity and light intensity in six replicate 50 cm × 50 cm × 50 cm glass tanks supplied with flow-through seawater and located inside a light-proof blind. Each tank was equipped with a feeding tube that allowed prey to be introduced from the other side of the blind with minimum disturbance of the experimental fish. The experimental system has been described in detail elsewhere (Ryer and Olla 1999) and will be described only briefly here. Visible illumination was provided by four green 555-nm light emitting diode (LED) illuminators that could be controlled to produce irradiances between 1.9×10^{-7} and 1.0×10^{-3} $\mu E \cdot m^{-2} \cdot s^{-1}$. Green LEDs were selected to mimic the predominant wavelengths of light in coastal marine waters during both day and night (McFarland 1986). Light levels above 1.0×10^{-3} $\mu E \cdot m^{-2} \cdot s^{-1}$ were achieved by supplementing the LED illuminators with additional light emitted by a rheostat-controlled 40-W incandescent light mounted above each tank and reflected from a white ceiling 150 cm above the tank.

Fish are differentially sensitive to different wavelengths of light, and it is unclear how a shift from green to white light may have affected the response of the planktivores. However, changes in spectral composition of light in the experiments are unlikely to have biased the results to a great degree as in both these and previous experiments (Ryer and Olla 1999), planktivorous feeding in the apparatus occurred well below the change from green to multispectral illumination, and there were no large changes in prey consumption when supplemental light was first used.

Light intensity was measured with a radiometer (model 1700; International Light, Inc., Newburyport, Mass.) equipped with a photosynthetically active radiation filtered, cosine response detector. Measurements were made at the water surface with the detector pointed upwards. Illumination in the six replicate tanks differed by 6–18% depending on light level, and the values reported here represent means of the six measurements. Light measurements were made at the beginning of the study and were periodically checked to confirm that light levels were consistent thought the study period.

Turbidity was controlled by adding a bentonite clay suspension to the experimental tanks. Clays are weakly absorptive of visible light, but highly scattering (Kirk 1994), and often are the primary contributor to reductions in beam attenuation coefficient in turbid environments (Vant 1990). A predetermined amount of clay was mixed into 2 L of seawater, and the suspension was slowly added to the experimental tanks through the feeding tube. In experiments in clear water, seawater without clay was added to the tanks in the same manner. Turbidity was measured with a Hach 2100A turbidimeter (Hach, Loveland, Colo.), which quantifies the amount of light from an incandescent bulb scattered at a 90° angle in nephelometric turbidity units (NTU). Preliminary observations indicated that turbidity was reduced by ~50% within 1 h as a result of settling and that fish were agitated by the increase in turbidity for <5 min. To minimize settling during experiments, but allow the fish to acclimate to changes in turbidity, the fish were allowed 30 min to acclimate. A series of preliminary experiments ($n = 25$) established that turbidity after 35 min (i.e., at the end of trials) was reproducible to within 10% of the average level over the range of 0–40 NTU. Turbidity values reported here represent the mean of these measurements.

General planktivory protocol

All planktivory experiments followed a similar experimental protocol: groups of five fish were selected haphazardly from holding tanks and were acclimated to experimental tanks for 16–20 h. Before starting the experiments, the lights were set to the desired intensities, and the flow-through seawater was turned off. To prevent the loss of prey through the outflow drains, the water level in the tank was siphoned down to a height of 37 cm, which is 5 cm below the tank drain. This reduced the water volume in the tank to 93 L. The fish were allowed to acclimate for 60 min before prey introduction.

Live *Artemia salina* were used as a proxy for zooplankton prey in planktivory experiments. Prey cultures were initiated 3–4 days apart, and a subsample of 25 prey was measured daily to ensure that prey size (~2.5 mm) did not vary appreciably between trials. In each trial, 100 prey were counted and placed in a beaker containing 300 mL of seawater. The prey were poured into the experimental tank through a funnel at the end of the feeding tube, and the beaker was rinsed with 750 mL of seawater, which was then poured into the feeding tube. The fish were allowed to feed for 5 min, and the experiment was then terminated by entering the blind and rapidly removing the fish with a dip net. Any prey removed with the fish were quickly separated. Fish were measured and returned to holding tanks and were not reused in subsequent trials. The remaining prey were removed by methodically straining the tank with a fine-mesh dip net for 5 min. Preliminary trials in which prey were added to the tanks without fish and subsequently recovered indicated that almost all prey ($\bar{x}$ ± standard deviation (SD), 98.9 ± 0.3%, $n = 6$) added through the feeding tubes were recovered, and the number of prey missing at the end of the feeding trial was taken to be the number of prey consumed. Experimental temperatures were ~11 °C and ranged between 9.9 °C and 11.8 °C. Five replicate trials were conducted for a given treatment, and the order of trials was randomized in blocks of 2 and 3.

