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The reactions of shoaling adult cod to a pelagic trawl: implications for commercial trawling

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The reactions of shoaling adult Atlantic cod to a pelagic trawl were measured during fishing off the north coast of Norway. Cod remaining in the trawl track dived at rates as fast as 0.35 m s^{-1} following vessel passage and swam away from the vessel, in the direction of the approaching trawl, at an average rate of 0.6 m s^{-1}. They did not attempt to swim ahead of the trawl as documented previously, but passed into the lower half of the trawl entrance and swam slowly in the direction of trawling at a rate of 0.2–0.5 m s^{-1} as the trawl's greater speed through water carried them deeper into the trawl. Shoals compressed vertically once inside the trawl, suggesting that packing density increased at least fourfold. Fish remained in the lower part of the trawl as they moved through its tapered section towards the codend, with little to no clearance above the bottom panel, but significant clearance beneath the top panel. Catches were sufficient to support commercial harvest, and the behaviour observed suggests that changes in trawl design and fishing strategy might improve fuel economy and species selectivity.

Keywords: cod behaviour, diving, fish capture, midwater trawl, swimming speed.

Introduction

Commercial fishing is coming under increased scrutiny for collateral environmental impact during harvest. Concerns have been raised about the impact of demersal trawling on the benthic community and ecosystem functioning (Kaiser *et al.*, 2002; Olsgard *et al.*, 2008; Hinz *et al.*, 2009), with experiments demonstrating a measurable decline in the biomass of large benthic organisms after trawling (Prena *et al.*, 1999), and less abundance and diversity in heavily trawled areas than in adjacent untrawled areas (McConnaughey *et al.*, 2000). High catch rates of non-target fish and invertebrates are a problem in many demersal trawl fisheries (Davies *et al.*, 2009), and criticism is growing about the large quantity of fossil fuel consumed per unit of fish captured (Tyedmers *et al.*, 2005; Schau *et al.*, 2009). One way to decrease the environmental consequences of trawl fisheries is to shift fishing effort from demersal to pelagic trawling. This would reduce or eliminate benthic impacts and the catch of non-target species over the seabed. Fuel consumption may be reduced too, through lessened drag when towing a large-mesh pelagic trawl with a reduced twine area and without bottom contact, although perhaps any benefit of a lower towing resistance would be negated by simply increasing the overall size of the trawl.

Pelagic trawls were first introduced in the late 1940s (Glanville, 1956), and they are used to harvest small pelagic species and large gadoids including hake and pollock (Chuenpagdee *et al.*, 2003), Pacific cod (*Gadus macrocephalus*; NMFS, 2011), and some grenadier species (e.g. *Macruronus novaezelandiae*; Graham *et al.*, 2003). Whereas pelagic trawls have been used to target Atlantic cod (*Gadus morhua*) in the Baltic Sea for decades (Madsen *et al.*, 2010), their use and development for targeting large gadoids in the Northeast Atlantic has been interrupted by regulatory changes and concerns about catches of juvenile fish (Hylen, 1973; Sævaldsson and Valtýsson, 2010). With little design undertaken specifically for the capture of large gadoid species, the trawls used there have generally been modified versions of those originally designed to capture small pelagic species with different life histories and behavioural reactions. This has likely led to suboptimal designs for the capture of economically important large gadoids such as Atlantic cod, haddock (*Melanogrammus aeglefinus*), and saithe (*Pollachius virens*).

Extensive literature exists on the behaviour of gadoid fish in relation to demersal trawls (Main and Sangster, 1981; Wardle, 1993; Engås, 1994; Kim and Wardle, 2003; Jones *et al.*, 2008). Fish react strongly to demersal trawls under light conditions and typically perform a "fountain manoeuvre", whereby they are herded towards the centre of the trawl entrance by visual perception of the trawl doors, mud clouds, netting, ropes, and the floats at the front of the trawl. Even under dark conditions, cod, haddock, and saithe enter at the horizontal centre of a demersal trawl (Engås and Ona, 1990), suggesting that non-visual stimuli may also play an important role in positioning fish ahead of the approaching trawl (though see Glass and Wardle, 1989). Studies of the behaviour of gadoids in relation to pelagic trawls are far fewer and have tended to concentrate on diving and horizontal herding in response to the vessel and the trawl (Ona and Godø, 1990) or on behaviour in the aft portion of the trawl (Pikitch *et al.*, 2002; Rose, 2004).

