

Effects of turbidity on the reactive distance, search time, and foraging success of juvenile Atlantic cod (*Gadus morhua*)

Justin J. Meager, Turid Solbakken, Anne C. Utne-Palm, and Tina Oen

Abstract: We investigated the effects of turbidity on the foraging behaviour of juvenile Atlantic cod (*Gadus morhua*) on mysid prey (*Praunus neglectus*) in the laboratory. The influence of turbidity on vision and chemoreception was examined by measuring reactive distances and search times to visual, chemical, and visual-chemical prey cues over turbidity levels ranging from 0.4 to 17·m⁻¹ (beam attenuation·m⁻¹). We also compared foraging rates of juvenile cod on mysids in highly turbid water and clear water under well lit and totally dark conditions. Juvenile cod using chemical cues were able to locate mysids from significantly longer distances than when only visual cues were available. Turbidity did not affect reactive distance to chemical cues, and had only a weak negative effect on reactive distance to visual and visual-chemical cues. Search time was variable, but tended to increase with turbidity. Turbidity did not affect predation rates on free-ranging mysids, but predation rates were significantly lower in dark conditions than in well lit conditions. We suggest that juvenile cod use chemoreception in conjunction with vision (at close ranges) to locate prey in highly turbid water.

Résumé : Nous avons étudié les effets de la turbidité sur le comportement de prédation de jeunes morues franches (*Gadus morhua*) sur des proies mysidacées (*Praunus neglectus*) en laboratoire. Nous avons déterminé l'influence de la turbidité sur la vision et la chimioréception en mesurant les distances de réaction et la durée de la recherche en fonction de signaux visuels, chimiques et chimiques-visuels des proies sur une gamme de turbidités de 0.4 à 17·m⁻¹ (atténuation du faisceau·m⁻¹). Nous avons aussi comparé les taux d'alimentation des jeunes morues sur les mysidacées dans de l'eau fortement turbide et de l'eau claire dans des conditions de bonne lumière et d'obscurité totale. Les jeunes morues sont capables de localiser les mysidacées à l'aide de signaux chimiques à des distances significativement plus grandes qu'à l'aide de seuls signaux visuels. La turbidité n'affecte pas la distance de réaction aux signaux chimiques et elle n'a qu'un faible effet négatif sur la distance de réaction aux signaux visuels et chimiques-visuels. La durée de la recherche des proies est variable, mais elle tend à augmenter en fonction de la turbidité. La turbidité n'affecte pas les taux de prédation sur les mysidacées libres, mais les taux de prédation sont significativement plus bas en conditions d'obscurité que de bon éclairage. Nous pensons que les jeunes morues utilisent la chimioréception en conjonction avec la vision (à courte distance) pour localiser leurs proies dans les eaux très troubles.

[Traduit par la Rédaction]

Introduction

Growth and survival of juvenile Atlantic cod (*Gadus morhua*) depends on their ability to detect and capture prey items, such as small crustaceans and fish (Hawkins et al. 1985; Grant and Brown 1998), which are often highly mobile and difficult to catch (Arnott et al. 1998; Arnott and Pihl 2000). The ability of fish to visually detect such prey can be limited by prey visibility and the optical environment (e.g., spectral composition, light intensity, turbidity; Vinyard and O'Brien 1976; Utne-Palm 1999). Turbidity from suspended sediment, dissolved organic matter, and plankton

scatters and absorbs light and can reduce the reactive distance of fish (Gregory and Northcote 1993; Vogel and Beauchamp 1999 and references herein).

Coastal habitats used as nurseries by juvenile cod (Godø et al. 1989; Grant and Brown 1998) may be affected by increases in turbidity from human activities that lead to eutrophication and suspension of sediments (Bonsdorff et al. 1997; Frid et al. 2003). However, the influence of turbidity on the foraging success of juvenile cod is unknown.

