

Effect of turbidity on habitat preference of juvenile Atlantic cod, *Gadus morhua*

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Abstract We examined the effects of turbidity on habitat preference of juvenile Atlantic cod in the laboratory, using a shuttle box where fish could select between two different habitats. In the first experiment, we compared three turbidity levels of kaolin (3, 8 and 21 beam attenuation m^{-1}). In the second experiment, we looked at the effect of turbidity media (kaolin versus algae), after controlling for spectral differences between turbidity media. Although cod preferred an intermediate turbidity of kaolin over low turbidity water, comparisons between low and high turbidity, and intermediate and high turbidity did not significantly influence habitat preference. Algae did not influence habitat preference by cod. Although other studies have found that turbidity affects both foraging and antipredator behaviour of juvenile cod, this study has shown that gradients in turbidity per se do not have a strong effect on their habitat preference.

Keywords Turbidity · Juvenile Atlantic cod · Habitat preference

Introduction

Human activities leading to the suspension of sediments or eutrophication are increasing the turbidity of coastal waters in the North Sea (Frid et al. 2003) and Baltic Oceans (Bonsdorff et al. 1997). This has led to concerns on possible impacts on commercial fish populations. In contrast to freshwater systems (see reviews by Henley et al. 2000; Bash et al. 2001), little is known on the influence of turbidity on the distribution of marine fish. In freshwater systems, changes in turbidity can affect fish distributions by influencing settlement, survival or patterns of habitat preference or avoidance (see review by Henley et al. 2000). Causes are varied, but range from effects on fish vision (e.g. Vinyard and O'Brien 1976), habitat quality (e.g. quality of sediments for egg laying, see review by Bash et al. 2001) or interference of physiological function (e.g. gill trauma, osmoregulation, Servizi and Martens 1992). Turbidity levels in marine systems are generally not as extreme as in freshwater, hence, turbidity is thought to affect fish distributions in marine systems primarily by limiting visual range (Utne-Palm 2002; Aksnes et al. 2004).

A reduced visual range in turbid water may affect social interactions (Berg and Northcote 1985), foraging (reviewed by Utne-Palm 2002) and predator avoidance behaviour of fish (Miner and Stein 1996). The relationship between

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turbidity and habitat preference may therefore be complex. For example, reduced foraging search volume in turbid water (e.g. Vogel and Beauchamp 1999) and the risk of predation in clear water (e.g. de Robertis et al. 2003), may result in a trade-off between foraging return and predator risk, favouring intermediate turbidities.

The influence of turbidity on marine fish populations is also likely to be species specific, depending on a range of factors, such as the contribution of vision to feeding and predator avoidance, and the effects of turbidity on prey availability. Visual perception of turbid environments is also likely to vary among fish species, because of differences in colour vision between species (Bowmaker 1995) and spectral differences in scattering and absorption between particles causing turbidity (Mobley 1994). It is therefore important to have a clear understanding of fish vision to understand the effects of turbidity on the distribution of fish. Although several studies have commented on the colour of turbidity media (e.g. Boubée et al. 1997), visual perception of turbid environments by fish has been largely ignored in habitat choice experiments.

Atlantic cod, *Gadus morhua*, are an ideal model species to investigate the effects of turbidity on habitat choice, as vision in this species is well understood (Anthony 1981; Anthony and Hawkins 1983). Coastal cod populations are also declining (Hutchings and Baum 2005) and the influence of turbidity on their distribution is poorly known. Recent experiments have focused on the role of turbidity on foraging and antipredator behaviour on juvenile cod, because they are often found in shallow, coastal waters (e.g. Gregory and Anderson 1997) that are often the most affected by turbidity (Mobley 1994). These experiments have shown that juvenile cod are likely to have higher energetic costs associated with foraging on evasive prey (Meager et al. 2005; Meager and Batty 2007) and reduced ability to escape from predators, in highly turbid water (Meager et al. 2006). We predict from these results that juvenile cod avoid areas of high turbidity. In this study, we tested this hypothesis by examining habitat preference of cod in relation to a range of turbidity levels. We also aimed to determine if this response to turbidity is similar

between two of the main particulate components of turbidity in coastal waters: clay and algae (Mobley 1994).