A series of preliminary experiments (5.02×10^{-1} $\mu E \cdot m^{-2} \cdot s^{-1}$, 0 NTU) were videotaped from above to investigate the possibility of quantifying the distance at which prey were detected by planktivores. Analysis of video records indicated that both chum and pollock began making rapid forward movements of up to 10–20 cm followed by sharp turns shortly after prey were introduced. Although prey were generally not resolved in the video records, in several cases we were able to confirm that prey were consumed as the planktivores turned. These observations suggest that prey-sighting distances by both planktivores were on the order of 20 cm at high light intensity in clear water. However, because position of individual prey could not be reliably resolved, we did not further characterize the distance at which prey were detected in the planktivory experiments.

Light threshold of chum salmon

Although the thresholds for visual feeding by sablefish and pollock have been previously established (Ryer and Olla 1999), the threshold for visual feeding by chum salmon, which was required to design the turbidity experiments, was unknown. We thus established the threshold for visual feeding by chum salmon in clear water (0.2 NTU, no added bentonite) by recording prey consumption at 1.14, 1.16×10^{-1}, 1.20×10^{-2}, 0.98×10^{-3}, 1.17×10^{-4}, and 0.91×10^{-5} $\mu E \cdot m^{-2} \cdot s^{-1}$ and in complete darkness ($<1.0 \times 10^{-8}$ $\mu E \cdot m^{-2} \cdot s^{-1}$). Mean *Artemia* length ranged from 2.2 mm to 2.6 mm. Fish length was 42.0 ± 3.3 mm ($\bar{x}$ ± SD), and the mean size of fish did not vary with illumination (analysis of variance (ANOVA), $F_{[6,168]} = 1.55$, $p = 0.17$). Prey consumption was analyzed by one-way ANOVA after a square-root transformation to homogenize variance (Bartlett's test $p = 0.21$) in order to meet ANOVA assumptions. A posteriori multiple comparisons were made using Tukey's test.

Effect of turbidity on planktivory

We investigated the effects of elevated turbidity on planktivory by chum and pollock at two light intensities. A high light intensity was selected such that additional light would not increase feeding rates, and a lower light intensity was selected such that feeding rates were below those observed at high light intensity but above those in the dark. Based on the results of the light threshold of experiment for chum salmon and previous studies of pollock in the same apparatus (Ryer and Olla 1999), trials were conducted at 5.02×10^{-1} (high light) and 4.80×10^{-4} $\mu E \cdot m^{-2} \cdot s^{-1}$ (low light). These light levels correspond approximately to illumination at the water surface during sunrise or sunset and under a half moon, respectively (Macy et al. 1998).

For each species, trials were conducted at 0.2 (no added bentonite), 5.1, 9.3, 19.6, and 39.9 NTU under both high and low light conditions. To remove the confounding effects of decreased light intensity in the turbid treatments (up to 59% reduction, measured at the bottom of the tank), illumination was increased such that the measured light level at the center of the tank was approximately constant (within 5%) over all turbidity levels.

Chum used in turbidity trials averaged 47.0 ± 5.2 mm in length, and size did not vary among treatments (ANOVA, $F_{[9,240]} = 0.87$, $p = 0.55$). Pollock averaged 71.6 ± 7.8 mm in total length, and size did not vary among treatments (ANOVA, $F_{[9,240]} = 0.345$, $p = 0.96$). Mean prey size ranged between 2.2 and 2.6 mm in chum experiments and between 2.4 and 2.9 mm in pollock experiments. Prey consumption was analyzed by two-way ANOVA after a square-root transformation to homogenize variance (Bartlett's test, $p > 0.05$ in both cases) to meet ANOVA assumptions. A posteriori multiple comparisons were made using Tukey's test.

Piscivory experiments

We investigated the effects of turbidity on piscivory by studying predation by 1-year-old sablefish on juvenile chum salmon at 0.4 ± 0.2, 5.1 ± 0.5, and 10.0 ± 0.5 ($\bar{x}$ ± SD) NTU, which correspond to the three lowest turbidity levels tested in the planktivory experiments. Before use in experiments, sablefish were fed shiner surfperch (*Cymatogaster aggregata*) for a week to habituate them to live prey, and then they were starved for 7–12 days to ensure that they would be motivated to feed. Six replicate trials at each turbidity level were conducted in three identical indoor flow-through circular tanks (1.3 m deep, 3 m diameter). To ensure that predator and prey would be visible to overhead video cameras under turbid conditions, water depth was held at 0.5 m at all times by means of an external standpipe. The experimental volume was 2700 L. One replicate at each of the three turbidity levels was tested in a single day, with the order of trials randomized within that day. The tanks were lit with overhead fluorescent lights, which produced a light intensity ranging from 1.29 to 1.45 $\mu E \cdot m^{-2} \cdot s^{-1}$ at the water surface. The highest turbidity level reduced light levels at the bottom of the tank by <15%, and no compensation was made for decreased light intensity in turbid treatments.

