Effects of turbidity on the spontaneous and prey-searching activity of juvenile Atlantic cod (*Gadus morhua*)

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Increasing turbidity in coastal waters in the North Atlantic and adjacent seas has raised concerns about impacts on Atlantic cod (*Gadus morhua*) using these areas as nurseries. A previous experiment (Meager *et al.* 2005 *Can. J. Fish. Aquat. Sci.* **62**, 1978–1984) has shown that turbidity (up to 28 beam attenuation m^{-1}) had little effect on the foraging rate of juvenile cod. Although this was attributed to cod using chemoreception in conjunction with vision to locate prey, foraging rates may also be maintained by increased activity. Higher activity, however, is energetically costly and may offset benefits from increased foraging return.

We examined the effects of turbidity on prey searching and spontaneous activity of juvenile cod in the laboratory, by measuring activity with and without prey cues. Activity of juvenile cod was nonlinearly affected by turbidity and was lower at intermediate turbidity, regardless of the presence of prey odour. Activity increased over time when prey odour was present and decreased when absent, but the effects of prey odour were similar across all turbidity levels. Position in the tank was unaffected by turbidity or prey odour. Reduced activity at intermediate turbidities is likely to offset longer prey-search times. At high turbidity (greater than 17 m^{-1}), both longer prey-search times and higher activity indicate that increased energetic costs are probable.

Keywords: turbidity; fish; activity; foraging; cod; juvenile

1. INTRODUCTION

Environmental factors such as temperature (Clark *et al.* 1995), dissolved oxygen (Schurmann & Steffensen 1994) and light (Trippel & Neil 2003) influence fish locomotor activity. Activity levels determine energy intake and predation risk (Werner & Anholt 1993), and are an important component of bioenergetic models predicting the effects of abiotic factors on growth and performance (Kerr 1982; Sweka & Hartman 2001). Although variations in light intensity are known to influence fish activity (see reviews by Blaxter 1970; Reeb 2002), much less is known of the influence of other aspects of the optical environment (e.g. spectral composition and turbidity) on fish activity. Turbidity from suspended sediment, dissolved organic matter and plankton scatters and absorbs light, and can modify fish behaviour by limiting visual perception of predators, prey and the environment (e.g. Vinyard & O'Brien 1976; Miner & Stein 1996; Utne-Palm 1999; reviewed by Utne-Palm 2002).

Recent anthropogenic increases in turbidity in coastal waters of Europe have led to concerns about the impact on fisheries species (Bonsdorff *et al.* 1997; Frid *et al.* 2003). Stocks of Atlantic cod are declining (Hutchings & Baum 2005) and juveniles are found in

shallow coastal waters (e.g. Godø *et al.* 1989; Grant & Brown 1998a) where turbidity levels are often high (Mobley 1994). Very little is known of the effects of turbidity on the distribution and behaviour of cod.

The influence of turbidity on prey-searching behaviour of fish depends on their foraging mode (Utne-Palm 2002; de Robertis *et al.* 2003): predators that locate prey with non-visual senses may be unaffected by turbidity (Rowe *et al.* 2003). Vision in cod is well developed (Anthony 1981) and considered to be the main sense used to forage on evasive prey items (Brawn 1969; Chinarina & Troshicheva 1975), but they are also able to locate prey by chemoreception (Ellingsen & Døving 1986; Harvey & Batty 1998; Løkkeborg 1998). In a recent laboratory study, foraging of cod on evasive prey in highly turbid water was attributed to the use of both visual and non-visual senses (Meager *et al.* 2005). However, cod may also increase their swimming speed in turbid water to compensate for a reduced visual range, which has energetic costs that may offset foraging return (Sweka & Hartman 2001). In brook trout (*Salvelinus fontinalis*), increased activity in turbid water (Gradall & Swenson 1982) has been associated with reduced growth (Sweka & Hartman 2001).

Until recently, poor visual resolution and contrast differentiation has limited detailed observations of locomotion, behaviour and activity of fish in highly turbid water. However, using infrared silhouette photography (Batty 1983) in turbid water, image quality can be improved by taking advantage of better transmission of

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One contribution of 18 to a Theme Issue 'Environmental constraints upon locomotion and predator-prey interactions in aquatic organisms'.

longer wavelengths of light in turbid water (Mobley 1994) and enhanced silhouette contrast.

