

Escape responses in juvenile Atlantic cod *Gadus morhua* L.: the effects of turbidity and predator speed

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Summary

We examined the effect of turbidity (0.5–14 beam attenuation m^{-1}) and predator attack speed (150 and 296 cm s^{-1}) on escape responses of juvenile cod *Gadus morhua* in the laboratory. We triggered escape responses using a predator model and measured escape timing, direction and locomotor performance. We also measured responsiveness and estimated the likelihood of fish escaping the ‘predator attack’ (putative escape success, PES).

Turbidity affected both PES and the type of escape response used by the fish, but these effects depended on predator speed. PES for the fast predator attack declined

from 73% in clear water to 21% in highly turbid water, due to decreased responsiveness and poorly timed escapes. Intermediate turbidity enhanced PES and responsiveness to the slow predator attack. Locomotor performance was reduced by turbidity, whereas predator speed had the opposite effect. Our results suggest that both predator attack speed and turbidity have important roles in determining the vulnerability of fish attacked by piscivorous predators.

Key words: turbidity, predator, speed, escape response, cod, *Gadus morhua*.

Introduction

Animals have a range of defences against predators, from minimising encounters to reducing the capture success of an attacking predator through evasion (Fuiman and Magurran, 1994). Most fish species evade predators by using escape responses involving a high-energy burst of swimming (for a review, see Domenici and Blake, 1997). Escape responses consist of a contraction of the axial musculature contralateral to the predator stimulus (stage 1), usually followed by a second contraction on the opposite side of the fish (stage 2) (Eaton et al., 1981; Domenici and Blake, 1993), resulting in a sudden acceleration away from the predator (Domenici and Blake, 1997). The factors affecting the success of an escape response have been studied by various authors and include the timing, direction and locomotor performance of escape responses (Dill, 1974a; Webb, 1984; Webb, 1986; Domenici and Blake, 1997; Lefrancois et al., 2005; Walker et al., 2005).

In aquatic systems, escape responses rely on sensory and motor systems that can be affected by environmental factors such as turbidity, temperature and dissolved oxygen (Webb and Zhang, 1994; Miner and Stein, 1996; Lefrancois et al., 2005). Vision has been studied extensively as one of the main sensory systems involved in escape responses (Dill, 1974a; Fuiman, 1993; Domenici, 2002) and provides a high spatial and temporal resolution of information of the identity,

distance, speed and direction of approaching predators (Curio, 1993; Hemmi, 2005b). Turbidity from suspended sediment, dissolved organic matter and plankton scatters and absorbs light and can reduce the visual abilities of fish (e.g. Gregory and Northcote, 1993) (for a review, see Utne-Palm, 2002). Turbidity may therefore shift the advantage of piscivorous predator–prey interactions in either direction, depending on relative effects on the detection abilities of predators and prey. Numerous studies have looked at the effect of turbidity on detection of prey by predators (e.g. Gregory and Northcote, 1993; Vogel and Beauchamp, 1999), but very few studies have looked at the effect of turbidity on detection of predators by prey (Miner and Stein, 1996).

Visual escape responses require both perception of the predator and a decision to escape (Blaxter and Fuiman, 1990; Hemmi, 2005a), based on the level of perceived risk (Ydenberg and Dill, 1986). Escaping from predators that pose no risk is energetically costly (Harper and Blake, 1988) and occurs at the expense of other fitness related behaviours (for a review, see Lima, 1998). Risk of directly approaching predators is conveyed by the magnifying retinal image; fish usually escape when the rate of change of this signal reaches a certain threshold (Dill, 1974a). Responding too early may allow predators to compensate for early reactions (Blaxter and Fuiman, 1990), while escaping at the latest possible moment

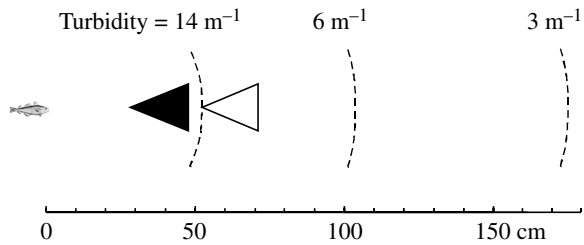


Fig. 1. Predicted effects of predator velocity and turbidity on escape responses of juvenile cod. Dotted lines indicate the influence of turbidity on visual fields [calculated from a visual model (Aksnes and Utne, 1997), using parameters from (Fiksen et al., 1998); the visual field in clear water exceeds 530 cm and is not shown]. Theory suggests that reactive distances are shorter to a slow predator attack (black triangle: 150 cm s^{-1}) than to a fast predator attack (white triangle: 296 cm s^{-1}), assuming a constant apparent looming threshold (Dill, 1974a) of 0.5 rad s^{-1} (Domenici, 2002). Reactive distance (distance to the predator's widest point) to the slow predator is within the visual field for all turbidity levels, but reactive distance to the fast predator is outside the visual range in the highest turbidity.

may be advantageous [the 'matador strategy' (Blaxter and Fuiman, 1990; Fuiman, 1993)].

The time available for prey to detect predators and decide on an appropriate response is limited by predator attack speed. Similarly, turbidity may limit the time prey have to evade a predator, by reducing visual distance. Hence, high turbidity or fast predator attacks may result in prey being caught before detecting the predator. Less time to respond to the predator and changes in stimulus characteristics such as image contrast and attack speed, may also lead to reduced escape performance in terms of timing, direction or locomotor performance.

As both predator speed and turbidity influence the distance from which prey respond to predators (prey reactive distance) (Dill, 1974a; Miner and Stein, 1996), their combined effects are likely to be more complex. While prey reactive distance is longer for faster predators (Dill, 1974a), it is limited by turbidity (Miner and Stein, 1996). We therefore predict that turbidity will have greater effects on fast predators (longer reactive distances) than slow predators (shorter reactive distances) (Fig. 1).

Atlantic cod *Gadus morhua* make an ideal model to test this prediction, as the visual sensory system of this species is quite well understood (e.g. Anthony, 1981; Anthony and Hawkins, 1983). Understanding how turbidity influences predator evasion by juvenile cod will also aid in predicting the impact of increases in turbidity from human activities (Bonsdorff et al., 1997; Frid et al., 2003) on its vulnerability to predation.