In each trial, two sablefish predators (mean length ± SD, 353.8 ± 17.8 mm) were haphazardly drawn from a holding tank and introduced to the arena to acclimate for 16–20 h. Before each trial, an overhead partition was lowered to confine the predators to half of the tank, and the seawater supply was turned off. A turbid suspension was prepared by adding pulverized kaolin to 120 L of seawater. Kaolin was used to produce the desired turbidity rather than bentonite because it was found that settling of kaolin was negligible over a period of 1–2 h. Half of the suspension was pumped into each side of the experimental tank, and an additional 30 L of seawater was used as a rinse. Preliminary turbidity measurements showed that the kaolin suspension mixed through small holes in the partition and dispersed evenly throughout the tank within several minutes. In the 0.4 NTU trials, water without kaolin was pumped into the tanks as a control. After introducing the suspension into the arena, six chum salmon (82.9 ± 11.5 mm) were drawn from a holding tank, measured, and added to the tank opposite the predators. The fish were then allowed to acclimate to conditions in the arena for 70 min. Trials were initiated by turning on the videotape recorders and raising the partition 50 cm above the water surface with a pulley system from a location outside of the field of view of the fish. Predator and prey were allowed to interact for a period of 15 min. After the conclusion of experiments, the lengths of the predators and remaining prey were measured, as were water temperature and turbidity. Tanks were drained and refilled before further use. Fish used in experiments were not used in subsequent trials. Predator size (ANOVA, $F_{[2,33]} = 0.24$, $p = 0.79$) and prey size (ANOVA, $F_{[2,105]} = 0.98$, $p = 0.38$) were not significantly different among turbidity treatments. Experimental temperatures ranged between 9.3 °C and 9.9 °C. Significant changes in prey consumption were identified using the Kruskal–Wallis test, followed with a posteriori multiple comparisons using the Nemenyi test.

To determine whether turbidity affected predator–prey encounter rates or capture success, the number of pursuits was quantified from the video records of experimental trials. Pursuits could be clearly distinguished from routine swimming by sudden acceleration, rapid changes in direction, and prey responses. In some of the clear-water trials, the predators consumed all of the prey in <15 min, and the number of encounters was normalized by the time until all prey were consumed. Capture success was calculated by dividing the number of pursuits by the number of prey consumed. Significant changes in pursuit rate and encounter rates were identified using the Kruskal–Wallis test, followed with a posteriori multiple comparisons using the Nemenyi test.

Effect of type of suspended material

The experiments with planktivores and piscivores differed in the material used to increase turbidity levels, which were measured in NTU. The beam attenuation coefficient of kaolin and bentonite suspensions was measured at nine turbidity levels ranging from 0 to 40 NTU with a Wetlabs C-Star 25 cm path length transmissometer (Wet Labs, Philomath, Oreg.). This instrument measures the sum of absorption and scattering coefficients at a wavelength of 660 nm.

To confirm that kaolin and bentonite had a similar effect on planktivory, the feeding rates of groups of five chum salmon on *Artemia* prey (mean length 2.7–2.9 mm) were measured at 0.3 NTU (no kaolin) and at 9.8 NTU of kaolin-induced turbidity and compared with the results of trials using bentonite (described above). Experiments were conducted at 5.02×10^{-1} $\mu E \cdot m^{-2} \cdot s^{-1}$. Experimental fish averaged 78.9 ± 12.2 mm ($\bar{x}$ ± SD) in length, and fish size did not vary between treatments (*t* test, $t_{48} = 1.40$, $p = 0.17$). Five trials were conducted at each turbidity level.

Results

Light threshold of chum salmon

The relationship between prey consumption by juvenile chum salmon and log light intensity was sigmoidal (Fig. 1). There was a significant decrease in prey consumption at low light intensities (ANOVA, $F_{[6,34]} = 33.5$, $p < 0.001$; Fig. 1). The threshold illumination at which feeding increased was between 10^{-5} $\mu E \cdot m^{-2} \cdot s^{-1}$ and 10^{-4} $\mu E \cdot m^{-2} \cdot s^{-1}$ (~5×10^{-5} $\mu E \cdot m^{-2} \cdot s^{-1}$). Prey consumption reached a maximum at ~1×10^{-1} $\mu E \cdot m^{-2} \cdot s^{-1}$ and did not increase with further illumination.

Effect of light and turbidity on planktivory

Turbidity at the tested levels of 0–40 NTU did not have a strong effect on prey consumption by juvenile chum salmon and walleye pollock except at the highest turbidity at the high illumination (Figs. 2*a*, 2*b*). Although there was a strong light effect for both species, there was a significant interaction between light and turbidity (Tables 1, 2), indicating that the effect of turbidity on prey consumption depends on light intensity. Pairwise comparisons (Tables 1, 2) identified significant turbidity effects only at the higher light intensity.