Norwegian fisheries managers and researchers hope to shift a portion of the current commercial demersal trawling effort for large gadoid species such as cod, haddock, and saithe to pelagic trawling. The investigation described here utilizes the observations of cod shoals beneath the vessel, at the trawl entrance, and at two locations inside the trawl to infer behaviour during the catch process. Understanding such behaviour is essential in developing more efficient pelagic trawl designs and fishing strategies for harvesting large gadoid species as well as for better understanding the catching efficiency of the trawls used in resource surveys.

Material and methods

Data were collected in the Barents Sea off the north coast of Norway (71°N 22°E) in April 2008 on board the 60-m 4590 bhp commercial trawler FV "Atlantic Star". Temperature at the fishing depth was 5°C (s.d. = 0.1). The trawl was placed with the headrope at the depth where most shoals were present, and its position in the water column was adjusted only marginally within each haul as the overall depth distribution of the shoals changed. The trawl was not moved up and down in the water column to target individual shoals.

The trawl used was a four-panel design, with a stretched opening circumference of 960 m and a stretched length of 262 m (excluding grid section, lengthening piece, and codend). The trawl entrance kept a consistent height of 45 m and a width of 65 m with a doorspread of 110 m at towing speeds of 1.7–2.0 m s^{-1} (3.3–3.9 knots, measured using GPS). Mesh size tapered from 32 m in the forward section and wings (16 m in the bottom panel) to 155 mm in the aft body. Consistent with fishing regulations, a 1.20 × 1.75-m stainless steel sort-V grid with 55 mm bar spacing was placed ahead of the codend. Codend and grid section were constructed of 135 mm mesh, and the grid exit and codend were covered by small-mesh nets of 52 and 50 mm, respectively, to retain escaping fish. More than 99% of the cod were captured in the codend, and <1% in the covers over the grid and codend.

Small catches during an earlier cruise led us to believe that fish may have been escaping through the large meshes in the belly of the trawl, so a 400-mm liner was sewn to the bottom panel of the trawl to provide a visual and hydrodynamic barrier. The liner extended 114 m from the footrope to the start of the 400 mm mesh. The trawl was fished with 10.5-m^2, 4400-kg trawl doors ("Supershark", Sp/f Rock, Vágur, Faroe Islands), with 12-m backstraps followed by 60-m bridles. A setback of 8 m of chain was attached between the lower bridle and the lower wing, and chain weights of 600 kg were used on each side of the trawl where the lower bridle joined the setback.

The geometry of the trawl under towing conditions was measured on a subsequent cruise using sonar observations made from a towed underwater vehicle. The vehicle was positioned above the trawl while towing in a protected fjord at the same speed as fishing had been conducted, and a scanning sonar image (Simrad MS1000, 300 kHz) was taken at the seam of each mesh panel (12 measurements in all). The vertical and horizontal openings were measured from the on-screen display, and the circumference was divided by the number of free meshes to calculate the average opening of each mesh. Overall, the trawl shortened 22% from its stretched length during towing. The geometry was consistent with measurements made on a 1:40 scale model of the trawl in a flume tank.

The twine area for each section was calculated following a method described by Ferro (1981) and was used to calculate the solidity ratio, the proportion of the trawl area occupied by the netting twine. In the most forward section, solidity was <1%, and the gap between adjacent twines was up to 6 m. At the end of the extension, solidity was >27%, with a maximum gap of <5 cm between adjacent twines. Calculations for the demersal trawl normally used by FV "Atlantic Star" (Selstad GR-520, Selstad AS, Måløy, Norway) predict the solidity of 8% in the forward section, assuming a similar 20% reduction from the stretched length during trawling.