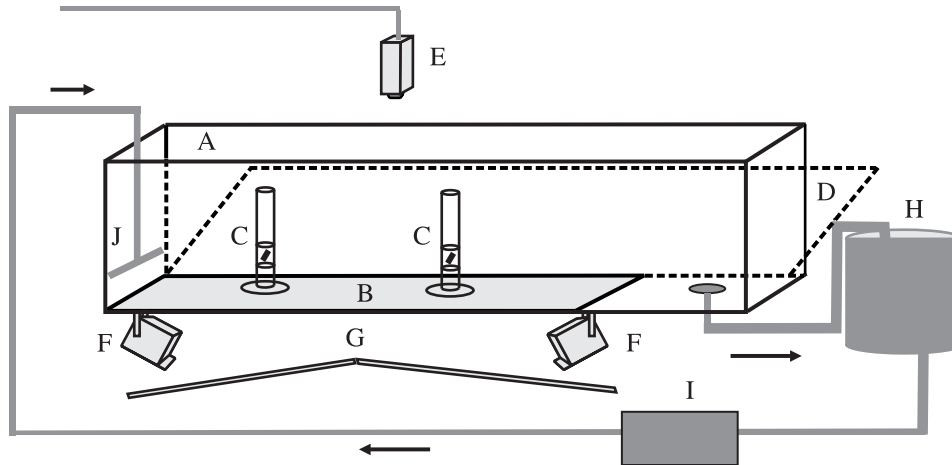
Turbidity can have varying effects on foraging by fishes depending on their search volume and foraging mode. For example, an intermediate increase in turbidity can have a positive effect on feeding rates of fish and fish larvae feeding on small prey by increasing contrast (Boehlert and Morgan 1985; Utne 1997). Predators that locate prey with nonvisual senses, such as chemoreception or mechanoreception, may be unaffected by turbidity (Rowe et al. 2003). Although vision is considered to be the main sense used by juvenile cod to detect mobile prey (Brawn 1969; Chinarina and Troshicheva 1975), chemosensory cues are also used (Harvey and Batty 1998; Løkkeborg 1998;

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Fig. 1. Experimental set-up: glass aquarium (A; 300 cm × 70 cm × 50 cm); experimental arena (B; 200 cm × 70 cm × 30 cm); poly-vinyl chloride prey cylinders (C; diameter, 7 cm) containing a mysid with vertical movement restricted by two clear disks; mirror providing side view (D), a 5-cm grid was painted on the back wall of the aquarium; overhead video camera (E; Panasonic WV BP550) with infrared filter (Optolite 50% IR); infrared lamps (F; 2 × Derwent 70 W, 830 nm); reflective white boards (G); tank (H) where saltwater and kaolin were mixed by air bubbling and circulation; pump (I; 58 L·m⁻¹) introducing turbid water mix into aquarium through jets (J).



Løkkeborg and Fernö 1999) and may be important in highly turbid water.

Our experiments aimed to examine the influence of turbidity on the reactive distance and search time of juvenile cod, and to determine if turbidity affects their foraging rates. We also tested the general hypothesis that cod mainly use visual cues to locate prey in clear water (in photopic conditions) and chemoreception in turbid water.

Materials and methods

Collection and maintenance of experimental animals

Juvenile *Gadus morhua* were collected at several sites around Bergen, western Norway (60°16'N; 4°58'E) using trammel nets. These fish were tagged with external Floy T-bar tags and kept in tanks (1000 L) for up to 3 months prior to the experiments. Juvenile cod were fed a diet of frozen gobies, decapods, pellets, and live mysids (the use of live decapods and fishes as prey items is prohibited by the Norwegian Council for Animal Research).

Mysids (*Praunus neglectus*) were used for experiments because they are common prey items of juvenile cod (e.g., Mattson 1990; Hüsey et al. 1997) and have an evasive response similar to other natantid prey of juvenile cod (tail-flip response; Neil and Ansell 1995). *Praunus neglectus* were collected using dip and seine net. Mysids were kept in tanks (90 L) for up to 2 months prior to the experiments and fed live artemia.