Materials and methods

Fish and experimental setup

Offspring of wild-caught parental cod (60°16' N; 4°58' E) were reared at the University of Bergen (spawned spring, 2003). Fish sizes in the experiment (summer 2004) ranged from 18 cm to 27 cm Standard Length (SL) (mean: 21.6 cm SL, standard deviation: 2.05).

We tested for behavioural responses of cod to turbidity gradients in shuttle boxes where fish could select between two different habitats (see Utne et al. 1997). Each shuttle box consisted of two tanks (150 l, 60 × 60 cm, 47 cm depth) connected by a transparent tube (15 cm diameter, 30 cm long). Inside the tubes, two funnels that tapered from 15 cm to 13 cm diameter were used to restrict the flow of water between tanks. Rocks (~10 cm in diameter) covered one-third of the bottom of each tank and provided shelter.

Diffuse light conditions were provided ($5.5 \mu\text{E m}^{-2} \text{s}^{-1}$) by indirectly illuminating (lights directed towards the walls and ceiling of the room) with halogen floodlights (4 × 150 W). Homogenous turbidity levels were maintained on each side of the shuttle box throughout the experiments by providing slight aeration through air stones. Turbidity was measured as % light transmitted (T) with a spectrophotometer (Shimadzu UV-VIS Recording Spectrophotometer UV-160) at a wavelength (λ) of 490 nm. Light transmission (T) was converted to beam attenuation (c) ($c = -10 \ln T$). To minimise bias due to forward-scattering, a 10 cm cuvette was used (see Meager et al. 2005 for more details). Turbidity samples were taken mid-water column at the start and finish of each trial, using syringes attached to plastic tubes mounted on each side of the shuttle boxes.

Experimental protocol

The first experiment tested for the effect of three turbidity levels on habitat preference of cod: low,

intermediate and high turbidity ($c = 3, 8$ and 21 m^{-1} ; 6.5, 21 and 47 NTU, measured with a Vernier turbidity sensor). These turbidity levels represent the range of coastal and estuarine habitats (McMahon et al. 1992; Bowers et al. 2000; Frette et al. 2004) used by juvenile Atlantic cod. At least 10 fish received each treatment: 21 vs. 3 m^{-1} , 3 vs. 8 m^{-1} and 8 vs. 21 m^{-1} . An additional 10 fish received a control to test for a tank effect (3 vs. 3 m^{-1}). Suspensions of pulverised kaolinite clay (Kaolin Polisperse 10, IMERYS) were used to make the water turbid.

The second experiment tested for the effect of turbidity media (algae and kaolin) on habitat preference by juvenile cod. In this experiment, at least 10 fish received each treatment: low turbidity versus intermediate algal turbidity (3 vs. 3 m^{-1}), and intermediate algal turbidity versus intermediate kaolin turbidity (8 vs. 8 m^{-1}). We used algal suspensions created from frozen microalgae (*Nannochloropsis* sp.: Reed Mariculture) that were defrosted prior to the experiments, and suspensions of kaolin (as above). We controlled for spectral differences between turbidity media by measuring beam attenuation level at the visual response peak for cod ($\lambda = 490 \text{ nm}$, Anthony and Hawkins 1983) (see Fig. 1).