Analyses of diving, passage rates, and changes in position relative to the trawl panels were made by matching shoals of fish visually as they sequentially passed acoustic sensors beneath the vessel, at the entrance of the trawl, and at locations 100 and 130 m inside the trawl (total horizontal distance between vessel and aft acoustic sensor ~600 m; see the Supplementary material for sensor specifications, and Figure 1 for their positions). This required that there be gaps between consecutive shoals, a condition satisfied in just three of the hauls. Fish in the remaining hauls were distributed in more continuous bands that could not be separated into distinct individual shoals during the analysis. In all, 244 shoals were recorded as the vessel passed over them in the three hauls that could be analysed, 150 of which were matched with net-entrances recorded at the trawl entrance. Patterns in the amount of time between shoals and shoal size and density indicated on the echograms provided ongoing references to keep the sequence correct. Alternate matching strategies based upon comparisons of vertical position in the water and measures of shoal dimension were explored, but there was insufficient variation in these characteristics. As the trawl sonar and TrawlEye instruments were mounted pointing directly down from the top panel of the trawl, their 20° athwartship beam angles ensonified only the central 10–16% of the trawl's cross section, and fish passing to the sides would not have been detected (see inset in Figure 1). Echograms from the acoustic sensors were used to establish the time shoals passed each sensor, as well as to measure shoal dimensions and their positions in the water column and relative to the panels of the trawl.

Data from the vessel-mounted echosounder and trawl sonar were logged and replayed using the instruments' operating software, and on-screen measurement tools were used to measure shoal dimension, depth, and position relative to the panels of the trawl. No thresholds or noise-suppression algorithms were applied. Raw hydrophone data from the TrawlEye were saved as wav format acoustic files and later played back through a SCANMAR ScanBas receiver unit. During replay, a frame grabber (VGA2USB, Epiphan Systems, Ottawa) was used to save the echogram output in .avi video format that could be scrolled

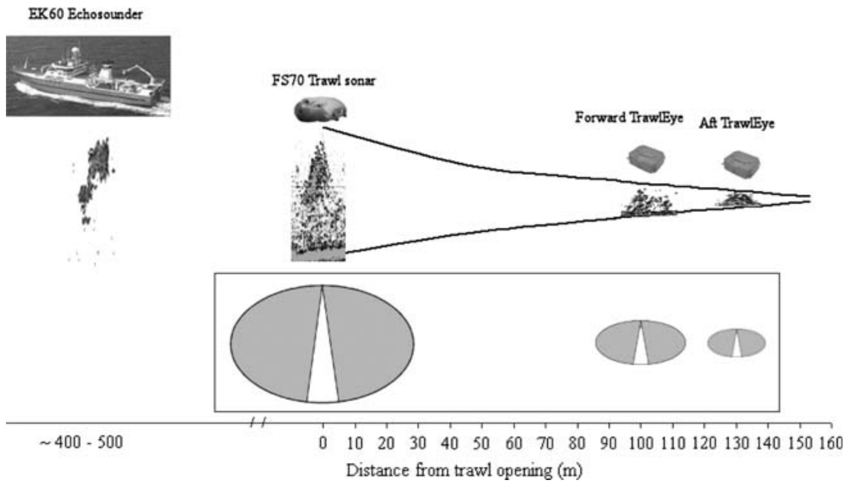

Figure 1. Side view of the pelagic trawl, showing the locations of the acoustic sensors used to study cod behaviour. Trawl wings, grid, and codend are not shown. The echograms beneath each sensor illustrate the passage of the same single shoal. The inset panel illustrates coverage of the trawl sonar's downsounder beam and TrawlEye out to 3 dB down-angle (white) relative to the trawl's cross section (grey).

and paused during analysis. Shoal dimension and position relative to the trawl panels were measured relative to a distance scale output on the echogram. The footrope and bottom panel were visible as consistent bands in the echograms from the trawl sonar and TrawlEye and were easily distinguished from passing fish shoals.

Horizontal distance between the vessel and trawl ranged from 400 to 500 m and was logged continuously. The precise distance at the time of each shoal passage was calculated from the instantaneous towing warp length, depth to the trawl doors, and the length and calculated angle of bridles between the trawl doors and wing tips (inferred from door and wing distance sensors). Distances between sensors mounted on the trawl were calculated based on their positions on the trawl and the calculated foreshortening of the trawl during towing.

Targets were detected within the conical beam of the echosounders and trawl sonar, and the outer limit of the beam was assumed to be the manufacturer's specified 3-dB down angle. For example, with the trawl's opening height of 45 m, the 10° alongship beam angle of the trawl sonar's downsounder beams would have placed its leading edge 4 m ahead of the footrope while the scanning sonar's 40° alongship beam angle would have had a leading edge 16 m ahead of the footrope.