Experiment 1: effect of turbidity on the reaction distance and search time of juvenile cod

In this experiment we looked at the influence of turbidity on prey localization by juvenile cod. Mysids were located inside closed (clear) or partially closed cylinders (clear and white) to provide cod with visual, visual-chemical, and chemical prey cues.

Experimental set-up

Experiments were conducted in a large rectangular glass aquarium (70 cm × 300 cm × 50 cm), filled to a depth of 20 cm with seawater (salinity 32‰–35‰; temperature maintained at 9.5 ± 1.5 °C). This depth allowed us to view the fish from above at the highest turbidity levels.

Diffuse light conditions were provided (9.5 ± 0.5 μmol·m⁻²·s⁻¹) by indirectly illuminating the aquarium with four halogen floodlights (2 × 150 W, 2 × 500 W). This irradiance level is equivalent to that found in juvenile cod habitat in coastal waters of western Norway (i.e., at a 20-m depth on a sunny clear summer day with 1000 μmol·m⁻²·s⁻¹ surface irradiance, or at a 3-m depth on a cloudy winter day with 20 μmol·m⁻²·s⁻¹ surface irradiance; Baliño and Aksnes 1993). The experimental aquarium was illuminated from underneath with disperse infrared light (>800 nm), and fish silhouettes were recorded using an overhead video camera fitted with an infrared filter (Fig. 1).

Pulverised kaolinite (Kaolin Polperse 10, ECC International) was used to make the water turbid. A kaolin-seawater suspension was introduced into a mixing tank and recirculated through the experimental tank (Fig. 1). Water flow was turned off 30 min prior to the experiments.

Experimental protocol

We examined the reactive distance and search time of juvenile cod in response to three prey treatments (visual, visual-chemical, and chemical cues) at five turbidity levels (beam attenuation: 0.4, 3, 5, 10, and 17·m⁻¹). Prey treatments consisted of mysids in clear cylinders (visual), mysids in clear cylinders with small holes (visual-chemical), and mysids in white cylinders with small holes (chemical). Additional empty cylinders (white, clear, and with holes) were used as controls for the effect of cylinders on reactive distance and search time. The size (2.5 mm diameter), number, and location (above and below the section containing the mysid) of holes were chosen to allow chemical cues to disperse from the cylinders while minimizing

mechano-auditory cues. Observations of dye tracers showed that chemical cues dispersed uniformly around each cylinder. The depth of mysids (from 7.5 to 12.5 cm) was constant throughout all trials (Fig. 1).

The turbidity levels correspond to 1.4, 10, 16, 32, and 55 nephelometric turbidity units (NTU; measured with a Vernier turbidity sensor) and represent the turbidity range in habitats used by juvenile Atlantic cod (based on turbidity data from E. Marken, Department of Physics and Technology, University of Bergen, N-5020 Bergen, Norway; McMahon et al. 1992; Bowers et al. 2000; Frette et al. 2004).

Turbidity levels were maintained to within ± 0.5 beam attenuation $\cdot \text{m}^{-1}$ throughout the experiments. Water samples from random locations at both the top and bottom of the tank at the start and finish of each trial were used to measure turbidity during a trial. Turbidity was measured as the percentage of light transmitted through a 10-cm cuvette in a spectrophotometer (Shimadzu UV-VIS Recording Spectrophotometer UV-160) at 800 nm (to minimize near-forward scattering) and converted to beam attenuation using the standard relationship $T = e^{-cr}$, where T is light transmitted through a path length r (in metres) and c is the beam attenuation coefficient.

A total of 18 fish (20–30 cm standard length, SL) were tested for each turbidity–prey cue treatment. Fish were tested in pairs following the randomized-blocks experimental design: nine pairs of fish received each treatment once in different orders. To maintain equal replication in each treatment (18 fish), fish that did not complete every treatment combination were replaced with new individuals (three fish grew too large, one died, and another seven developed exophthalmia).