Effect of turbidity on piscivory

The number of chum salmon consumed by sablefish decreased significantly under elevated turbidity (Kruskal–Wallis test, $H = 13.0$, df = 2, $p < 0.001$). Pairwise comparisons revealed that the number of prey consumed was significantly higher at 0 than at 10 NTU, but prey consumption at these

Fig. 1. Mean number of prey (± standard error) consumed by groups of five juvenile chum salmon (*Oncorhynchus keta*) in clear (0.2 nephelometric turbidity units (NTU)) water at illuminations ranging from $<1 \times 10^{-8}$ (darkness) to 1 $\mu E \cdot m^{-2} \cdot s^{-1}$. Prey consumption at underlined light intensities does not differ significantly (Tukey's test, $p < 0.05$). Five replicate trials were conducted at each illumination, with 100 prey per trial and fish allowed 5 min to feed.

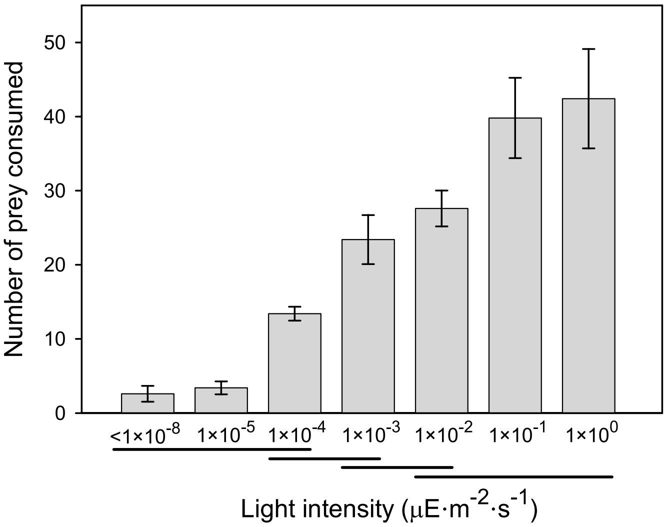
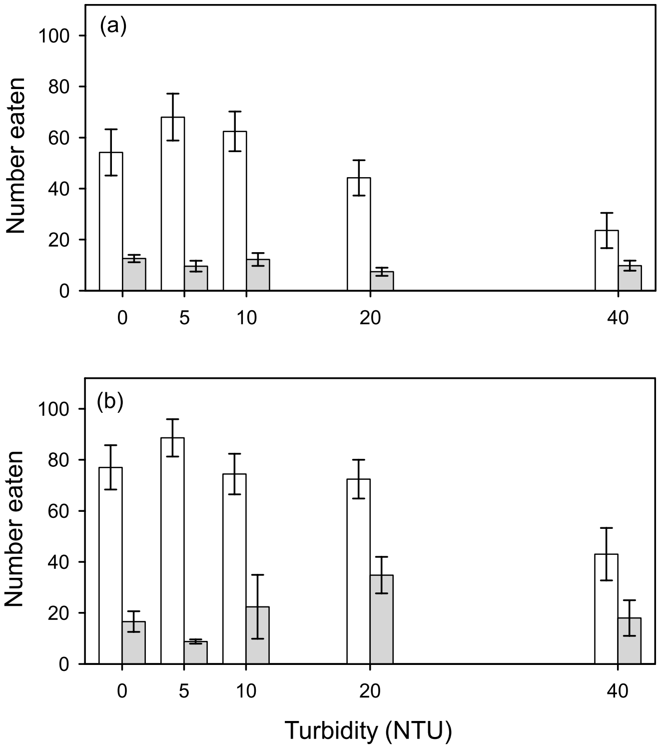


Fig. 2. Effect of turbidity (in nephelometric turbidity units (NTU)) on planktivory by juvenile (*a*) chum salmon (*Oncorhynchus keta*) and (*b*) walleye pollock (*Theragra chalcogramma*). Bars indicate the mean number (± standard error) of prey consumed by groups of five fish at five turbidity levels and two light intensities. Open bars indicate high light conditions (5.02×10^{-1} $\mu E \cdot m^{-2} \cdot s^{-1}$) and shaded bars indicate low light conditions (4.80×10^{-4} $\mu E \cdot m^{-2} \cdot s^{-1}$). Five replicate trials were conducted at each illumination, with 100 prey per trial and fish allowed 5 min to feed.



turbidities could not be distinguished from that at 5 NTU (Nemenyi test). Predation rates were about threefold lower at 5 NTU than in clear water, and no prey were consumed in the 10 NTU trials (Fig. 3).

Analysis of the video records indicated that as turbidity increased, sablefish pursued the chum prey less often (H = 9.76, df = 2, p = 0.008; Fig. 4*a*). Pairwise comparisons revealed that pursuit rates were higher at 0 than at 10 NTU, but pursuit rates at neither of these turbidities could be statistically distinguished from those at 5 NTU (Nemenyi test). In clear water, the sablefish generally responded to the chum immediately after the barrier was raised, crossing the tank and initiating pursuit. Under elevated turbidity, the sablefish did not respond as rapidly to the chum and were often observed to swim around the periphery of the tank as they typically did when no prey were present in the tank. In many cases, the prey tended to occupy the central areas of the tank while the sablefish, which appeared not to detect the prey, swam around the periphery of the tank. In addition to reducing the frequency of pursuits, elevated turbidity reduced the rate of prey capture (H = 11.92, df = 2, p = 0.003; Fig. 4*b*). Pairwise comparisons revealed that pursuit rates were significantly higher at 0 than at 10 NTU, but capture success at either turbidity could not be statistically distinguished from that at 5 NTU (Nemenyi test).