Shoal length was calculated as the length of time the shoal was visible in the echogram multiplied by the trawl's speed though the water. If the shoal was swimming in a coordinated direction, this would affect the calculated shoal length (swimming in the direction of tow would make the shoal appear longer, and vice versa). The trawl's speed through water was measured by a trawl speed sensor (SCANMAR HC4 –TSS). Initial attempts to mount the sensor were unsuccessful; the sensor was placed successfully on the final haul of the cruise (haul C) by fixing it around a round stainless steel pipe attached to the footrope of the trawl. Only data from that haul were used for analyses of shoal length and swimming speed relative to trawling speed.

The conical beam of the acoustic sensors can lead to an overestimate of shoal length because of the "attack angle" of the acoustic beam (Misund, 1993). Shoal lengths measured at the trawl sonar and TrawlEye sensors were corrected as described in Diner (2001), but it was not possible to apply the correction for measurements made by the vessel's echosounder because of the large beam width relative to shoal length at the ~100 m range where shoals were present. Only the corrected lengths measured by the trawl sonar and TrawlEye sensors were used in the analyses. Shoal thickness was calculated as the difference in depth between the shallowest and the deepest portions of the shoal, as detected by the echosounder, corrected for pulse length as described by Misund (1993).

Rates of shoal passage were calculated by dividing the distance between the sensors by the difference in time between when the leading edge was detected at each sensor. The distance the shoals travelled was calculated as a vector, including both the horizontal distance between sensors and the vertical displacement attributable to diving.

The position of shoals relative to the cross section of the trawl opening was measured using the scanning beam of the trawl sonar. The sonar's range was set at 60 m and traced an arc of a plane perpendicular to the centreline of the trawl, sweeping from 72 to 288° (straight up = 0°). As the sonar did not sweep between 288 and 72°, a 144° sector above the trawl was not sampled, and the numbers of fish escaping above the trawl are therefore likely underestimated. The sonar was set to a full 360° sweep on several occasions when fish were entering, but no fish were observed escaping above the trawl.

An image of the screen's display was saved each time the beam traversed the trawl entrance (every 20 s), resulting in 1016 images. A cell grid (2 × 2 m) was overlaid on the sonar images; each cell overlapping a portion of a shoal was assigned a value of 1, and cells without fish were assigned a value of zero. This procedure was repeated for each image, and the results were summed to create an aggregate distribution pattern.

Data on diving rate were analysed using version 2.9.1 of the R statistical package (R Development Core Team, 2010). Shoal depth, length, and thickness were investigated as potential explanatory variables for the diving rate. Data were examined for outliers using Cleveland dotplots and tested for collinearity using pairwise scatterplots. Normality was verified *a posteriori* by examining normal Q–Q plots and a histogram of residuals from the model. Homogeneity was verified by examining conditional boxplots of the diving rate for each of the three hauls.

Shoal depth, length, and thickness were $\log_{10}$-transformed to reduce the effect of extreme values (no true outliers were detected). Shoal length and thickness were highly collinear (Pearson's correlation coefficient 0.73 on log-transformed data), so thickness alone was used as a representative measure of shoal size. Diving rate was modelled as a function of haul, depth, and shoal thickness using multiple linear regression. The initial model included first-order interactions of haul (a categorical variable), shoal depth, and size (continuous variables), plus the second-order interaction. By backward selection, terms were removed from the model if they did not reduce the Akaike information criterion by >2 (Zuur *et al.*, 2007).

Results

Significant pelagic aggregations of post-spawning cod were located during daylight, but the fish descended to the seabed at night. Over seven days, 168 t of large post-spawning cod were harvested in nine pelagic trawl hauls. Saithe, haddock, and lumpsucker (*Cyclopterus lumpus*) were the next most common species, but combined represented <2% of the catch by weight. Only three of the hauls contained data suitable for behavioural analysis. The total catch of cod in the three hauls was 49 t, along with <500 kg of other species. Weighted mean length was 79 cm, with the s.d. of the individual hauls ranging from 11 to 12 ($n = 230$, 208, 432). Of the cod sampled, 81% had empty stomachs.