This paper examines escape responses of juvenile Atlantic cod under laboratory conditions. We tested the hypothesis that the influence of turbidity on escape responses depends on predator attack speed, with greater effects at faster speeds (Fig. 1). We also aimed to determine which characteristics of an escape response are affected by turbidity and predator speed.

Materials and methods

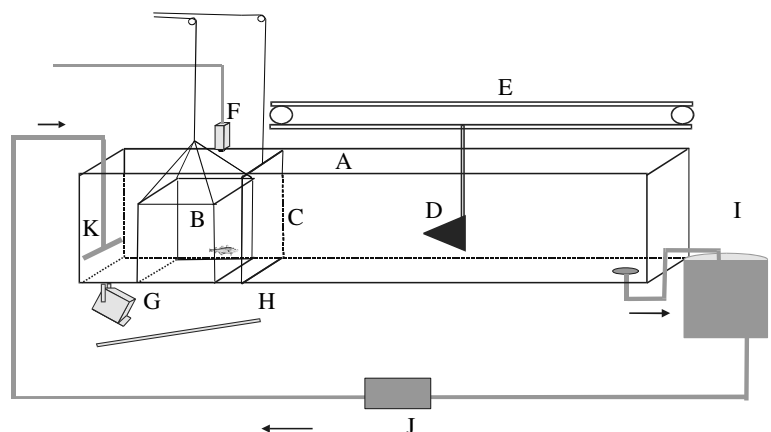
Experimental animals and observation tank

Offspring of wild caught parental cod *Gadus morhua* L. ($60^{\circ}16'N$; $4^{\circ}58'E$) were reared at the University of Bergen (spawned spring 2003) and fed a mixture of pellets, mysids, frozen gobies and decapods.

Experiments were conducted in a large rectangular glass aquarium ($70 \text{ cm} \times 300 \text{ cm} \times 50 \text{ cm}$), filled to a depth of 20 cm with seawater (salinity: 32–35‰, temperature: $9 \pm 1^{\circ}\text{C}$) from a flow-through seawater system (Fig. 2). This depth was used so fish could be viewed from above in the highest turbidity treatments. Prey were located in an experimental arena (5 mm thick glass) that was lowered down into the aquarium and further separated from the predator model by a clear, removable divide that consisted of one 5 mm thick glass sheet and one 5 mm thick Perspex sheet with rubber shock absorbers placed between (Fig. 2). The walls of the fish compartment rested on a silicon cushion (10 mm thick). The opposing end of the aquarium was painted white.

Diffuse light conditions were provided ($9.5 \pm 0.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$) by indirectly illuminating (lights directed towards the white walls and ceiling of the room) the aquarium with four halogen floodlights ($2 \times 150 \text{ W}$, $2 \times 500 \text{ W}$). This irradiance level is equivalent to that found in

Fig. 2. Experiment set-up. (A) Glass aquarium ($300 \text{ cm} \times 70 \text{ cm} \times 50 \text{ cm}$). (B) Removable fish compartment ($40 \text{ cm} \times 54 \text{ cm} \times 40 \text{ cm}$, bottomless). (C) Removable glass and Perspex barrier. (D) Predator model (conical shape). (E) Predator model track (200 cm long). (F) Overhead video camera (250 Hz, Redlake, Motion Scope PCI) with infrared filter (Optolite 50% IR). (G) Infrared lamp (Derwent 70W, 830 nm). (H) Reflective white board. (I) Tank where saltwater and kaolin were mixed by air-bubbling and circulation. (J) Pump (58 l m^{-1}) introducing turbid water mix into aquarium through jets (K).



juvenile cod habitat in coastal waters of western Norway [i.e. at a 20-m depth on a clear summer day or 3 m depth on a cloudy winter day (Baliño and Aksnes, 1993)]. The experimental aquarium was illuminated from underneath with diffuse infrared light (>800 nm wavelength) and fish silhouettes were recorded at 250 frames s^{-1} using an overhead high-speed video camera (Redlake Motion Scope 1000S PCI, Tucson, AZ, USA) fitted with an infrared filter (Optolite 50% IR, Instrument Plastics Ltd., Maidenhead, Berks, UK). Turbidity levels were established by combining clay particles (pulverised kaolinite, Polisperse 10, IMERYS, Oslo, Norway) and seawater in a mixing tank and recirculating the water through the experimental tank (Fig. 2) (for details, see Meager et al., 2005).

Predator model

Predator attacks were simulated by a predator model that was computer controlled, and hence able to move through the experimental aquarium at highly repeatable speeds. This model was based on the frontal profile of a 60 cm generalised teleost predator, i.e. with a conical shape and 15 cm wide (i.e. 0.25 body lengths; BL) at a point 18 cm from the tip of the snout (0.3 BL) (Domenici, 2002). Predator length was based on field data for predators of Atlantic cod (Scharf et al., 2000). The model was painted matte black to give it an inherent contrast of -1 against the white background.

The predator model was driven by an electric motor with a variable-speed transformer. A computer server (Omron Corporation, Xmonwin 1.0) regulated model speed every 2.5 ms to maintain the predator model to within 10% of the designated speed for approximately 90% of the predator path (slow speed: 92% of path; fast speed: 87% of path). Cruising speed of the model was measured with a high-speed camera at 250 frames s^{-1} (Redlake, Motion Scope PCI) and was the same for five separate trials of each speed. The model was then synchronised with the high-speed camera to allow us to determine the position of the predator model in each frame, at each predator speed. The predator model and high-speed camera were triggered simultaneously from a control room (5 m away).

Experimental protocol

We examined the visual-escape response of juvenile cod to two predator model speeds: 150 $cm s^{-1}$ and 296 $cm s^{-1}$ (2.5 $BL s^{-1}$ and 4.9 $BL s^{-1}$ for a 60 cm predator) and four turbidity levels: 0.5, 3, 6 and 14 beam attenuation m^{-1} (1.8, 11, 20 and 44 NTU nephelometric turbidity units, measured using a Vernier Turbidity Sensor, Sarasota, FL, USA). Predator speeds were based on values from a review (Domenici, 2002) and turbidities represented the range of habitats used by juvenile Atlantic cod (see Meager et al., 2005). Turbidity was measured as the percent of light transmitted through a 10 cm cuvette in a spectrophotometer (Shimadzu UV-VIS Recording Spectrophotometer UV-160, Duisburg, Germany) at 800 nm (to minimise near-forward scattering) and converted to beam attenuation using the standard relationship: $T = \exp^{-cT}$, where T

is light transmitted through a path length r (in m) and c is the beam attenuation coefficient.