In this study, we used infrared silhouette photography to examine locomotor activity of juvenile cod across a broad range of turbidity levels. We tested the hypothesis that cod are more active in turbid water to increase prey encounter rate by comparing the effects of turbidity on activity in the presence and absence of prey odorants. Turbidity may affect the behaviour of prey as well as predators and could bias the outcome of an experiment where the focus is on the predator's behaviour (Granqvist & Matila 2004). Prey odorants were therefore used because low concentrations are known to stimulate prey-searching behaviour (Johnstone 1980; Ellingsen & Døving 1986).

2. MATERIAL AND METHODS

(a) 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 fish traps and kept in tanks (1000 l) for up to three months prior to the experiments. Juvenile cod were tagged individually with Floy T-bar tags and fed a diet of frozen gobies and decapods, pellets and live mysids. Mysids (*Praunus neglectus*) were used to create prey odour in the experiments as they are common prey items of juvenile cod (e.g. Hüsey et al. 1997). *Praunus neglectus* were collected using dip and seine nets and were kept in tanks (90 l) for up to two months prior to the experiments.

(b) 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 $9.5 \pm 1.5^\circ\text{C}$). Diffuse light conditions were provided ($9.5 \pm 0.5 \mu\text{mol m}^{-2}\text{s}^{-1}$) by indirectly illuminating the aquarium with four halogen floodlights (2 × 150 W, 2 × 500 W). The experimental aquarium was illuminated from underneath with diffuse infrared light (more than 800 nm wavelength, 2 × Derwent 70 W lights reflected off white boards) and fish silhouettes were recorded using an overhead video camera (Panasonic WV BP550) fitted with an infrared filter (Optolite 50% IR). Pulverized kaolinite (Kaolin Polisperse 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 (see Meager et al. 2005 for full details). Water flow was turned off 30 min prior to the experiments.

(c) Experimental protocol

Activity of juvenile cod was measured at five turbidity levels (beam attenuation: 0.4, 3, 5, 10 and 17 m^{-1}) over 60 min, in the presence and absence of prey odorants (prey-cue treatment). Prey-cue treatments consisted of two white cylinders, each containing one mysid (14–23 mm total length, TL) or two empty white cylinders. Mysids 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 and carefully introduced into the prey cylinders at the start of each trial. Prey odorants dispersed from the cylinders through small holes (see Meager et al. 2005 for further details) and one cylinder was placed randomly in each half of the experimental area.

The turbidity levels correspond to 1.4, 10, 16, 32 and 55 nephelometric turbidity units (NTU, measured with a

Vernier turbidity sensor) for our turbidity media, and represent the turbidity range in habitats used by juvenile Atlantic cod (e.g. McMahon et al. 1992; Bowers et al. 2000; Frette et al. 2004). Turbidity levels were maintained within $\pm 0.5 \text{ m}^{-1}$ 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 per cent 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. Fish were tested in pairs as earlier experiments indicated that fish tested in groups were more likely to react to prey within a trial than solitary individuals (J. Meager 2003, personal observation). Fish were starved for between four and five days (to increase feeding motivation, e.g. Confer et al. 1978) prior to the experiments, acclimated overnight to the experimental tank and to the turbidity level for 1.5 h. Following trials, live mysids were introduced into the tank ad hoc to reinforce the feeding behaviour of fish for subsequent trials. Every three weeks throughout the experiments, the fish were sedated (metacaine) and eye size (diameter, mm), standard length (cm) and weight (g, wet weight) were measured.

(d) Video and data analysis

Of the 90 films recorded, 15 were not analysed due to differences in image alignment and physical degradation of video tapes. Swimming activity was measured using a spatial actograph program (MOTIONGRAB, R. S. Batty 2004, unpublished data), which analysed video footage by comparing consecutive captured frames at five frames per second and recording differences between them. If movement was detected within predefined trigger zones, frames with fish movement were saved as an audio video interleaved (AVI) file for later viewing and verification of activity. Activity was detected and scored in two zones. The focal zone was a 0.65 m^{-2} area in the centre of the tank, surrounding the prey-cue cylinders (focal area, figure 1). In this area, activity was measured by reviewing the captured files and scoring the number of fish active within a given frame. This value was summed to give fish activity indices for 10 min (fish activity 10 min^{-1}) and 1 h (fish activity per hour) time-intervals. Activity around the edges of the focal area (edge area, figure 1) was measured using an index of movement per unit time that did not differentiate between individuals (active frames 10 min^{-1}), due to limitations in image contrast.