Fish were starved for between 4 and 5 days (to increase feeding motivation; e.g., Confer et al. 1978) prior to the experiments, and acclimated overnight to the experimental tank. Trials lasted for 1.5 h or until each fish reacted to prey at least three times. Every 3 weeks throughout the experiments, the fish were anaesthetised (Metacaine) and eye size (diameter, mm), standard length (cm), and weight (g, wet weight) were measured.

Mysids (14–23 mm total length, TL) were acclimated to the experimental room in 200 mL of water from the experimental aquarium (one mysid per 200 mL) for 30–45 min before experiments. Mysids were subsequently introduced into the prey cylinders at the start of each trial, when fish were general facing away from the cylinders and at the opposing end of the tank. Two cylinders were placed in the experimental tank in each trial; one cylinder was placed randomly in each half of the experimental area.

Search time and reactive distances were determined by analyzing video recordings. Reactive distance was defined as the distance at which fish first orient toward prey (Vinyard and O'Brien 1976; Vogel and Beauchamp 1999). This behaviour was easily distinguished from more random and slower search activity by fish; initiation of pursuit was accompanied by direct orientation of the long axis of the fish towards the prey. Reactions of cod to prey were digitized, and distances were measured using Image-Pro Plus (Version 5, Media Cybernetics Inc., Silver Spring, Maryland). The maximum reactive distance of the first three observations for

each fish was used to represent reactive distance (Utne 1997; Utne-Palm 1999). A side mirror and 5-cm grid (Fig. 1) were used to determine the vertical location of cod (where possible). We determined search time by recording the time from when mysids were introduced into the cylinders to the first reaction for each fish.

Data analysis

Data were analysed using SPSS (Release 11.5, SPSS Inc. 1999). The effect of turbidity and prey cues on the responsiveness of cod to prey was tested with logistic regression. The goodness of fit of a particular model was determined using the Likelihood Ratio statistic (G^2 ; Sokal and Rohlf 1995). We used a χ^2 test to test for an association between reactive depth category (5–10 cm, 10–15 cm, and 15–20 cm) and turbidity.

Factorial, random-blocks analysis of variance (ANOVA) was used to test for the differences in reactive distance and search time between turbidity levels and prey cues. Both individual fish and pairs of fish were used as blocks in the analysis to remove variability associated with individuals or interactions between pairs. Before analysis, reactive distance and search time were tested for normality and homoscedasticity using the Shapiro–Wilk and Levene's tests, respectively. No transformation was necessary for reactive distance, but search times were \log_{10} -transformed. Tukey's test was used for post hoc comparisons of means.

As any differences in turbidity within each category would increase the variability within the treatments in the ANOVAs, relationships between turbidity and reactive distance, as well as between turbidity and search time, were also investigated using a linear regression approach. We used multiple regression to determine whether turbidity, fish size (SL and weight), fish eye size, and mysid size (TL) significantly affected reactive distance and search time (\log_{10} -transformed). The forward stepwise model was used, and the standardized residuals were examined to test for homoscedasticity (Sokal and Rohlf 1995). The turbidity variable was the \log_e -transformed mean of measurements taken at the start and finish of each trial.

Experiment 2: effect of turbidity on the foraging rate of juvenile cod

We aimed to test if an ecologically relevant maximum turbidity (upper estuary; e.g., McMahon et al. 1992) affected foraging rates of juvenile cod on free-ranging mysids.

Experimental set-up

Experiments were conducted in a large, rectangular glass aquarium (70 cm \times 300 cm \times 50 cm), filled to 35 cm with seawater (Fig. 1). As in all laboratory experimental studies, enclosure effects were unavoidable. These experiments were therefore not intended to represent actual foraging rates and search times in nature but rather the relative changes in feeding rate and prey detection in response to changes in turbidity.