A minimum of 10 fish (mean total length ± 1 s.e.m. = 12.9 ± 0.1 cm; 101 fish tested in total) were tested for each predator speed–turbidity treatment. Higher numbers of fish were tested where necessary to provide a minimum of 7 responders in each treatment. Each trial used a different fish to avoid learning effects (Dill, 1974b).

After turbidity levels ($\pm 0.5 m^{-1}$) were established in the aquarium, the fish compartment and divides were lowered into place (Fig. 2). Fish were then transported from holding tanks using plastic bags filled with water to minimise handling stress and each fish was acclimated to the fish compartment for 1.5 h (Artigas et al., 2005). The predator stimulus and high-speed camera were triggered when cod entered into a ‘target area’ that was trapezium shaped (base: 15 cm, height: 10 cm, area: 300 cm^2) and 8–28 cm from where the predator model stopped. We used this target area to standardise the prey’s visual perspective of the model (i.e. to avoid a lateral view of the model) and to avoid effects of compartment walls on escape trajectories (Eaton and Emberley, 1991). Prey reactions were recorded at 250 frames s^{-1} .

After each trial was completed, fish were anaesthetised and eye size (diameter; mm), standard length (cm) and weight (g) were measured. Water samples from random locations at 7–8 cm depth in both the predator and prey sections of the aquarium at the start and finish of each trial were used to measure turbidity during a trial.

Trials were also conducted with a black screen (0.16 mm thick black polyethylene plastic) fixed to the front of the fish compartment (Fig. 2B) to control for potential non-visual responses, e.g. due to noise or vibrations generated by the motor or predator model. 26 different fish were tested in clear (beam attenuation coefficient $c = 0.5 m^{-1}$) and highly turbid water ($c = 14 m^{-1}$) at both predator model speeds. No non-visual responses were recorded.

Behavioural and kinematic analysis

Trials were analysed using frame-by-frame replay (Win Analyse, Version 1.6, Mikromak, Berlin, Germany) to measure the effect of turbidity and predator speed on responsiveness, and escape timing, direction and locomotor performance. The following conventions were used to analyse escape responses: stage 1, the initial turn; stage 2, rotation of the head in the opposite direction (Domenici and Blake, 1997).

Responsiveness

Responsiveness (% of individuals responding to predator stimulus) was measured for all fish tested. Fish that turned as the predator model approached, or up to 100 ms after the model stopped, were classified as ‘responders’, and all other fish were classified as ‘non-responders’.

Escape locomotor performance

Escape locomotor performance was measured by turning rate, and distance covered over a fixed-time interval. Turning

rate was calculated as the stage 1 angle, i.e. difference in orientation of the head between the initial position and at the end of stage 1, divided by the duration of the turn (Domenici and Batty, 1997). This was determined for the midline of the fish, which was measured as the straight line passing from the centre of mass (when stretched straight, i.e. 0.35 *BL*) to the tip of the head (Domenici and Blake, 1997).

Turning rates were used to classify escape types (Domenici and Batty, 1997; Domenici et al., 2004). To compare escape types with turns during spontaneous swimming, we also measured turning rates of fish of the same size range in the tank during routine activity (i.e. same experimental conditions, but without the predator model).

Distance covered (D_{80}) was defined as the distance between the centre of mass of the fish at time 0 and 80 ms after the initiation of the escape response (80 ms was chosen as the maximum duration for which all escapes were in the field of view of the camera and within the propulsive phases of the escape).

Escape direction

Escape trajectory and initial orientation were determined for each fish by measuring the angle between the midline of the fish (anterior to the centre of mass) and the attack path of the predator (for details, see Domenici and Blake, 1993). Hence, an angle of 0° represented a fish heading towards the predator. Escape trajectory was determined as the final angle of the escape (i.e. when the fish was swimming in a straight direction or gliding), relative to the attack path of the predator. All fish were observed to swim on a straight course or glide at the end of the escape response, while they were within the field of view of the camera. Initial orientation was measured at frame 0 (1 frame before the first detectable movement).

Escape timing

Reactive distance (*RD*) was calculated as the distance between the nearest prey eye and the posterior section (i.e. widest point) of the predator model, at frame 1 (frame with first detectable movement). We also estimated 'true reactive distance' (*TRD*), which took into account the delay between perception of the stimulus and the first detectable movement of fish (or latency) (Batty and Domenici, 2000). *TRD* was calculated for a range of latencies from the literature [50 and 100 ms: based on visual escape latencies (Batty, 1989)].

We also calculated apparent predator size as the angular size of the predator's image on the retina of the prey (O'Brien et al., 1976) (in degrees). Apparent looming threshold (*ALT*) was calculated as the rate of change of this angle (rad s^{-1}), using the following equation (Dill, 1974a):

$$\text{ALT} = \frac{4U_a S}{4D_a^2 + S^2}, \quad (1)$$

where *S* was the widest diameter of the predator model (0.15 m), D_a was reactive distance and U_a was the speed of the predator model. The *ALT* of each fish was therefore calculated

in the frame in which the escape response started. We also calculated 'true looming threshold' (*TLT*) (Paglianti and Domenici, 2006), based on *TRD*.

Putative escape performance (*PES*)

Fish were grouped into two categories: 'caught' or 'escaped', based on the likelihood of escaping the initial 'predator attack'. This calculation was defined as 'putative escape performance' (*PES*) and was based on the predator model continuing to move in a straight line with a constant speed. We used a predator gape size of 0.1 *BL*, which was representative of a generalist predator (for a review, see Domenici, 2002) and within the range of predators of juvenile Atlantic cod (Scharf et al., 2000). We measured *PES* by superimposing the putative path of the predator model over the prey footage. Prey were assumed to have escaped the predator once the whole body reached the outer limit of the path of the predator's gape projection.