The sablefish did not exhibit stereotyped orienting responses before pursuing chum prey, making it difficult to establish when prey detection occurred. This precluded the calculation of prey-sighting distances from the video records. However, the ability of sablefish to detect prey appeared to decrease substantially as turbidity increased. At 0 NTU, the predators often crossed the 3-m-diameter tank to pursue prey, indicating that prey were visible at distances of over 3 m. At 5 NTU, pursuits were initiated at predator–prey distances of less than 1 m, and pursuit ended when predator and prey were separated by more than 1 m. Pursuits at 10 NTU were initiated when predator and prey were separated by <40 cm.

Effect of type of suspended material

The beam attenuation coefficient (α) measured at 660 nm was linearly related to turbidity in NTU for both the bentonite ($y = 1.44x$, $r^2 = 0.99$) and kaolin ($y = 0.63x$, $r^2 = 0.99$) suspensions. Given that the bentonite suspension had a higher α at a given NTU value, this indicates that bentonite is more absorptive than kaolin at this wavelength. However, the effect of elevated turbidity on the feeding rates of chum salmon was similar regardless of the material used to generate the turbidity. At high light intensity, chum salmon consumed 56.8 ± 10.0 ($\bar{x}$ ± standard error (SE)) prey in clear water compared with 75.4 ± 6.6 at a kaolin-induced turbidity of 10 NTU. Prey consumption in clear water and 10 NTU of kaolin-induced turbidity was not significantly different (t_8 = 1.52, p = 0.16). Although these fish were ~30 mm larger than the fish used in bentonite planktivory trials (see above), the observed 33% increase in prey consumption at kaolin-induced turbidity of 10 NTU relative to control fish of the same size in clear water is comparable to the 15% increase above control observed at 10 NTU generated using bentonite (Fig. 2*a*).

Table 1. Two-way analysis of variance of juvenile chum salmon prey consumption at turbidities ranging from 0 to 40 NTU (nephelometric turbidity units) at light intensities of 5×10^{-4} and 5×10^{-1} $\mu E \cdot m^{-2} \cdot s^{-1}$. Turbidity levels are listed in order of descending prey consumption. Prey consumption at the underlined turbidity levels does not differ significantly (Tukey's test, $p < 0.05$). Degrees of freedom, df.

Factor	*F* ratio	df	*p*
Light	149.1	1,49	<0.001
Turbidity	5.1	4,49	0.002
Turbidity × light	3.8	4,49	0.01

	Turbidity (NTU)				
High light	5	10	0	20	40
Low light	0	10	40	5	20

Table 2. Two-way analysis of variance of prey consumption by juvenile walleye pollock at turbidities ranging from 0 to 40 NTU (nephelometric turbidity units) at light intensities of 5×10^{-4} and 5×10^{-1} $\mu E \cdot m^{-2} \cdot s^{-1}$. Turbidity levels are listed in order of descending prey consumption. Prey consumption at the underlined turbidity levels does not differ significantly (Tukey's test, $p < 0.05$). Degrees of freedom, df; NS, not significant.

Factor	*F* ratio	df	*p*
Light	95.3	1,49	<0.001
Turbidity	2.4	4,49	NS (0.07)
Turbidity × light	3.2	4,49	0.02

	Turbidity (NTU)				
High light	5	0	10	20	40
Low light	20	10	40	0	5

Fig. 3. Effect of turbidity (in nephelometric turbidity units (NTU)) on piscivory by sablefish (*Anoplopoma fimbria*). Bars indicate the mean (± standard error) number of chum salmon consumed by pairs of sablefish in 15-min trials ($n = 6$), with six prey per trial.