Experimental protocol

Predation rates on free-swimming mysids were compared between clear ($c = 0.2 \cdot \text{m}^{-1}$, 0.8 NTU) and highly turbid water ($c = 28 \cdot \text{m}^{-1}$, 91 NTU). We also measured predation rates

in the complete absence of light (a sealed, dark room and clear water: $c = 0.2 \cdot \text{m}^{-1}$, 0.8 NTU) to determine if visual cues were used to locate and capture mysids. Cod were tested individually to determine foraging rates for each fish, with nine different fish tested in each treatment (clear, photopic; turbid, photopic; clear, no light). We used the same protocol as we did in the previous experiment to establish and measure turbidity levels.

Prior to each trial, one juvenile cod (20–30 cm SL) was starved for 48 h and acclimated to the experimental tank for 24 h. Ten mysids (14–23 mm TL) were acclimated to an adjacent glass aquarium that was maintained at the same turbidity level as that in the experimental tank using a recirculating pump system. At the start of experiments, mysids were released into the opposing end of the tank from the fish. The length and weight of mysids was measured prior to each experiment. After 2 h, the fish was removed, the tank was completely drained through a filter, and the remaining mysids were counted, weighed, and measured (TL, mm). The predation rate was measured as both the number of mysids consumed per h and the proportion of total mysid weight consumed.

Data analysis

Analysis of covariance (ANCOVA) was used to test for differences in predation rate (mysids eaten $\cdot\text{h}^{-1}$) and proportion of mysid weight consumed (arcsine-transformed) between turbidity and light levels (turbid, clear, and dark), after variance associated with cod weight was removed. The homogeneity of regression coefficients in ANCOVAs was tested by examining the interaction between the covariate and factors (Dunn and Clark 1987; SPSS Inc. 1999).

Results

Experiment 1: effect of turbidity on the reaction distance and search time of juvenile cod

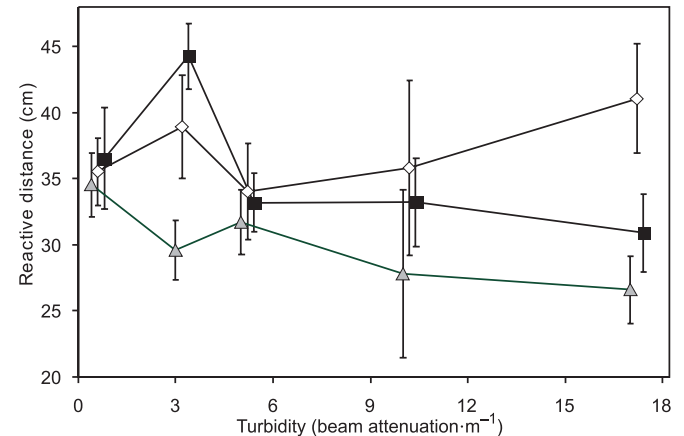
Approximately half of the 18 fish tested responded to prey in each treatment. The probability of cod responding to prey was not significantly affected by turbidity, prey cues, or interactions between turbidity and prey cues (logistic regression: turbidity, $p = 0.30$; prey cue, $p = 0.64$; interaction term, $p = 0.63$). Since no attacks were recorded on empty cylinders (from 84 observations), further analyses on reactive distances excluded trials with empty cylinders.

Most fish (87%) responded to prey at depths between 10 and 15 cm (112 reactions to prey were visible in the side mirror from a total of 355 reactions). Reactive depth was not significantly associated with turbidity ($\chi^2_8 = 11.7$, $p = 0.16$). Consequently, we ignored depth-related changes in fish position in our analyses of reactive distance.