Data analysis

Data were analysed using SPSS [Release 13, (SPSS Inc., 1999-2004)], Statistica (Release 6.1, StatSoft Inc., 2003) and Oriana (Release 2.02, Kovach Computing Services). The relationships between responsiveness, and turbidity and predator speed were analysed using logistic regression. We also used logistic regression to test for the influence of turbidity and speed on locomotor performance category, and on *PES*. The goodness of fit of a particular model was determined using the Likelihood Ratio statistic (G^2). Logit models were used to compare treatments and the odds of an occurrence were calculated as the exponential transformation of the corresponding logit value (Agresti, 1990).

Differences in escape direction between turbidities and predator speeds were tested using the Mardia-Watson-Wheeler tests (Batschelet, 1981).

Non-linear regression of treatment medians was used to test for the standard relationship between turbidity (*c*) and reactive distance (Gregory and Northcote, 1992). Conceptually, non-responders may have had a higher *ALT* had the stimulus been close enough. Hence, *ALT* data were treated as Type 1 censored samples (Webb, 1982; Blaxter and Fuiman, 1990) and the Generalised Wilcoxon Test (StatSoft Inc., 2003) test for comparing survival curves was used to test for differences in *ALT* between turbidity levels. *ALT* values were log-normally distributed and were log-transformed. We also used the Generalised Wilcoxon Test to test for differences in reactive distance between predator speeds.

To determine which factors had the most influence on *PES* we used forward-stepwise logistic regression. The following variables were included: timing (*ALT* and *RD*), locomotor performance (D_{80} , *S1* angle, *S1* duration, turning rate) and direction (escape trajectory). We also included initial orientation in the model. In this analysis, escape trajectory and initial orientation were transformed into angular displacement from the predator path (i.e. from 0 to 180°) (Batschelet, 1981).

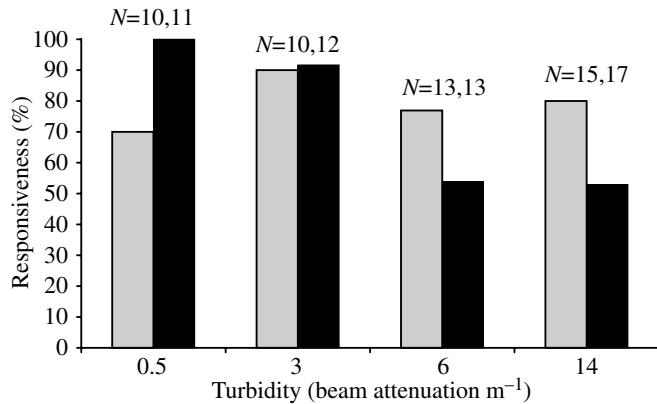


Fig. 3. Responsiveness (%) of juvenile cod with increasing turbidity to the fast (black) and slow predator attack speeds (grey). *N*, total number of fish used in each treatment.

Results

Responsiveness

An interaction between speed and turbidity significantly affected responsiveness to the predator model (interaction term: $G^2=7.97$, d.f.=1, $P=0.005$; turbidity $G^2=5.24$, d.f.=1, $P=0.022$; speed $G^2=0.76$, d.f.=1, $P=0.38$). Responsiveness to the fast predator model speed declined with turbidity (from 100% in clear water to 53% in highly turbid water, Fig. 3). Responsiveness to the slow predator model was higher at low turbidity ($c=3\text{ m}^{-1}$), but similar at other turbidity levels (Fig. 3). Fish were significantly more likely to respond to the fast predator speed than the slow predator speed in clear water. At a turbidity of 3 m^{-1} , the likelihood of responding was similar between predator speeds. At higher turbidities, the fish were more likely to respond to the slow predator speed than the fast predator speed (logit model: fish were 2.7 and 3.2 times more likely to respond to the slow predator speed at turbidities 6 m^{-1} and 14 m^{-1} , respectively).

Escape locomotor performance

Kinematic type of escape responses

Fish evaded the model with three types of responses based on a frequency distribution of turning rates (Fig. 4): slow

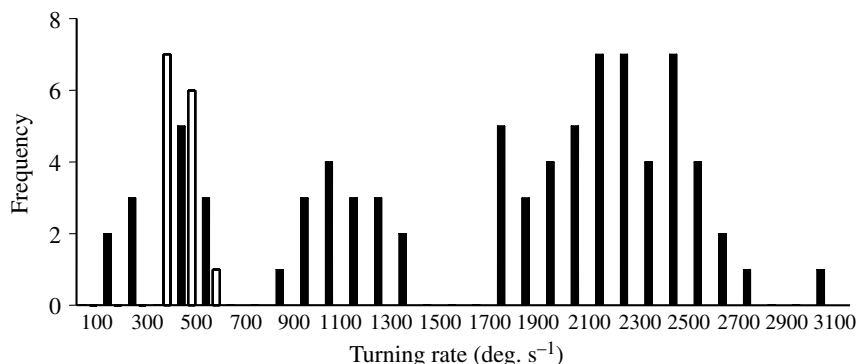


Fig. 4. Frequency distribution of juvenile cod turning rates during escapes (black bars) and spontaneous swimming (white bars).

Table 1. Escape locomotor performance categories of juvenile cod to predator model and results of ANOVAs testing for differences between categories

| Escape performance | Responses | | | $F_{2,74}$ |
|---------------------------------|------------|--------------|----------|------------|
| | Slow | Intermediate | Fast | |
| D_{80} (mm) ⁺ | 8.6±1.2 | 26.7±6.2 | 56.4±2.9 | 70.5** |
| S1 angle (degrees) ⁺ | 63.9±8.6 | 75±11.3 | 79.9±4.2 | 1.3 |
| S1 duration (ms) ⁺ | 174.1±12.6 | 68±10.3 | 35.8±1.8 | 142.5** |
| <i>N</i> | 12 | 14 | 49 | |

Values are means ± s.e.m. (*N*=sample size).