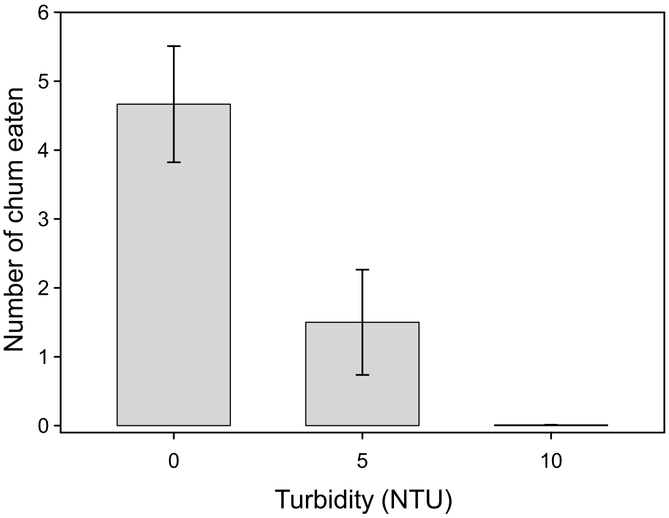
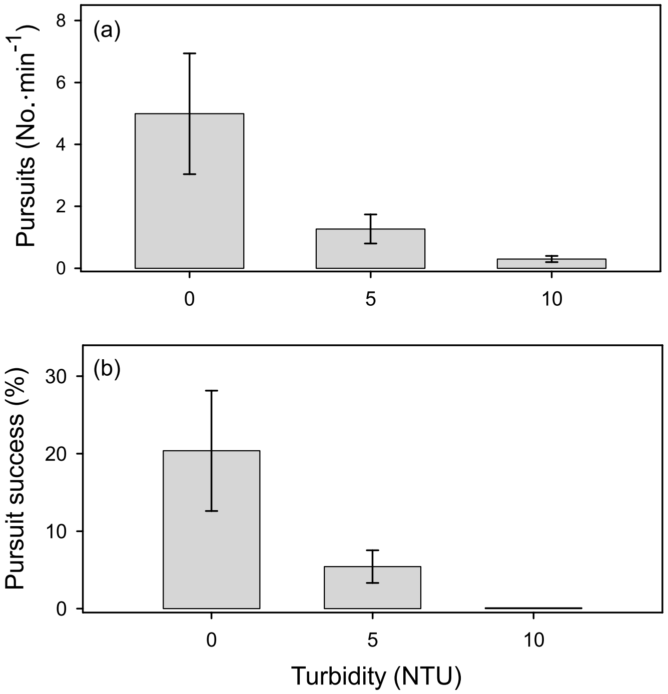


Fig. 4. Effect of turbidity (in nephelometric turbidity units (NTU)) on mean (± standard error) (*a*) pursuit frequency and (*b*) capture success of sablefish (*Anoplopoma fimbria*) feeding on chum salmon (*Oncorhynchus keta*) in 15-min trials ($n = 6$).



Discussion

These experiments indicate that piscivorous feeding by sablefish is substantially more sensitive to elevated turbidity than planktivorous feeding by chum salmon and walleye pollock. At 10 NTU, sablefish did not successfully consume juvenile chum salmon in 15-min trials, whereas feeding by both of the planktivores was unaffected relative to clear water conditions at this turbidity level. Our behavioral observations of sablefish are consistent with the interpretation that their ability to detect and capture prey was substantially impaired at this turbidity level. Although our experiments were designed to measure prey consumption, our observations of foraging fish are similar to previous reports that at high light in clear water, piscivores are able to detect their prey at distances of metres (Breck 1993; Vogel and Beauchamp 1999), whereas planktivores are able to detect prey at distances of 10s of centimetres (O'Brien 1987; Utne 1997).

Our results are consistent with contrast degradation theory, which predicts that the visibility of objects that can be seen at a large distance in clear water will be disproportionately reduced in turbid waters compared with that of objects that are visible at a shorter distance in clear water. This effect is analogous to the familiar situation where fog has little effect on short-range vision but can greatly diminish the visibility of objects at a distance (Lythgoe 1979). These results support the “turbidity as cover” hypothesis (Gregory 1993) and suggest that elevated turbidity may be advantageous for planktivorous fish because they will be less vulnerable to piscivores but will not experience a substantial decrease in feeding opportunity. Although our experiments were conducted with saltwater species, the implications of contrast degradation should be generally applicable and should also apply to freshwater species.

Increased turbidity decreased both the rate at which sablefish pursued chum prey and the probability of prey capture. The reduction in pursuits likely reflects reduced predator–prey encounter rates resulting from a decrease in visibility. Capture success averaged ~20% in clear water, and no successful pursuits were observed at 10 NTU. The generally low capture success reflects the high mobility and maneuverability of the chum prey. Reduced capture success at elevated turbidity indicates that lower prey consumption in turbid water cannot be attributed solely to a reduction in encounter rate, as has been proposed previously (Gregory and Levings 1996). Increased turbidity likely decreases capture success by increasing the probability that prey escape responses will displace the prey outside of an attacking predator’s field of view. Visual encounter models based on piscivore reactive distances (e.g., Beauchamp et al. 1999), which implicitly assume constant capture success, will overestimate feeding opportunities under turbid conditions if capture success decreases in turbid environments.

Our experiment was designed to eliminate the confounding effect of decreased ambient light intensity due to light attenuation under elevated turbidities, and the effects of turbidity on planktivorous feeding observed in the experiments can be attributed primarily to increased scattering of light by suspended materials. High turbidity significantly decreased prey consumption by the two planktivores at the higher illumination, but not at the lower illumination. At lower illuminations, prey will be visible at shorter distances (Aksnes and Utne 1997), which will reduce the effects of contrast degradation relative to high illuminations resulting from a decreased path length between predator and prey. It should be noted that prey depletion over the course of planktivory experiments has the potential to result in an underestimation of prey consumption, particularly in the high light trials in which larger fractions of available prey were consumed. However, given that the trends observed in chum salmon are similar to those of pollock, which consumed more prey, the effects of prey depletion should not alter our primary conclusion that feeding by planktivores is less sensitive to turbidity than piscivores.