The influence of turbidity, time category (10–60 min) and prey-cue treatment on the distribution of cod activity was examined using logit-loglinear modelling (SPSS, Release 11.5, SPSS, Inc. 1989–2002). In this analysis, we converted activity in the focal area into an index of activity (active frames 10 min^{-1}) to make it comparable with activity in the edge area. Turbidity, time category and prey cue were the explanatory variables and location (edge or focal area) was the binomial response variable. The goodness of fit of a

Figure 1. Areas used for video analysis within the experiment tank. Focal (50×130 cm) and edge areas (top: 15×152 cm, left: 19×50 cm). C, prey-cue cylinders.

Figure 2. Effect of turbidity (beam attenuation) on activity of juvenile cod (mean fish activity per hour ± 1 s.e.). Also shown are the results of the Waller–Duncan test (A, homogenous subset 1; B, homogenous subset 2) and sample size (below line).

particular model was determined using the likelihood ratio statistic (G^2 ; Agresti 1990).

Repeated-measures analysis of variance (ANOVA) was used to test for the differences in activity (fish activity 10 min⁻¹) between turbidity levels and prey-cue treatments (SPSS). To remove variability associated with different fish groups, we included fish pairs as random-blocks in the analysis. Time within the trial was the within-subjects factor (10 min categories) and we tested for normality, homoscedasticity and sphericity using the Shapiro–Wilk, Levene and Mauchly tests, respectively. The main odorants used by fishes to detect live, intact crustacean prey are metabolites that increase in concentration in surrounding water as a function of time (among other variables, Zimmer *et al.* 1999; Weissburg *et al.* 2002). Hence, to test for the effects of fish that have perceived prey odorants, we analysed activity over the last 20 min (i.e. more than 40 min) of the experiments separately using a random-blocks ANOVA. Owing to unequal sample sizes, all *post hoc* multiple comparisons were made using the Waller–Duncan test (SPSS, Inc. 1999).

3. RESULTS

(a) Position in the tank

Most fish activity occurred at the edge of the tank (85% of overall activity in 33% of total tank area analysed), significantly more than expected when corrected for area (Chi-squared goodness of fit test, $p < 0.001$). Neither turbidity, time category and prey-cue treatment nor interactions between factors significantly affected the distribution of fish activity in the tank (no significant fit of logit models at $\alpha = 0.05$).

(b) Activity

Turbidity significantly affected activity ($F_{4,44} = 2.84$, $p = 0.035$), but there were no significant differences between prey-cue treatments ($F_{1,44} = 0.33$, $p = 0.57$), and no significant interaction between turbidity and prey-cue treatment ($F_{4,44} = 1.68$, $p = 0.17$). Activity was significantly lower at a turbidity of 10 m⁻¹ (mean $\pm$ s.e.: 277.5 $\pm$ 75.7 fish activity per hour) than at high (17 m⁻¹: 675.2 $\pm$ 130.6 fish activity per hour) or low turbidity (3 m⁻¹: 599.1 $\pm$ 96.5 fish activity per hour) (Waller–Duncan, $p < 0.05$, figure 2). Activity also varied over the experiment period (Pillai's trace: $F_{5,40} = 3.65$, $p = 0.008$), but this effect depended on the prey-cue treatment (time $\times$ prey-cue interaction: $F_{5,40} = 2.69$, $p = 0.035$). Activity tended to increase in the presence of prey odorants up to 60 min and decrease when no prey odorants were present (figure 3). However, this effect was independent of turbidity (time $\times$ prey cue $\times$ turbidity interaction: $F_{20,172} = 1.30$, $p = 0.19$). Similarly, there was no significant interaction between turbidity and experimental time ($F_{20,172} = 0.93$, $p = 0.55$). Additional data points that were not included in the statistical analysis owing to lower sample sizes indicated that the trend of increasing activity in the presence of prey odorants continued up to 70 min and that activity continued to decline when there were no prey odorants (figure 3).

The patterns of significance were similar when only the activity for the final 20 min of the experiment was examined (40–60 min), i.e. only turbidity significantly affected cod activity (turbidity: $F_{4,44} = 2.8$,

Figure 3. Activity of juvenile cod (mean fish activity $10 \text{ min}^{-1} \pm 1 \text{ s.e.}$) over experimental period, with prey odour (white diamonds, sample size above line) and without prey odour (black squares, sample size below line). Additional data points that were not included in the statistical analysis owing to low sample sizes are also provided (*).

Figure 4. (a) Prey-search times (mean search time $\pm 1 \text{ s.e.}$) and (b) activity (mean fish activity per hour $\pm 1 \text{ s.e.}$) with increasing turbidity (beam attenuation). Search times represent time taken to locate mysid prey (adapted from Meager *et al.* 2005, aggregate means for prey-cue treatments).