** $P<0.001$; ⁺data were log-transformed prior to analysis to correct for heteroscedasticity (Cochran *C*-test); D_{80} , distance covered in 80 ms; S1, stage 1 of escape response.

responses, with turns of similar turning rates as during routine swimming (mean turning rate ± s.e.m.) of $395.3\pm 41.2\text{ deg. s}^{-1}$ (range: $119.6\text{--}591.9\text{ deg. s}^{-1}$), intermediate responses with a mean turning rate of $1117.3\pm 41.3\text{ deg. s}^{-1}$ (range: $942.8\text{--}1335.9\text{ deg. s}^{-1}$) and fast responses with a mean turning rate of $2215.7\pm 41.2\text{ deg. s}^{-1}$ (range: $1718.5\text{--}3002.7\text{ deg. s}^{-1}$). These response categories differed significantly in escape speed (D_{80} and S1 duration), but not in S1 angle (Table 1; ANOVA analysis). The average speed (over first 80 ms) of slow escape responses was $10.7\pm 1.5\text{ cm s}^{-1}$ ($0.8\pm 0.1\text{ BL s}^{-1}$), compared with $33.2\pm 6.8\text{ cm s}^{-1}$ ($2.4\pm 0.5\text{ BL s}^{-1}$) for intermediate responses and $72.4\pm 3.6\text{ cm s}^{-1}$ ($5.7\pm 0.3\text{ BL s}^{-1}$) for fast responses.

Effects of turbidity and predator speed on locomotor performance

Because of limited numbers of slow responses (Fig. 4), slow and intermediate responses were pooled as 'slow-intermediate responses'. The proportion of slow-intermediate responses and fast responses was significantly affected by predator attack speed and turbidity (predator speed: $G^2=10.5$, d.f.=1, $P=0.001$; turbidity: $G^2=5.4$, d.f.=1, $P=0.02$). Slow-intermediate responses were more commonly elicited by the slow predator attack speed and fast responses were more often triggered by the fast predator attack.

The logit model predicted that the odds of fish responding with a fast response were 4.4 times higher for the fast predator speed than for the slow predator speed. The proportion of slow-intermediate responses was greater in turbid ($3\text{--}14\text{ m}^{-1}$) than clear water (Fig. 5). The logit model predicted that the odds of a fast response ranged from 4.2 in clear water to 1 in highly turbid water (i.e. the probability of fish responding with a fast response in clear water was 0.81, compared with 0.5 at a turbidity of 14 m^{-1}). Although there was a trend for the proportion of fast responses to decrease at a turbidity of 3 m^{-1} for the slow predator speed, and increase for the fast predator velocity, there was no

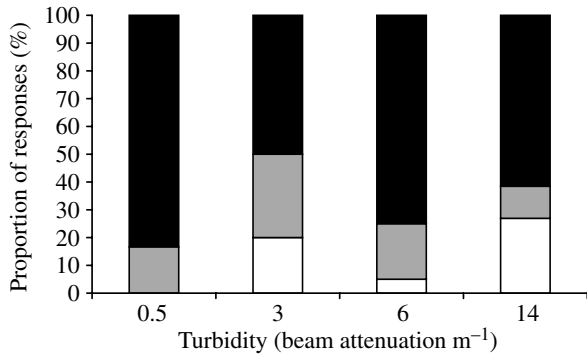


Fig. 5. Effect of turbidity on kinematic escape categories of juvenile cod to predator model (slow responses, white; intermediate response, grey; fast responses: black). Responses to fast and slow predator speeds were pooled because there was no significant interaction between turbidity and predator speed ($P=0.93$).

significant interaction between turbidity and predator speed (interaction term: $G^2=0.01$, d.f.=1, $P=0.93$).

Escape direction

Turbidity did not significantly affect the direction of escape from the predator model (Mardia–Watson–Wheeler Test: $W=4.79$, $P=0.571$, $N=17-21$). Similarly, escape direction was not significantly affected by predator speed (Mardia–Watson–Wheeler Test: $W=1.29$, $P=0.524$, $N_1=31$, $N_2=38$). Although most fish were close to perpendicular to the line of predator at the start of the ‘predator attack’ (circular mean \pm s.e.m. = $88.1 \pm 3.4^\circ$), initial orientations ranged from 5° to 160° . The mean escape trajectory (\pm s.e.m.) was $165.8 \pm 3.7^\circ$ (relative to an approaching predator at 0°). The distribution of escape trajectories, however, tended to be bimodal with peaks around

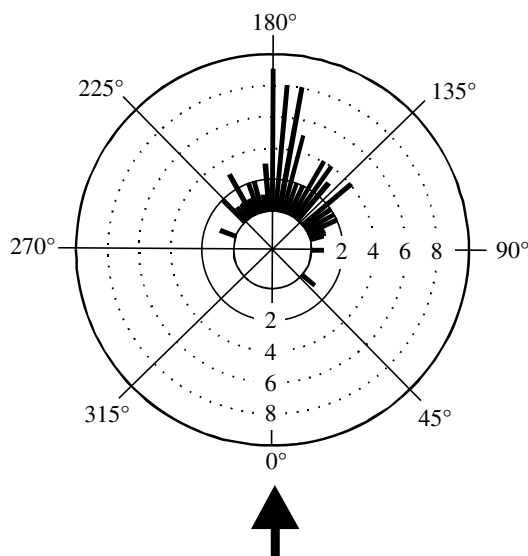


Fig. 6. Circular frequency distribution of escape trajectories of juvenile cod to predator model (black arrow) (trajectory category size: 5°).

140° and 180° (Fig. 6). There were no significant differences in direction or initial orientation between the kinematic type of escapes (Mardia–Watson–Wheeler Test: $P=0.49-0.98$).

Escape timing

Fish were between 206 and 225 cm from the predator model when the model was triggered, and the model stopped between 11 and 28 cm from the initial position of the fish (mean \pm 1 s.e.m.: 18.1 ± 5.1 cm). In clear water, reactive distance did not significantly differ between predator attack speeds (mean $RD \pm$ 1 s.e.m.: slow attack, 91.3 ± 25.3 cm; fast attack: 96.9 ± 22.1 cm) (Generalised Wilcoxon test: $Z=0.092$, $P=0.089$).

Reactive distance (cm) to the fast predator model declined as a negative power function of turbidity (c , m^{-1}) ($RD=67.01 \times \text{turbidity}^{-0.705}$, $r^2=0.99$, $P=0.009$ for 4 treatment medians, Fig. 7A). However, the relationship between reactive distance and turbidity was not significant for the slowest predator speed ($RD=70.3 \times \text{turbidity}^{-0.252}$, $r^2=0.34$, $P=0.416$ for 4 treatment medians, Fig. 7B). Apparent predator size followed an inverse function of reactive distance i.e. the predator appeared larger when it was closer (Fig. 7A,B).