Experiments one and two followed the same basic protocol; one juvenile cod was released into a random side of each shuttle box during the afternoon and allowed to move freely between sides overnight. The following day, turbidity media was introduced by carefully pouring a 300 ml suspension of turbidity media and seawater into the shuttle boxes. In tanks receiving the low turbidity (3 m^{-1}) treatment, 300 ml of seawater was introduced as a procedural control. We also counterbalanced the effects of the starting turbidity level on fish behaviour; hence, half of the replicates in each treatment received the turbidity media in the reverse order. For example, in the comparison of intermediate versus high turbidity (8 vs. 21 m^{-1}), an intermediate turbidity level was established on side of the shuttle box containing the fish for five replicates (intermediate vs. high turbidity), and into the opposing side for the remaining five replicates (high vs. intermediate turbidity). Experiments commenced

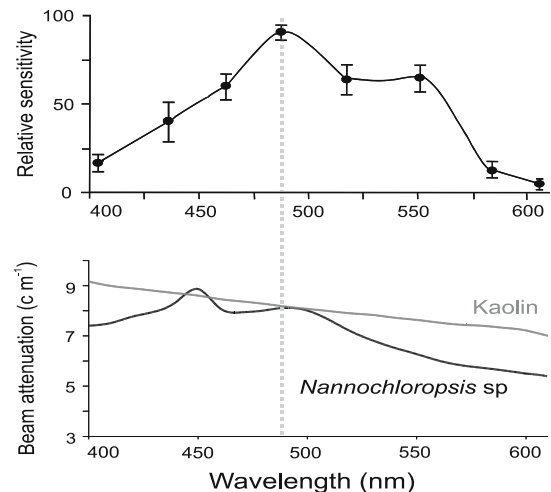


Fig. 1 Comparison of the visual effects of clay (kaolin, grey line) and algae, *Nannochloropsis* sp., (black line) on juvenile cod. The spectral distribution of the beam attenuation coefficient for each turbidity media is shown in the lower panel and the relative spectral sensitivity (mean \pm SE) of juvenile cod is shown in the upper panel (redrawn from Anthony and Hawkins 1983, with permission from Taylor & Francis Ltd.). The vertical dashed line indicates the visual response peak of cod and the wavelength where we measured beam attenuation in our experiments

15 min after the introduction of the turbidity media and lasted for 1 h.

The tubes connecting the tanks were illuminated with infrared lights ($\lambda > 800 \text{ nm}$) and filmed from above (Panasonic WV BP550). We also used an observer to verify fish movements in the intermediate versus high turbidity experiments, where image contrast was very low. We recorded the time and duration of movements between shuttles and calculated the total time spent on each side over the experimental period (60 min). These data were used to assign a binomial preference response category to each fish: either “preference response”, “no preference response”.

Preference responses were based on two criteria: (1) fish spent more than 37.5 min in total in the habitat during a trial, representing a deviation of greater than 25% from the neutral response and (2) fish that demonstrated an awareness of the alternative habitat by moving either between tanks or into the tube separating tanks. Log-likelihood ratio tests (2×2 G tests) were

used to test for effect of water turbidity on preference responses in each experiment. The effect of fish starting turbidity level on preference responses and fish movement was also examined with log-likelihood ratio tests.

Results

In the control experiments, preference responses were not significantly affected by shuttle box side ($G^1 = 0.26$, $P = 0.61$).

Experiment 1

Significantly more cod preferred intermediate turbidity (8 m^{-1}), from low turbidity water (3 m^{-1})