Although we did not observe a strong effect of turbidity on prey consumption by planktivores, lower levels of turbidity than those tested here will substantially increase light attenuation with depth. Decreased light penetration will restrict feeding by visually foraging planktivorous fish to shallower water where light levels are higher (Eiane et al. 1999). Because light attenuation increases exponentially with depth (Kirk 1985), the effects of light attenuation will be most pronounced for species that live at greater depths. As a result, the primary effect of turbidity on feeding by planktivorous fish in all but the most turbid waters may be to reduce illumination at depth and thus limit the depth at which fish are able to feed effectively.

The experiments with planktivores and piscivores differed in the material used to manipulate turbidity. The beam attenuation coefficient at 660 nm at a given turbidity (NTU) was measured to be higher for a bentonite than for a kaolin suspension. Given that NTUs are a measure of light scatter, this indicates that bentonite absorbs more light at this wavelength. This suggests that bentonite may be more disturbing to the visual system than kaolin, although this depends on light absorption at other wavelengths, the spectral distribution of ambient light, and the spectral sensitivity of the fish. If this were the case, then our interpretations would be conservative, as the experiments with planktivores were conducted with more visually disturbing suspended materials than experiments with piscivores. However, at 10 NTU, neither bentonite nor kaolin resulted in a significant change in prey consumption by chum salmon, which indicates that the use of different suspended materials does not introduce a substantial bias and cannot account for the difference in turbidity-induced prey consumption between piscivores and planktivores.

In our experiments, we used model species to simulate natural predator–prey interactions. Although all predator species are able to consume prey in complete darkness, they should be considered primarily visual predators as feeding rates in well-illuminated conditions are substantially higher than in the dark (Ryer and Olla 1999; this study). Thus, the results are primarily applicable to fish that visually search for individual prey. Although the *Artemia* used as prey were approximately the same size as natural prey consumed by juvenile chum salmon and walleye pollock (Bailey et al. 1975; Schabetsberger et al. 2000), *Artemia* have poorly developed escape responses and are less likely to escape once attacked by a planktivore. When visibility is poor, prey with more developed escape responses may decrease capture success by moving outside of the predator’s reduced field of vision. Thus, although the use of *Artemia* as prey may adequately reflect encounter rates with small prey, their limited escape responses may bias our experiments as consumption of *Artemia* may be overestimated at low light intensity and high turbidity compared with consumption of more evasive prey. However, given that turbidity at the levels tested had only weak effects on planktivore feeding rate, it is unlikely that elevated turbidity greatly reduced the planktivore’s visual field to the point that it would have greatly increased the ability of more evasive prey to escape. Even if *Artemia* never successfully escape planktivores and the results of the planktivory experiments can be ascribed purely to changes in encounter rate, this does not invalidate the conclusion that piscivores are more sensitive to increases in turbidity than planktivores, as significant decreases in pursuit rate by piscivorous sablefish were observed at 10 NTU, whereas no changes in prey consumption by the two planktivores were observed at this turbidity level.

A substantial body of work has demonstrated that high turbidity decreases the distance at which planktivorous fish are able to detect prey (e.g., Vinyard and O’Brien 1976; Confer et al. 1978; Utne 1997). Turbidity in many of these studies was measured based either on light absorbance or on measures of visibility to human observers, and these studies are thus not directly comparable to our experiments. Studies of particle-feeding planktivorous fish in which turbidity was measured in a comparable manner support our conclusions, as they suggest that relatively high turbidity is required to reduce prey consumption. In a comparative study of diadromous planktivores, a significant decrease in feeding rate was observed in three species at turbidities of 20, 160, and 640 NTU, whereas three other species were unaffected by turbidities as high as 640 NTU (Rowe and Dean 1998). Feeding of juvenile chinook salmon on adult *Artemia* decreases at >150 NTU, although prey-sighting distance decreases by ~50% by 25 NTU (Gregory and Northcote 1993). Planktivory by bluegills is reduced at turbidities of 60 NTU (Gardner 1981). Overall, these studies indicate that moderately high levels of turbidity are required to impair feeding by planktivorous fish.