ALT was significantly affected by turbidity, but only for the highest speed (Generalised Wilcoxon test for multiple samples: fast predator: $\chi^2=14.1$, d.f.=3, $P=0.003$; slow predator:

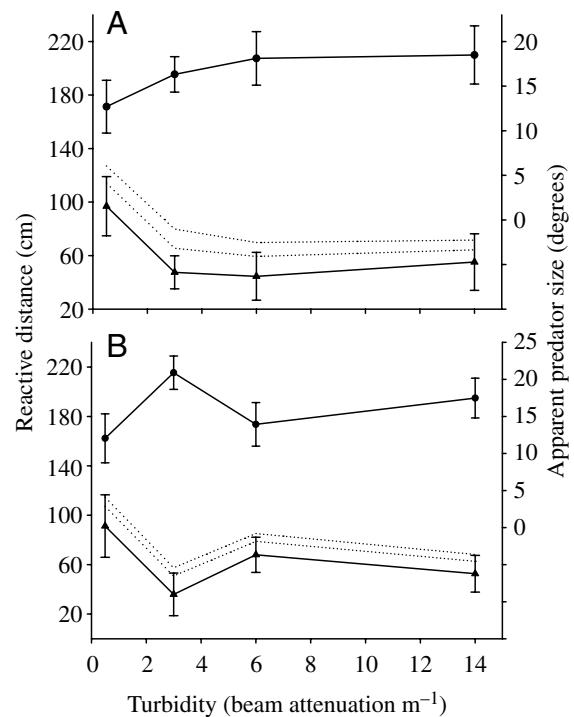


Fig. 7. Effect of turbidity on reactive distance (triangles) and apparent predator size (or retinal size) (circles) of juvenile cod to two predator attack speeds: (A) 296 cm s^{-1} or 4.9 BL s^{-1} and (B) 150 cm s^{-1} or 2.5 BL s^{-1} . Values are means \pm 1 s.e.m. Dotted lines are estimates of TRD (true reactive distance), assuming 50 ms latency (bottom) and 100 ms latency (top).

$\chi^2=0.31$, d.f.=3, $P=0.96$). ALT increased from clear water (1.11 ± 0.15 rad s^{-1}) to the highest turbidity (2.16 ± 1.75 rad s^{-1}) for the fast predator attack speed, indicating a higher response threshold at higher turbidities. Mean response threshold (ALT \pm s.e.m.) was 1.11 ± 0.15 rad s^{-1} to the slow predator speed ($TLT_{50ms}=0.66\pm 0.091$ rad s^{-1} ; $TLT_{100ms}=0.55\pm 0.081$ rad s^{-1}) and 2.16 ± 1.75 rad s^{-1} ($TLT_{50ms}=1.44\pm 0.22$ rad s^{-1} , $TLT_{100ms}=1.18\pm 0.21$ rad s^{-1}) to the fast predator speed.

Putative escape success

None of the non-responders were likely to have evaded the simulated predator attack. Putative escape success (PES) was significantly affected by an interaction between turbidity and speed (interaction term: $G^2=10.2$, d.f.=1, $P=0.001$; speed: $G^2=4.3$, d.f.=1, $P=0.38$; turbidity: $G^2=3.7$, d.f.=1, $P=0.06$). PES was higher for the slow predator speed in all turbidities except clear water (Fig. 8A). Increasing turbidity reduced putative escape success for the fast predator attack speed, in a similar manner to reactive distance (Fig. 8A and Fig. 7A). Hence, the logit model predicted that fish were 7.3 times more likely to evade the fast predator model in clear water than in turbid water (6–14 m^{-1}). However, for the slowest predator speed, putative escape success was the highest at intermediate turbidity (80% PES at $c=3$ m^{-1}), but similar between clear water and other turbidity categories (0.5, 6 and 14 m^{-1}) (Fig. 8A).

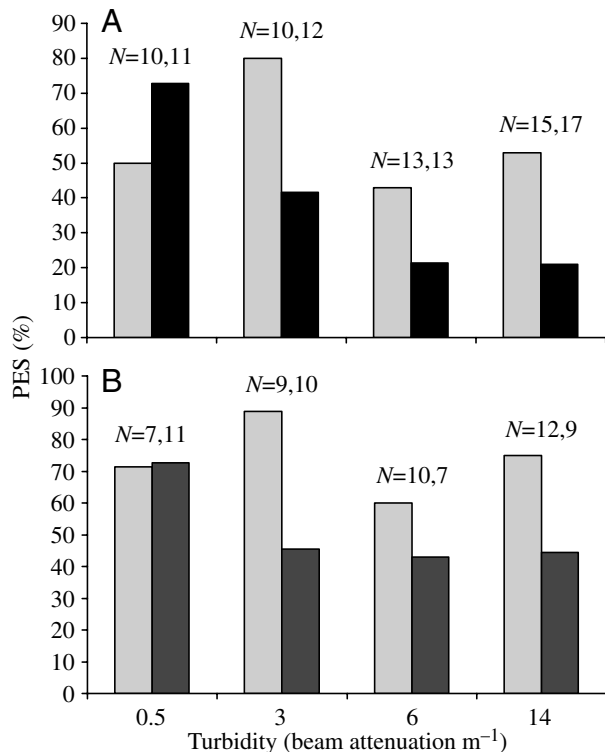


Fig. 8. Putative escape success (PES, %) of juvenile cod to the fast (black columns) and slow predator attacks (grey columns), with increasing turbidity. (A) Overall PES (B) PES of responders only. N , sample size.

We analysed 'responders' separately to remove variation associated with responsiveness. An interaction between turbidity and predator attack speed also significantly influenced PES of responders (interaction term: $G^2=4.16$, d.f.=1, $P=0.041$; predator speed: $G^2=3.68$, d.f.=1, $P=0.06$; turbidity: $G^2=0.68$, d.f.=1, $P=0.41$). Patterns of significance of PES between treatments were similar to the complete data set, i.e. PES was significantly lower in turbid water than clear water for the fast predator speed and significantly higher at 3 m^{-1} than other turbidity levels for the slow predator speed (Fig. 8B). In contrast to the complete data set, however, PES to the fast predator speed was similar between turbidities from 3 to 14 m^{-1} and PES was similar between predator attack speeds in clear water (logit analysis, Fig. 8A,B). 60–89% of the responders escaped the slow predator model, compared with 43–73% for the fast predator model (Fig. 8B).