$p=0.04$; prey cue: $F_{1,44}=1.1$, $p=0.30$, turbidity $\times$ prey cue: $F_{4,44}=1.1$, $p=0.17$). Activity was significantly lower in intermediate turbidity (10 m^{-1}) than in high (17 m^{-1}) or low turbidity (3 m^{-1}) (Waller-Duncan, $p<0.05$).

4. DISCUSSION

Our experiments revealed a nonlinear effect of turbidity on spontaneous and prey-searching activity of juvenile cod, with less activity at an intermediate turbidity level

(figure 2). These results have consequences for the foraging energetics of cod. A comparison of our results with Meager *et al.* (2005) indicates that low activity at intermediate turbidity levels (e.g. 45% less activity at 10 m^{-1} than in clear water) is likely to offset longer prey search times (figure 4). Hence, although fish are taking longer time to find prey at intermediate turbidity levels, they are likely to expend less energy in doing so. In contrast, longer prey search times and higher activity levels indicate that increased energetic costs are probable at high turbidity levels (greater than 17 m^{-1} , figure 4).

Such turbidity levels would only be encountered by cod in upper regions of highly turbid estuaries (e.g. McMahon *et al.* 1992; Kocum *et al.* 2002).

The similar influence of turbidity on spontaneous and prey-searching activity in our experiments may indicate that foraging behaviour does not explain the observed pattern. Alternatively, it may indicate that cod were searching for food even when no prey odourants were present. We consider the latter explanation more likely, since the fish were trained to feed in the tank. Cod activity increased when prey odourants were present, as has been observed in earlier studies (e.g. Hammer 1997; Løkkeborg 1998). This increased activity may be the result of fish maximizing the probability of encountering prey within an odour plume, or a competitive strategy towards other fish (Løkkeborg 1998). Nevertheless, the effect of prey odour on fish activity was constant across all turbidity levels in our study.

Although very few studies have compared the influence of turbidity on prey searching and spontaneous activity of fish, nonlinear relationships between foraging rates and turbidity (Boehlert & Morgan 1985; Vandenbyllaardt *et al.* 1991; Gregory & Northcote 1993), and between prey-searching activity and turbidity (Miner & Stein 1996) have been noted in several studies. An increase in foraging in intermediate turbidity has been explained in terms of contrast enhancement (Boehlert & Morgan 1985), visual asymmetries between predator and prey (Vandenbyllaardt *et al.* 1991) or behavioural plasticity (Gregory & Northcote 1993; Miner & Stein 1996). Even though activity decreased in intermediate turbidities in our experiment, we attribute our results to behavioural plasticity rather than visual effects, as no visual prey cues were available to the fish. However, the ultimate basis for this behavioural plasticity maybe the visual effect of turbidity on prey detection acting through either evolution or learning.

In cod, the results of laboratory and field experiments indicate a plasticity in foraging strategies that depends on the optical environment. Although they can feed throughout the diel cycle (e.g. Turuk 1973; Løkkeborg 1998), the response of cod to odour plumes from bait differs between day and night (Løkkeborg & Fernö 1999). Cod reduce swimming speed and restrict their search area after encountering bait odour plumes during the day but not at night (Løkkeborg & Fernö 1999). This was attributed to the role of vision in prey localization during the day (Løkkeborg 1998; Løkkeborg & Fernö 1999). Laboratory experiments have indicated that juvenile cod use both vision and chemoreception to locate prey in both clear and turbid water, and that turbidity did not affect feeding motivation (Meager *et al.* 2005). We suggest that foraging modes in our experiments changed with turbidity, or with the amount of visual information available. In clear water, optimal prey searching and rapid localization of prey using both visual and chemical cues was probable. As turbidity increased, we suggest that greater reliance on chemical cues reduced prey-searching speed (slower search speeds are likely to be better for prey localization in low flow environments; Weissburg *et al.* 2002). In highly turbid water, the increased activity (when compared to intermediate

turbidity; figure 2) may indicate more random searching at faster swimming speeds. This would increase the probability of an encounter with mobile prey (*sensu* Gerritsen & Strickler 1977) and act as compensation for the further reduction in the visual field. Although increased activity and longer search times may be energetically costly, the alternative may be reduced growth from fewer prey located. Such a flexible foraging strategy may therefore maximize energy intake per unit time, within the constraints imposed by optical environment. No information, however, is available on the search pattern used to locate prey, which may also vary with turbidity.