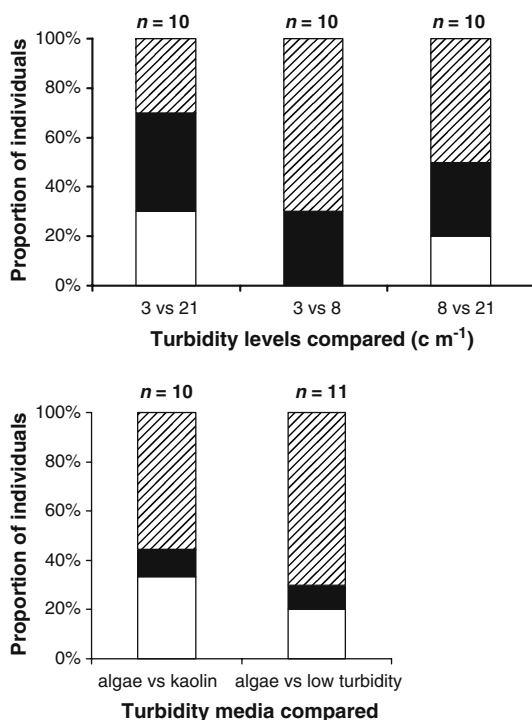


Fig. 2 Influence of turbidity (kaolin) on habitat preference patterns of juvenile cod in experiments 1 and 2. In the upper panel (experiment 1), the white sections of the bars indicate preference for the lowest turbidity level of the two tested, black sections indicate preference for the highest turbidity level, cross hatched sections indicate no preference. In the lower panel (experiment 2), white sections of the bars indicate preference for algal turbidity, black sections indicate preference for kaolin turbidity and cross hatched sections indicate no preference. n , total of number of fish tested

($G_1 = 4.8$, $P = 0.029$; Fig. 2). Both fish movement, and preference responses were significantly associated with fish starting turbidity (movement: $G^1 = 13.97$, $P < 0.001$; response: $G_1 = 7.9$, $P = 0.005$). Fish started in low turbidity water were more likely to move between habitats and hence, more likely to have a preference response, than fish started in water of intermediate turbidity.

Habitat preference was not significantly associated with turbidity in the intermediate versus high turbidity treatment (8 vs. 21 m^{-1}) ($G_1 = 0.27$, $P = 0.580$). Similarly preference responses were not significantly associated with starting turbidity ($G_1 = 0.31$, $P = 0.58$). However, fish movement was significantly associated with starting turbidity ($G_1 = 4.07$, $P = 0.044$) and fish were less likely to move between habitats if they started at intermediate turbidity.

Habitat preference was not significantly affected by the low turbidity water versus high turbidity treatment (3 vs. 21 m^{-1} : $G_1 = 0.22$, $P = 0.639$). Neither preference responses nor fish movement were significantly affected by the initial turbidity of fish (movement: $G_1 = 1.29$, $P = 0.256$; preference responses: $G_1 = 0.60$, $P = 0.439$).

Experiment 2

Neither algae (low turbidity water versus intermediate *Nannochloropsis* sp. turbidity, $G_1 = 0.67$, $P = 0.412$; Fig. 2), nor turbidity media (intermediate kaolin turbidity versus intermediate *Nannochloropsis* sp., $G_1 = 1.27$, $P = 0.260$; Fig. 2) significantly affected preference responses. Fish starting position did not affect either preference responses or fish movement in either treatment (preference responses: P from 0.260 to 0.412; movement: P from 0.888 to 0.937).

Discussion

Juvenile cod did not avoid highly turbid water, even when exposed to the steepest turbidity gradient (i.e. a difference in c of 18 m^{-1} between high and low turbidity water). Instead, a weak preference was found for an intermediate turbidity (8 m^{-1}) of kaolin from low turbidity water.

Fish started in intermediate turbidity also had reduced movement between habitats when compared to either low turbidity water or high turbidity. This is supported by recent experiments that indicated lower activity levels at an intermediate turbidity ($c = 10 \text{ m}^{-1}$), and may indicate that lower activity is a strategy to remain in their preferred habitat (Meager and Batty 2007).

No comparable data (i.e. beam attenuation or light extinction coefficients) are available for the distribution of cod in field in relation to turbidity. Juvenile cod are found in habitats ranging from clear coastal water (e.g. Godø et al. 1989; Grant and Brown 1998a) to highly turbid water of estuaries (Marshall and Elliot 1998). It is, however, difficult to ascertain from field evidence if cod prefer or avoid turbidity in the wild. One reason for this is that turbidity and cod abundance have rarely been measured simultaneously and we are aware of no studies that have recorded beam attenuation and cod abundances. An additional problem is covariance between turbidity and other environmental factors that may affect cod distributions (e.g. oxygen, temperature, salinity and habitat structure), and that the influence of turbidity in the field is also dependent on light intensity (Aksnes and Giske 1993) and hence, depth and season (among other factors).