Diving between vessel passage and trawl entrance

The shoals were on average 149 m (s.d. = 35) above the seabed when the vessel passed over them. Fish dived following vessel passage (Figure 2a). In total, 91% of the 150 matched shoals exhibited a diving response of >5 m (six shoals were shallower at the time of trawl passage than vessel passage, maximum ascent 16 m). The maximum recorded dive was 75 m, at an estimated rate of 0.35 m s^{-1}. Average diving rates cannot be calculated because of the statistically significant negative correlation with shoal depth ($p < 0.005$).

Diving rate was negatively correlated with shoal depth and positively correlated with shoal size (Table 1, Figure 2b). Shoal thickness did not vary systematically with haul, but the interaction between shoal depth and haul was significant. The final model is

$$\text{diving rate}_{ij} = \alpha_i + \beta \times \log_{10}(\text{shoal thickness}) + \gamma_i \times \log_{10}(\text{shoal depth}_{ij}) + \varepsilon_{ij},$$

where i and j are the indices for haul and shoal, and ε is an error term.

Behaviour ahead of the trawl entrance

The data were examined in three ways to test whether cod attempted to avoid capture by swimming ahead of the trawl entrance. First, for nine shoals split by the footrope of the trawl, with the upper portion entering the trawl and the lower portion escaping beneath, the timing of entering each portion was examined. If fish located in front of the trawl attempted to swim ahead of the trawl to avoid capture, we would expect the portion of the shoal passing beneath the trawl to be detected first by the sonar mounted on the headrope. The data showed some evidence for this. In six shoals, the portion passing below the footrope was detected before the portion passing above it and into the trawl, but in three instances, the opposite was observed. The maximum absolute difference in time of first detection between upper and lower portions of the split shoals was 18 s (mean = 8 s, s.d. = 5 s).

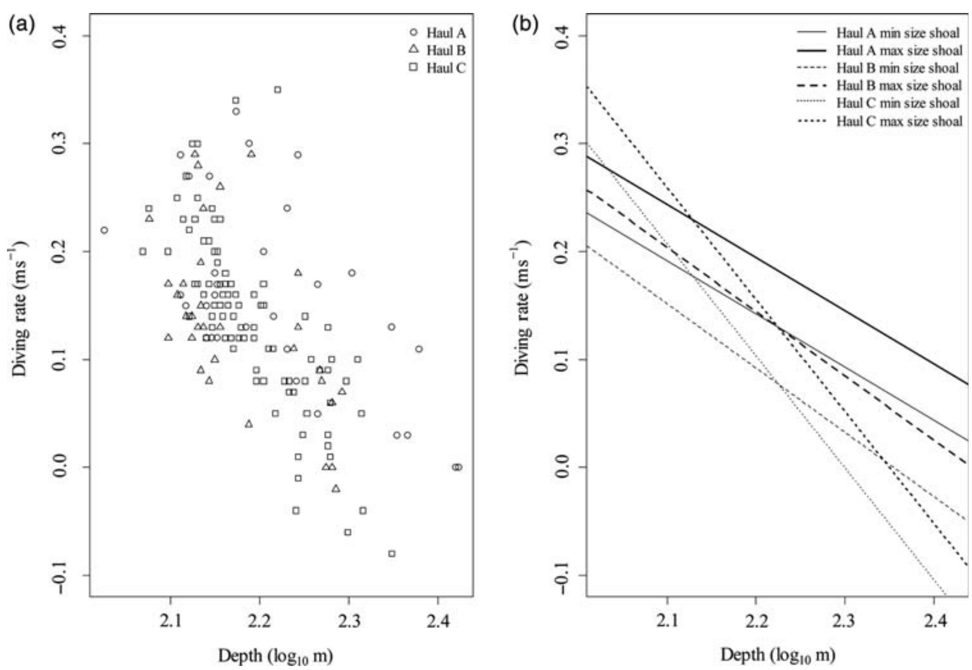

Figure 2. Diving rate vs. depth for cod. (a) The diving of a single shoal between detection beneath the vessel and again at the trawl entrance. Negative diving rates indicate shoals that rose following vessel passage. (b) Linear models of diving rate as a function of shoal depth and shoal thickness. Thin lines represent modelled diving rate for the smallest shoal observed (0.7 m thick), thick lines showing the largest shoal (42.5 m thick).