Influence of escape parameters on putative escape success

Of the various escape parameters examined, response timing (ALT and RD) had the greatest influence on putative escape success (Table 2). ALT had the most significant affect on PES, but responsiveness and reactive distance were also significant (Table 2). Although ALT was derived from reactive distance, ALT took into account predator speed and predator size (Eqn 1).

ALT was also the most important variable affecting the fish that responded (Table 2). We also tested for other factors that may have influenced PES (minor variations in temperature, fish condition factor, eye size and length), but found no significant effects (P values from 0.108 to 0.999).

Table 2. Variables affecting the putative escape success of juvenile cod

| | All fish | | Fish that responded | |
|----------------------------------|-------------------|--------|---------------------|--------|
| | G^2 | P | G^2 | P |
| Locomotor performance | | | | |
| D_{80} | 0.12 | 0.725 | 0.001 | 0.978 |
| S1 angle | 0.24 | 0.621 | 0.66 | 0.415 |
| S1 duration | 0.01 | 0.929 | 0.28 | 0.599 |
| Turning rate | 0.49 | 0.484 | 1.70 | 0.193 |
| Escape direction | | | | |
| Escape trajectory ^a | 0.80 | 0.372 | 0.28 | 0.595 |
| Initial orientation ^a | 0.44 | 0.505 | 0.21 | 0.643 |
| Escape timing | | | | |
| ALT | 14.8 ⁺ | <0.001 | 14.8 ⁺ | <0.001 |
| Reactive distance | 9.9 | 0.002 | 8.77 | 0.003 |
| Responsiveness | | | | |
| | 39.7 | <0.001 | – | – |

G^2 , logistic regression analysis.

^aAngular displacement from predator; ⁺inclusion of the component makes a significant contribution to the multiple logistic regression model ($P<0.05$: forward stepwise); D_{80} , distance covered in 80 ms; S1, stage 1 of escape response; ALT, apparent looming threshold.

Discussion

Responsiveness and escape timing

The effect of turbidity on predator evasion by juvenile cod depended on the speed of the predator attack. Reactive distance to the fast predator attack decreased sharply with turbidity and followed a negative power relationship often evident in fish–fish interactions [i.e. *RD* to predators (Miner and Stein, 1996), and *RD* to prey (Vogel and Beauchamp, 1999; de Robertis et al., 2003)]. This is because visual impairment from turbidity is greater for large and conspicuous visual targets, such as other fish, than for smaller or cryptic targets (Aksnes and Giske, 1993; de Robertis et al., 2003). Fish in turbid water therefore responded to the fast attack later, when there was less time to evade the model. The probability of responding was also low at high turbidities (Fig. 3), due to limited time to perceive and react to the fast model. For example, if we assume that the fish reacted to the predator at close to the limits of their visual range and had a visual latency of 50 ms, they would have had only around 0.2 s to perceive and react to the fast predator at the highest turbidity level. Low vigilance in turbid water may have also contributed to this reduced responsiveness, as numerous studies have shown that turbidity reduces antipredator behaviour (Gregory, 1993; Abrahams and Kattenfeld, 1997; Van de Meutter et al., 2005).

The effect of turbidity on responsiveness and response timing was more complex for the slow predator attack. Responsiveness was similar between clear water and high turbidity (6–14 m⁻¹), but there was an unexpected increase at intermediate turbidity ($c=3$ m⁻¹, Fig. 3). Reactive distance was also variable and did not follow the relationship shown for the fast predator speed (Fig. 7). Furthermore, responsiveness to the slow predator attack in clear water was considerably less than to the fast attack (Fig. 3).

It is unlikely that the fish in our experiment were less vigilant in clear water, as all fish responded to the fast predator attack in clear water (Fig. 3). An alternative explanation for these results is that perceived risk to the slow predator attack was low in clear water and increased in intermediate turbidity. In our system, risk is represented by time to contact with the ‘predator’ after it enters the visual field of the prey. Hence, higher turbidity levels (and faster predator speeds) imply increased risk. Even at intermediate turbidity, fish have considerably less time to visually assess the risk imposed by an approaching object and less visual information. Due to the exponential attenuation of image-forming light in turbid water, visual distance in intermediate turbidity is considerably less than in clear water (Aksnes and Giske, 1993). Hence, the predator model was substantially closer (and appeared larger) by the time it was first detected by prey in intermediate turbidity, compared to clear water (Fig. 7). This would give the predator model a tendency to rapidly increase the area of the prey’s retina stimulated in intermediate turbidity. Such a sudden appearance of large image may have enhanced responsiveness in intermediate turbidity (compared to clear water) by increasing perceived

risk or startling the fish. In this context, such increased perceived risk or larger retinal stimulation may not have occurred in higher turbidity levels, because of a further reduction of visual range at high turbidity levels (6–14 m⁻¹), reducing the probability of fish seeing the slow predator model in time to respond. Contrast degradation at high turbidity levels water may have also reduced the visual information to a level that was below the threshold required for a response by some fish (Aksnes and Giske, 1993).

This explanation, however, remains speculative as we did not quantify perceived risk (Abrahams and Dill, 1989). Very little is known of visual predator recognition and predator-risk assessment in conditions of poor visibility and this subject needs further investigation. It is also interesting to note that contrary to theoretical predictions and previous work (Dill, 1974a) (Fig. 1), reactive distances were quite similar between predator speeds in clear water. Fish therefore had a higher response threshold (i.e. higher ALT) to the fast predator attack. The basis for discrepancies between our results and those of Dill (Dill, 1974a), who obtained a constant ALT independent of predator speed, are unclear but may be due to differences in methodology, temporal resolution or the species used. This indicates that further research into the relationship between predator speed and ALT may be warranted.