Effect of turbidity and prey cue on the reactive distance of juvenile cod to prey

The mean reactive distances to chemical cues (mean \pm 1 standard error (SE), 36.9 ± 1.8 cm) and visual–chemical cues (35.4 ± 1.4 cm) were similar (Tukey's test, $p > 0.05$), and longer than to visual cues (29.9 ± 1.3 cm; Tukey's test, $p < 0.05$; ANOVA, $F_{[2,98]} = 7.42$, $p = 0.001$). There was no significant effect of turbidity on cod reactive distance (ANOVA, $F_{[4,98]} = 0.32$, $p = 0.87$), but there was a near-

Fig. 2. Reactive distance (mean \pm 1 standard error) of juvenile *Gadus morhua* to visual (shaded triangles), visual–chemical (solid squares), and chemical cues (open diamonds) with increasing turbidity. Data were offset slightly horizontally to display standard error bars.



significant interaction between turbidity and prey cue (ANOVA, $F_{[8,98]} = 1.76$, $p = 0.094$). Reaction distances to visual cues tended to decrease with turbidity, while reactive distances to visual–chemical cues tended to decrease after an initial increase (Fig. 2). Reactive distances to chemical cues tended to increase with turbidity (Fig. 2).

We further investigated the relationship between reactive distance and turbidity with multiple linear regression. Turbidity reduced reactive distance to visual ($r^2 = 0.09$; $df = 1,45$; $p = 0.044$) and visual–chemical prey cues ($r^2 = 0.08$; $df = 1,50$; $p = 0.049$), but not to chemical prey cues ($r^2 = 0.01$; $df = 1,40$; $p = 0.466$). However, the relationship between turbidity and reactive distance was very weak and explained only 7.6% of variation for visual–chemical cues and 8.7% of variation for visual cues. Fish size, fish eye size, and mysid size did not contribute significantly to any of the regression models.

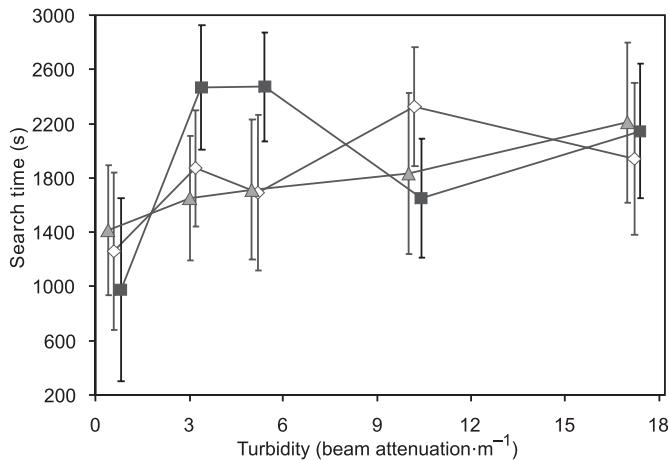
Effect of turbidity and prey cue on the search time of juvenile cod for prey

Although highly variable, search time tended to increase with turbidity (Fig. 3). There were no significant differences in mean search times between turbidity levels, prey cues, or interactions (ANOVA: turbidity, $F_{[4,75]} = 0.72$, $p = 0.58$; prey cues, $F_{[2,74]} = 0.35$, $p = 0.71$; interaction term, $F_{[8,74]} = 0.68$, $p = 0.71$). Further analysis with multiple linear regression revealed a weak but significant increase in search time with turbidity for chemical ($r^2 = 0.12$; $df = 1,36$; $p = 0.037$) and visual–chemical prey cues ($r^2 = 0.18$; $df = 1,48$; $p = 0.009$; Fig. 3). Turbidity did not significantly affect search time for visual prey cues ($r^2 = 0.01$; $df = 1,39$; $p = 0.54$), although predator length had a weak positive effect on search time ($r^2 = 0.18$; $df = 1,39$; $p = 0.006$). Fish size, fish eye size, and mysid size did not contribute significantly to regression models for chemical or visual–chemical prey cues.