The second approach looked for differences in the rate of passage between the vessel and the trawl entrance between shoals that entered the trawl (107) and those that passed completely beneath it (34). The shoals passing beneath the trawl would be expected to cover the distance more quickly if fish located in the path of the trawl swam forward to avoid entering it. There was no statistically significant difference between the passage rates of the two groups (Student's t-test, $p > 0.1$ for all hauls).

Finally, the trawl sonar records were analysed for long echotraces, which would indicate fish remaining ahead of or just inside the trawl entrance. No such traces were recorded by either the downwards echosounder or the scanning sonar beam.

Table 1. Coefficients for the linear model parameters for the diving rate as a function of shoal thickness and depth by haul.

Coefficient	Estimate	Standard error	t	Pr (>|t|)
Intercept (α_A)	1.2286	0.2449	5.0160	0.0000
Haul B adjustment to intercept	0.1781	0.4236	0.4200	0.6748
Haul C adjustment to intercept	1.1626	0.3363	3.4570	0.0007
Shoal depth (γ_A)	−0.4918	0.1100	−4.4710	<0.0001
Shoal thickness (β)	0.0292	0.0118	2.4830	0.0142
Haul B adjustment to depth	−0.1038	0.1935	−0.5360	0.5926
Haul C adjustment to depth	−0.5463	0.1525	−3.5820	0.0005

Distribution of cod in the trawl entrance

The fish distribution in the trawl entrance was similar in all three hauls, fish passing in the centre in the lower part of the trawl (Figure 3). On average, 68% of the fish passages recorded by the scanning beam of the trawl sonar resulted in fish entering the trawl. Just 8% of the passages represented fish escaping over the headrope of the trawl or to the sides, and 23% of fish passed beneath the footrope of the trawl (Table 2). No single shoal exceeded the height of the trawl opening.

Swimming velocity and direction

In all, 86 shoals were successfully matched between their passage beneath the vessel and at the mouth of the trawl (data only from haul C, with trawl speed through the water measured). Of these, 68 entered the trawl and 16 passed beneath the footrope (two shoals were split by the footrope, with part entering the trawl and part escaping below). Of the shoals entering the trawl, 33 were matched again with detections 100 and 130 m inside the trawl. Shoal velocity over the distance between the vessel and the trawl entrance was greater than the measured speed of the trawl through water, suggesting that the shoals swam away from the vessel, against the direction of tow (Table 3). Average velocities once the shoals entered the trawl were lower than the trawl's speed through water, indicating that the fish changed orientation and swam in the direction of tow once inside the trawl.

Vertical distribution inside the trawl

Average shoal length did not change as fish passed inside the first 130 m of the trawl, but shoals compressed vertically as the trawl tapered from the opening at the mouth 45 m high to 11.5 m some 100 m into the trawl and to 6 m some 130 m into the