Escape locomotor performance

Turbidity and predator attack speed affected escape locomotor performance. Fish responded to the predator model with three categories of responses that varied in turning rates, and escapes with high turning rates were more commonly elicited by a fast predator attack and/or in clear water (Fig. 5). Enhanced locomotor performance to a fast predator attack speed indicates that escape responses depended on the immediacy of the threat, i.e. faster predators need to be evaded more quickly than slower predators. Decreased locomotor performance at higher turbidity levels, however, seems counterintuitive as the predator model was also closer to fish at the time of the response (Fig. 7). This is likely to be because of less visual information from the predator model (i.e. reduced contrast) over a shorter duration of time, hence, fish may not have received sufficient ‘threat’ information.

Our results indicated that escape behaviour was not maximised as an ‘all or nothing’ manoeuvre and are supported by numerous other studies (e.g. Webb, 1982; Webb, 1986; Domenici and Batty, 1994; Domenici and Batty, 1997; Domenici et al., 2004). The several kinematically discrete escape behaviours may be the result of different neural circuits or muscle activation patterns, as suggested elsewhere (Domenici and Batty, 1994; Domenici and Batty, 1997) [for a review of the neural basis of behaviour, see also DiDomenico and Eaton (DiDomenico and Eaton, 1988)].

Neither predator speed nor turbidity affected the direction of escape responses. Our study was the first to examine escape direction in cod and shows that escape trajectories are similar to those found in other fish species startled by mechano-acoustic stimuli (e.g. Domenici and Blake, 1993; Domenici and

Batty, 1997). It has been suggested that bimodal distributions of escape trajectories may imply sensory and biomechanical optimisations (Domenici and Blake, 1993). Our results suggest that escape trajectories may be relatively independent of the sensory systems involved.

Putative escape success

Turbidity and predator attack speed affected PES in a similar way to responsiveness. PES was largely determinant upon fish responding to the predator attack, and responding early enough to escape (i.e. timing and responsiveness). For example, of the 79% of fish that were 'caught' by the fast predator attack in high turbidity (14 m^{-1} , Fig. 8A), 57% were non-responders and the remaining 22% responded either too late or were too slow to escape.

Fish had approximately half the time to respond to the fast predator model than to the slow predator speed (since RD was relatively constant), hence, had lower PES to the fast predator model (between turbidity levels of 3 and 14 m^{-1} , Fig. 8A). Similarly, fish had less time to evade the model as turbidity increased and visual range decreased (Fig. 7). The effects of turbidity and speed were therefore additive, and PES was the lowest for the fast predator speed in turbid water, because fish were unable to see the model until it was close. Low PES to the slow predator attack in clear water was the exception to this pattern and was likely to be due to factors other than time/distance constraints, because the fish had considerable time to respond to the model (approx. 1.3 s) (Figs 3 and 8).

Response timing and responsiveness also determine escape success of larval fish from a fish predator (Fuiman, 1993) and of fish to avian predators (Katzir, 1993), and are critical in determining the outcome of predator-prey interactions (Domenici and Blake, 1997). Although it did not influence escape success significantly in our study, escape locomotor performance also varied with turbidity and predator speed. Locomotor performance is likely to be much more important in real predator-prey interactions, where the predator pursues the prey after the first strike (Webb, 1986). In these situations, escape locomotor performance can determine both evasion of the first predator strike and whether predators abort or give chase (Webb, 1986).

Ecological implications

The results of our study indicate that turbidity affected both the probability of juvenile cod detecting predators with enough time to respond, and the locomotor performance of their escapes. These effects depended upon predator attack speed: fish were more likely to evade a fast predator attack in clear water and a slow predator attack in intermediate turbidity.

The increased probability of capture by fast predators in turbid water indicates that faster attacks on prey in turbid water are less likely to elicit an early or fast prey response. Although these results suggest that predators may increase attack speeds in high turbidity, there are likely to be sensory-motor limits to this potential strategy. A recent study attributed reduced attack speeds of a planktivorous fish species in turbid water to less

visual information (Park and Park, 2005), but we are aware of no studies on the effect of turbidity on attack speeds of piscivorous fish. If attack speeds of piscivorous predators in turbid water are limited by sensory-motor constraints, then turbidity may have a stronger effect on attack rates than capture rates.

Our results suggest that the effects of turbidity on piscivorous predator-prey interactions are complex and depend on more than reactive distances or encounter rates (e.g. Miner and Stein, 1996; Abrahams and Kattenfeld, 1997). Knowledge of predator attack speed, and of prey evasive performance and behaviour, is also important. The probability of prey escaping may also be related to the searching speed of the predator, i.e. prey may be more likely to escape predators that are swimming slowly. Conversely, predators using faster searching speeds in turbid water may both maximise prey encounter (e.g. Sweka and Hartman, 2001) and reduce the probability of eliciting an early or fast escape response.

Mechano-reception is also used by fish to detect approaching predators (e.g. Bleckmann et al., 1996) and may increase in importance in turbid water [i.e. sensory compensation (Hartman and Abrahams, 2000)]. Hence, the outcome of predator-prey interactions in turbid water depends on the relative sensory abilities of both predator and prey, both in terms of vision and other sensory modalities (Vandenbyllaardt et al., 1991) (for a review, see Fuiman and Magurran, 1994). When considering multiple sensory modalities, asymmetries in predator-prey interactions are likely to be complex as information is integrated over different spatial and temporal scales by predators and prey (New et al., 2001; Montgomery et al., 2002).

This study has shown that even a small increase in turbidity can have a significant effect on visually mediated escape performance of juvenile cod. Escape performance to a fast predator attack was reduced at a turbidity level of 3 m^{-1} , which corresponds to summer algal blooms in coastal Norwegian waters and Baltic waters (Hamre et al., 2003; Kratzer et al., 2003). Cod in deeper waters or in waters with less surface irradiance are likely to be affected by even lower turbidity levels (Aksnes and Giske, 1993). This suggests turbidity may have an important role in regulating predation mortality in cod and indicates that further field-based investigation is required.

List of symbols and abbreviations

| | |
|----------------------|--|
| ALT | apparent looming threshold |
| BL | body length |
| c | beam attenuation coefficient (units: m^{-1}) |
| D_{80} | distance covered in 80 ms |
| PES | putative escape performance |
| RD | reactive distance |
| S1, S2 | stage 1, 2 of escape response |
| $TLT_{100\text{ms}}$ | true looming threshold (100 ms visual latency) |
| $TLT_{50\text{ms}}$ | true looming threshold (50 ms visual latency) |
| TRD | true reactive distance |

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