Experiment 2: Effect of turbidity on the foraging rate of juvenile cod

Mean predation rates (mysids $\cdot\text{h}^{-1}$) did not differ significantly between highly turbid (mean \pm 1 SE, 1.9 ± 0.6 mysids $\cdot\text{h}^{-1}$) and

Fig. 3. Search time to reaction (mean \pm 1 standard error) of juvenile *Gadus morhua* to visual (shaded triangles), visual-chemical (solid squares), and chemical cues (open diamonds) with increasing turbidity. Data were offset slightly horizontally to display standard error bars.



clear water (1.9 ± 0.6 mysids·h⁻¹), but were lower in complete darkness (0.79 ± 0.3 mysids·h⁻¹) (ANCOVA, $F_{[2,23]} = 4.25$, $p = 0.03$; Tukey's test, $p < 0.05$; Fig. 4). The same pattern was evident when predation rates were expressed as the proportion of mysid weight eaten (ANCOVA, $F_{[2,23]} = 8.80$, $p = 0.007$; Tukey's test, $p < 0.05$).

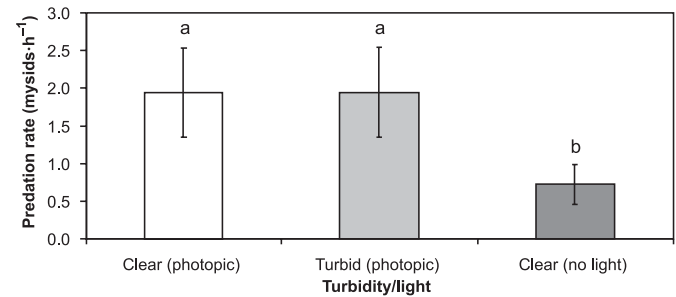
Discussion

Our results suggest that juvenile cod use vision and chemoreception to locate mysids in both clear and turbid water. Turbidity had little influence on the ability of cod to locate stationary mysids or to consume free-ranging mysids.

The lower predation rates in complete darkness and the weak effect of turbidity on visual reactive distance indicate that vision was used in highly turbid water. This reduced predation rate in the dark was unlikely to be caused by diel differences in feeding motivation, because all experiments were conducted at approximately the same time. Furthermore, numerous studies have indicated that diel foraging patterns of juvenile cod (> age 1) are variable, depending on prey availability (e.g., Turuk 1973; Mattson 1990; Gibson and Robb 1996).

Juvenile cod were able to accurately localize prey from longer distances using chemical cues rather than visual prey cues. Chemosensory response distance varies with the release rate and chemical composition of the prey odour, and with the fluid dynamic conditions in the habitat (Finelli et al. 2000). In the field, cod have been shown to respond to bait within a simple current from substantial distances outside visual range through rheotaxis (up to 698 m; Løkkeborg 1998; Løkkeborg and Fernö 1999). The present study shows that juvenile cod can use chemoreception to locate small, intact prey from outside visual range, even when water flow is limited to that created by fish movements (observations on dye tracers; J.J. Meager, unpublished data). However, the reliance of juvenile cod on chemoreception may be diminished in turbulent habitats or on other prey items (Weissburg et al. 2002).

Fig. 4. Foraging success of *Gadus morhua*, predation rate (mean mysids eaten·h⁻¹ \pm 1 standard error), with turbidity and light (clear, $c = 0.2$ m⁻¹; turbid, $c = 28$ m⁻¹). Also shown are the results of Tukey's tests (a, homogenous subset 1; b, homogenous subset 2).



The longer reactive distances, and similar search times in response to chemical prey cues when compared with visual cues, indicates that chemoreception alone can be sufficient for foraging on stationary or slow moving prey items, such as polychaetes or bivalves (Mattson 1990; Hüsey et al. 1997). However, foraging rates of juvenile cod on free-ranging mysids were reduced in the absence of visual cues. Observations under infrared lighting suggest that this is a result of reduced attack success and not a lower encounter rate (J. Meager, unpublished data). Chemical cues last beyond the moment of production and may be less effective in the final stages of localizing and capturing rapidly moving or evasive prey (New et al. 2001; Brown 2003). The demands of these prey encounters are such that both visual and mechano-auditory information are likely to be required (New et al. 2001; Montgomery et al. 2002). A combination of distance chemoreception, vision at closer ranges, and possibly mechano-auditory reception may be an effective foraging strategy for juvenile cod to use with evasive prey items in well lit, highly turbid water.