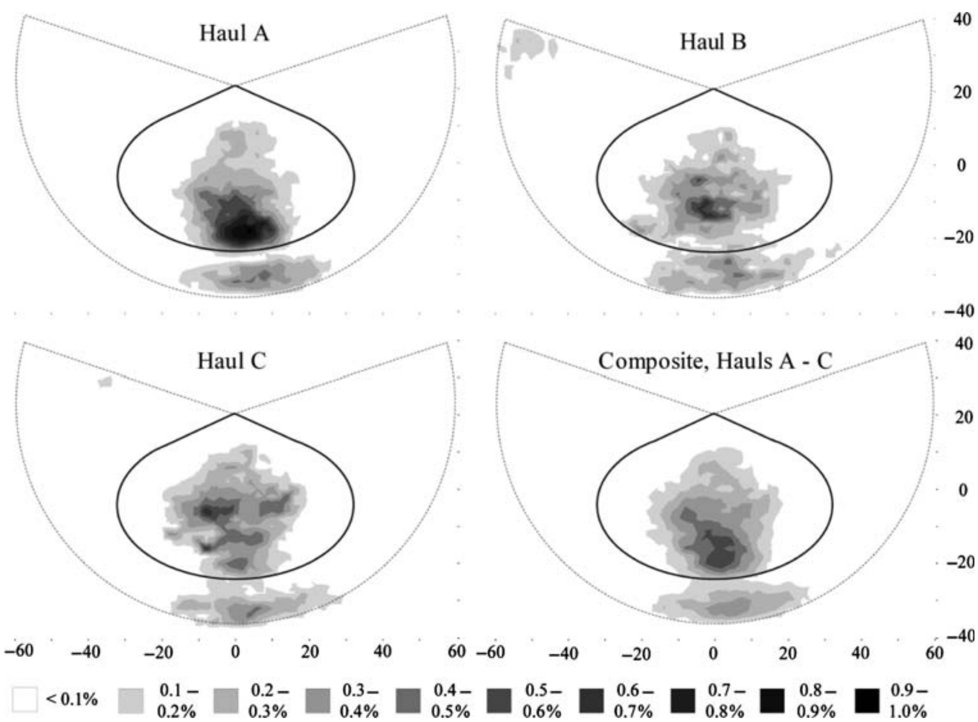

Figure 3. Distribution of cod at the trawl entrance (percentage of passages per 2 × 2 m cell). The outline of the trawl entrance is indicated by a thick elliptical outline, and the area ensonified by the trawl sonar is outlined by the dashed line sector. Numbers indicate distance from the centre of the trawl entrance (m).

Table 2. Summary of the hauls, passage velocity between vessel, and trawl opening and fish passages, as recorded by trawl sonar.

Parameter	Haul A	Haul B	Haul C	Combined[b]
Time of day (haul start)	11:30	09:35	12:58	–
Duration (h:min)	2:00	2:40	1:52	6:32
Catch (t)	5.0	22.1	21.5	48.6
Average bottom depth (m, ± s.d.)	312 ± 13	320 ± 12	305 ± 16	313 ± 16
Average shoal depth (m, ± s.d.)	168 ± 41	151 ± 25	157 ± 23	158 ± 29
Average headrope depth (m, ± s.d.)	164 ± 13	149 ± 14	153 ± 7	155 ± 11
Number of shoals entering the trawl	17	22	68	107
Number of shoals passing beneath the trawl	14	4	6	34
Number of shoals split by the trawl	1	6	2	9
Passage velocity of shoals entering the trawl ($m\ s^{-1}$, ± s.d.)	1.9 ± 0.4	2.1 ± 0.4	2.3 ± 0.3	2.2 ± 0.3
Passage velocity of shoals passing beneath the trawl ($m\ s^{-1}$, ± s.d.)	2.1 ± 0.3	2.1 ± <0.1	2.2 ± 0.2	2.2 ± 0.3
Total number of passages recorded by the trawl sonar	5 009	2 347	4 250	11 606
Percentage entering the upper half of the trawl (%)	11	8	14	11
Percentage entering the lower half of the trawl (%)	61	51	56	57
Percentage passing above the trawl (%)[a]	4	11	6	6
Percentage passing below the trawl (%)	23	26	23	23
Percentage passing to the side of the trawl (%)	1	4	2	2
Location of maximum passage (m below vertical centre, to the right of horizontal centre)	18, 4	10, −2	6, −8	18, 4

Percentages do not always add up to 100% because of rounding.
[a]The sonar did not scan a 144° sector above the trawl. Counts of fish passing above the trawl are therefore incomplete.
[b]Values in the combined column are calculated from an analysis of aggregate data and are not an average of values for the three hauls.

Table 3. Passage velocities between vessel and trawl opening, first 100 m into the trawl, and 100–130 m into the trawl, during haul C.

Interval	Trawl speed through water ($m\ s^{-1}$, ± s.d.)	Number of shoals	Mean passage velocity ($m\ s^{-1}$, ± s.d.)	Mean swimming velocity ($m\ s^{-1}$, ± s.d., direction)
Vessel to trawl opening (~500 m)	1.6 ± <0.1	86	2.3 ± 0.3	0.6 ± 0.2 against tow direction
Trawl opening to 100 m into the trawl	1.6 ± <0.1	33	1.4 ± 0.3	0.2 ± 0.3 with tow direction
100–130 m into the trawl	1.6 ± <0.1	33	1.1 ± 0.3	0.5 ± 0.3 with tow direction

Differences in passage velocity between intervals were statistically significant (Student's *t*-test, $p < 0.001$).