Behavioural responses of cod in our experiment differed between *Nannochloropsis* algae and kaolin, i.e. cod had a weak preference for intermediate turbidity over low turbidity water for kaolin, but not for *Nannochloropsis* algae. It is, however, unlikely that cod preferred for kaolin clay per se, because they showed no preference for turbidity media (algae or clay) when similar turbidity levels were used. Clay (white) and algae (green) differ both in colour composition as well as in optical properties (algae are highly absorbing and clay are highly scattering). In our experiment, we controlled for these differences by (1) matching the beam attenuation of both media at the visual response peak of cod ($\lambda = 490 \text{ nm}$) and (2) controlling for both scattering and absorbing properties of the particles by measuring turbidity as beam attenuation $= a + b$, where a is absorption and b is the scattering coefficient (Zaneveld et al. 1979). However, clay attenuates more light at other wavelengths perceived by cod (Fig. 1).

Hence, although visual distances are likely to be similar for cod in each turbidity media (i.e. brightness contrast at peak visual sensitivity, Johnsen and Sosik 2003), their perceived background colour will differ. This may have accounted for differences in habitat preference between turbidity media, i.e. preference for an intermediate turbidity of kaolin over low turbidity water, but not for an intermediate turbidity of algae. The relative roles of visual distance and perceived background colour in determining preferences of turbidity media by fish are therefore likely to be complex. Very little is known of the role of the spectral composition of light on habitat choice in fishes, hence, further investigation may be warranted.

Despite a weak preference for intermediate kaolin turbidity over low turbidity water, no strong preference/avoidance responses were observed in this study. Individual variability in cod responses to turbidity was high and varied from fish that did not explore either the shuttle box or the tube connecting the shuttle box, to an individual that entered the tube 37 times in 1 h. However, it is unlikely that this variability masked substantial differences between treatments, because we estimate that we had an 80% chance of detecting a 20% difference in habitat choice in each experiment (following the procedure of Agresti 1990).

An alternative explanation is that within moderate ranges, turbidity per se has a weak effect on juvenile cod distributions. Unlike other environmental factors such as temperature, salinity and dissolved oxygen (e.g. Claireaux and Dutil 1992; Claireaux et al. 1995), turbidity in our study was unlikely to have had direct energetic costs. In a recent study of juvenile cod, habitat preferences for oxygen concentrations in the laboratory were only affected when the fish were physiologically challenged by exposure to acute hypoxia (Herbert et al., unpublished data).

Differences in turbidity between habitats may therefore not be sufficient to generate strong habitat preference patterns in cod unless there is a potential fitness benefit, such as increased foraging return, or predator risk. Field data support this indirectly, by suggesting that food availability and vulnerability to predation are the

key factors affecting the distribution of juvenile cod (e.g. Grant and Brown 1998a, b; Linehan et al. 2001; Cote et al. 2002). Similarly, choice of habitat structure by juvenile cod in the laboratory depends on predator risk, with stronger habitat preferences in response to an actively foraging predator (Gotceitas et al. 1995). Although not tested in the current study, turbidity may also influence habitat preference by altering patterns of foraging return or predation risk (e.g. Abrahams and Kattenfeld 1997; Engström-Öst et al. 2006). Recent experiments have shown that both foraging and antipredator behaviour of juvenile cod are influenced by turbidity (Meager et al. 2005; Meager and Batty 2007; Meager et al. 2006), hence, a detailed study into the effect of turbidity on the distribution of juvenile cod should focus upon such indirect effects on habitat choice.

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