It is also important to consider the influence of turbidity on the ability of prey to detect and avoid predators (Giske et al. 1994). In other studies, the absence of turbidity effects on predation has been attributed to compensatory factors acting on the reduced visual ability of predators, such as increased prey encounter or reduced antipredator behaviour of prey (Granqvist and Mattila 2004). Although littoral mysids are more active at lower light levels (Mauchline 1980; Viherluoto and Viitasalo 2001), the influence of turbidity on encounter rates between cod and mysids is unknown. Turbidity may also affect more the ability of mysids to see and evade the cod predator than the ability of cod to see mysids because cod present a larger visual target (Giske et al. 1994; de Robertis et al. 2003). The visual system of fishes also differs fundamentally from that of crustaceans; hence, mysid vision may not be affected by turbidity in the same way as their predators.

Juvenile cod had long reactive distances to visual cues in highly turbid water (mean \pm 1 SE, 26.6 ± 2.6 cm at $c = 17$ ·m⁻¹ for 800 nm, or 61 NTU), supporting observations that cod have a well developed visual system (Chinarina and Troshicheva 1975) and high visual acuity (Anthony 1981). The exact nature of the relationship between turbidity and visual reactive distance was difficult to determine in the current study because of the high variation in reactive distance.

As fish and prey sizes, temperature, acclimation, and starvation time were all controlled for, this was attributed to differences in feeding motivation between individuals. Variation in movement, transparency, and position of mysids in the cylinders may have also affected reactive distance (Aksnes and Giske 1993; Thetmeyer and Kils 1995; Utne-Palm 1999). However, initial observations suggested that mysids were inactive and perched on one side of the prey cylinders.

The importance of vision in prey localization will obviously decrease at higher turbidity levels ($c > 28\text{-m}^{-1}$) and lower ambient light levels (e.g., at night or during arctic winters; dos Santos and Falk-Petersen 1989) than were used in this study. Juvenile cod in coastal waters of western Norway are unlikely to encounter turbidity levels greater than 5-m^{-1} (c ; Godø et al. 1989; Frette et al. 2004; E. Marken, Department of Physics and Technology, University of Bergen, N-5020 Bergen, Norway, unpublished data). Elsewhere, turbidity levels of 20-m^{-1} (c) or above would only be encountered by cod in upper regions of highly turbid estuaries (McMahon et al. 1992; Kocum et al. 2002, based on estimates of c from diffuse attenuation coefficients K following Aksnes and Giske 1993).

The ability of juvenile cod to locate and capture a variety of prey items using a combination of sensory systems (e.g., Mattson 1990) explains, in part, how this species is able to exploit habitats ranging from clear coastal waters (Godø et al. 1989; Grant and Brown 1998) to turbid estuaries (Riley and Parnell 1984; Marshall and Elliot 1998). Although it has been suggested that cod may prey on mobile prey items when visibility is high and on benthic prey items at low visibility (Løkkeborg 1998; Løkkeborg and Fernö 1999), little is known of how the optical environment effects prey choice.

In summary, juvenile cod were able to locate prey in highly turbid water using a combination of vision and chemoreception (and possibly other senses). Hence, turbidity had little effect on the ability of juvenile cod to locate and consume mysids. Predicting the effects of turbidity on foraging by juvenile cod in the field will require further experiments on other prey items, such as fishes and decapods. Fully resolving the effects of turbidity on predation by cod on mobile prey will require an integrative approach, considering encounter rates and reactive distances from the perspective of both predator and prey.

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