Perceived predation risk may have also affected activity patterns in our experiment. Although the fish in our experiments were not exposed to differences in predation risk, their perception of risk may have still been affected by turbidity. These fish were wild-caught and highly likely to have encountered predators in the past. Increased turbidity reduces visual encounters with predators (Gregory 1993); hence, fish in turbid water often use less antipredator behaviour (e.g. Gregory 1993; Abrahams & Kattenfeld 1997; Lehtiniemi *et al.* 2005). As with many other animals (Werner & Anholt 1993), reducing activity is an antipredator behaviour in juvenile cod (Nordeide & Svåsand 1990; Laurel & Brown 2006). A decrease in perceived risk in turbid water would therefore be expected to lead to higher activity levels, as has recently been shown for damselfly larvae (*Ischnura elegans*; Van De Meutter *et al.* 2005). While this effect may explain the increase in cod activity from intermediate to highly turbid water in our study, it does not explain the decrease in activity from clear to intermediate turbidity (figure 2).

Similarly, it is unlikely that changes in activity with turbidity were the result of an avoidance response to the turbidity media. Very high levels of turbidity and long exposures are required for a physiological response by cod (550 mg l⁻¹ of suspended sediment for five days, Humborstad *et al.* 2006) and other fish species (Servizi & Martens 1992; see also review by Newcombe & McDonald 1991). Similar responses in our experiments were unlikely as the concentration of turbidity media was low (less than 47 mg l⁻¹) and exposure times were short (less than 2.5 h). In the field, juvenile cod are found in habitats ranging from clear coastal water (e.g. Godø *et al.* 1989; Grant & Brown 1998a) to highly turbid water (Marshall & Elliot 1998). Recent laboratory experiments indicate that cod prefer intermediate turbidity (7 beam attenuation m⁻¹) over clear water (Meager & Utne-Palm *in press*), which may indicate that the reduced activity in our experiments represented a preferred turbidity level and a part of the behavioural mechanism by which cod remain in their preferred environment. However, as there were no differences in habitat choice between intermediate and high turbidity (i.e. 7 versus 15 m⁻¹, Meager & Utne-Palm *in press*), it is unlikely that preference alone explains the results from the current experiment.

The potential behavioural effects of turbidity on foraging mode, perceived risk of predation and habitat preference are not mutually exclusive. Although the results cannot be entirely explained by the theoretical expectation that reduced antipredator behaviour and

prey encounter rate will favour higher activity in turbid water than in clear water (Abrahams & Kattenfeld 1997; Sweka & Hartman 2001), the activity patterns observed may represent a trade-off between foraging intake and predation risk (see review by Dill 1987). Fish may, for example, associate high predation risk with clear water and low foraging return with highly turbid water; and hence, higher activities may be an avoidance response to these turbidity levels. It is, however, difficult to determine proximate behavioural causes of responses to these factors if we do not know the motivational state of the fish, even if external factors such as predators and food are controlled for in the experiment (Colgan 1993).

No field data exist for cod activity and turbidity and it is difficult to extrapolate the results of laboratory experiments to the field. Our experiments were designed to test for the effect of turbidity on activity in controlled conditions, not to predict swimming speeds in the wild. The influence of turbidity in the field will also depend on light intensity (Mazur & Beauchamp 2003) and hence, depth and season (among other factors). Although few experiments have looked at the effects of light intensity *per se* on foraging by cod, spatial and temporal variation in their diel activity patterns are associated with varying levels of food availability (e.g. Turuk 1973; Cote *et al.* 2002) and vulnerability to predators (in early life-history stages, e.g. Grant & Brown 1998a,b; Linehan *et al.* 2001). We know very little of the role of the optical environment on availability of prey items or on prey choice by cod. Clearly, further research into effects of turbidity on cod foraging return and growth in the field is warranted. Further research into the effects of turbidity on activity and growth of cod will also have relevance to the development of the cod aquaculture industry, given the tendency to use net pens in coastal areas.

Financial support was provided by the European Union Fisheries Directorate, through contract QLRS-2002-00799, Project ETHOFISH. Thanks to all of the staff at the University of Bergen, but special mention to Turid Solbakken, Tina Oen and Frank Midtøy for technical assistance, and to Karsten Øvretveit and Martin Midtøy for supplying the cod. We would also like to thank Anne Christine Utne Palm, Anders Fernö, Ian Mayer, Mark Abrahams and an anonymous reviewer for helpful comments on the manuscript. Experimental procedures complied with the Norwegian Council for Animal Research.

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