The distance at which fish are able to respond to other fish is known to decrease sharply with small increases in turbidity. Measurements of the reactive distance of lake trout to salmonid prey indicate that turbidities as low as 3 NTU will decrease reactive distances by ~40% under well-illuminated conditions (Vogel and Beauchamp 1999). The distance at which bluegills are able to detect largemouth bass predators is highly dependent on turbidity, decreasing from ~210 cm in clear water to ~35 cm at 5 NTU (Miner and Stein 1996). These measurements are consistent with our results and suggest that turbidity greatly impairs the ability of fish to detect large, visible objects. However, previous experimental studies of prey consumption by piscivores (Vandenbyllaardt et al. 1991; Reid et al. 1999) have demonstrated statistically significant decreases in prey consumption only at substantially higher turbidities than those tested in this study (37 NTU and 100 NTU), respectively. Gregory and Levings (1996) did not detect a significant difference in predation by cutthroat trout on juvenile salmonids at turbidities as high as 87 NTU. These results may be attributable to methodological differences. Previous studies used comparatively long experimental periods (1–162 h), which constrained highly mobile predators in fairly small volumes for extended periods, and predator satiation may have masked changes in predator–prey encounter rates (Gregory and Levings 1998). This experimental bias is consistent with previous experiments in which elevated turbidity was observed to decrease feeding by piscivores in 1-h but not 4-h trials (Vandenbyllaardt et al. 1991). In addition, the piscivores in our experiments were starved, which motivated them to feed.

Increases in turbidity alter the background against which a prey item is viewed and can lead to increases in the inherent contrast between the prey and the background. This makes the prey more visible and can compensate for turbidity-induced degradation of apparent contrast. However, this does not appear to be a primary effect in our study, as piscivory by sablefish decreased sharply at elevated turbidity, and prey consumption by both species of planktivores was not significantly elevated in turbid vs. clear water. The relative importance of turbidity in increasing prey background inherent contrast decreases sharply with the distance at which prey can be seen (Fiksen et al. 2002). Thus, turbidity-induced changes in prey inherent contrast should be most important for larval fish and least important for piscivorous fish. This prediction is consistent with studies of larval fish that have shown that under well-lit conditions, elevated turbidity either has a minor effect on feeding rate (Breitburg 1988) or leads to an increase in feeding rate (Boehlert and Morgan 1985; Miner and Stein 1993).

If, as our experiments suggest, feeding by piscivores is substantially more sensitive to elevated turbidity than feeding by planktivores, then turbid habitats may be favorable for planktivorous fish, as they will be less vulnerable to attack by piscivores. Recent studies indicating that elevated turbidity makes planktivores less susceptible to predation by piscivores (Gregory and Levings 1998; Beauchamp et al. 1999; Johnson and Hines 1999) support the notion that turbid waters may be favorable habitats for planktivores. This is consistent with the distribution of small fishes in both freshwater and marine environments, where small fish are often associated with more turbid waters (e.g., Blaber and Blaber 1980; Heege and Appenzeller 1998). For example, 16 of 20 species of juvenile fishes studied in a turbid estuary were disproportionately found in waters with turbidities exceeding 10 NTU (Cyrus and Blaber 1987). In addition, planktivorous fish may respond to turbid water by decreasing predator-avoidance behaviors (Gregory 1993; Miner and Stein 1996; Abrahams and Kattenfeld 1997). This may be advantageous, as predator-avoidance behavior often comes at the cost of decreased feeding opportunities (Gilliam and Fraser 1987; Lima and Dill 1990).

Turbidity levels sufficient to reduce the effectiveness of piscivory are more likely to occur in freshwater and estuarine environments than in marine environments. Turbidity in these habitats is often high as a result of inputs of inorganic particles from land (Kirk 1985). However, turbidity may have a locally important effect in productive coastal marine habitats during dense phytoplankton blooms (Lovvorn et al. 2001), in river plumes (Grimes and Kingsford 1996), or in areas where bottom sediments are resuspended (Churchill et al. 1994). Estuaries serve as nursery areas for many marine fishes; turbidity in these habitats may often be sufficient to reduce vulnerability to visual predators (Blaber and Blaber 1980; Miller et al. 1985; Vant 1990). For instance, turbidity has the potential to reduce the mortality of juvenile salmon, such as the chum used as both predator and prey in our experiments, which often inhabit turbid freshwater and estuarine habitats. Salmonids are often associated with river plumes in the coastal ocean during their first months in the ocean, and decreased visibility in these environments is unlikely to affect planktivorous feeding but may be sufficient to reduce vulnerability to piscivorous fish and seabirds. Focused field studies (e.g., Gregory and Levings 1998) should be conducted to evaluate if turbidity reduces predation risk for planktivorous fish exposed to natural environmental conditions and predator assemblages.

In conclusion, turbidity decreases visibility in aquatic systems by decreasing light penetration and reducing apparent contrast. Our experiments suggest that there is an asymmetry in how turbidity-induced contrast degradation affects the feeding rates of visually hunting piscivorous and planktivorous fish. This asymmetry has important ecological implications, as moderately turbid aquatic environments may provide an advantage for planktivorous fish. Increased turbidity will decrease predation risk substantially more than the ability to feed on zooplankton prey. Our inferences are limited in scope because they are based on experiments with two species of planktivores and a single piscivore. However, we anticipate that our results are broadly relevant to these two trophic levels, as the expectation that piscivores are more sensitive to turbidity is based on fundamental optical principles.

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