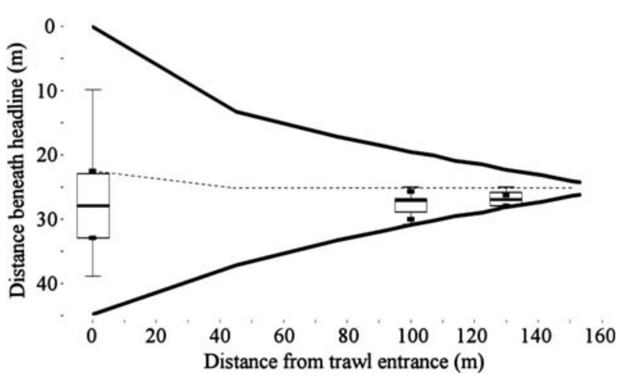

Figure 4. Trawl cross section and shoal position at the trawl entrance, 100 m into the trawl, and 130 m into the trawl. The vertical scale is exaggerated 2 × relative to the horizontal scale. Sloped lines show the upper and lower panels of the trawl, and the dashed line indicates the centreline of the trawl. Short solid lines represent the average upper and lower extents of shoals. Box and whisker plots indicate the range in shoal position (vertical centre of shoal), with the median position indicated by the thick line inside each box and the upper and lower limits of the boxes delimiting the 25th and 75th percentiles. The ends of the whiskers indicate minimum and maximum values.

trawl (Figure 4). No significant vertical compression or shortening was measured between the time when shoals passed beneath the vessel and when they were detected at the trawl entrance. Average clearance beneath the top panel was 22 m at the trawl entrance, 8 m when shoals were 100 m inside the trawl, and 5 m when they were 130 m inside the trawl, whereas clearance above the bottom panel was just 12, 1.3, and 0.4 m, respectively, at the same locations (Table 4).

Discussion

Cod reacted to the passage of the vessel by diving and swimming in a direction opposite the direction of tow, towards the approaching trawl. They did not attempt to avoid entering the trawl by swimming ahead of the entrance and entered primarily in the lower part of the opening. Once inside the trawl, cod swam slowly in the direction of tow, but were overtaken by the trawl's greater speed and passed back towards the extension and codend. The shoals compressed vertically and remained in the lower portion of the trawl, with minimal separation above the bottom panel.

This study is based on acoustic instruments available during commercial fishing operations. A potential source of error could be the matching of shoals at the four locations. During the interval between the vessel passing and trawl entrance, some shoals could move horizontally out of the path of the trawl-mounted sensors, and other shoals not passing beneath the vessel could move into the path of the trawl. The sampling volume of the acoustic instruments could also permit some shoals to pass to the sides without being registered. Mismatching of shoals would affect the calculations of swimming and diving rates, but would not impact the analyses of shoal position relative to the trawl opening or the panels of the trawl.

Table 4. Shoal dimensions and distance from the trawl panels.

Parameter	Shoal length (m)			Shoal thickness (m)				Clearance above bottom panel (m)			Clearance beneath top panel (m)		
	Trawl entrance	100 m in	130 m in	Under vessel	Trawl entrance	100 m in	130 m in	Trawl entrance	100 m in	130 m in	Trawl entrance	100 m in	130 m in
Number of observations[a]	27	31	31	33	33	33	33	33	33	33	33	33	33
Maximum	91	161	163	19	19	10.7	5.7	31	4.0	3.5	34	14.0	7.9
Minimum	5	1	2	2	3	0.3	0.3	2	0.3	0.3	7	3.0	2.0
Mean	33[b]	29[b]	31[b]	9[b]	10[b]	5.2	2.1	12	1.3	0.4	22	8.0	5.2
s.d.	25	32	32	5	4	3.1	0.8	7	1.1	0.6	8	3.1	1.8

Vertical distances were measured with a resolution of 0.3 m 100 and 130 m into the trawl. Resolution for all other measurements was 1 m.

[a]Six shoal lengths measured in the trawl entrance and two lengths inside the trawl were too short to correct for attack angle of the acoustic beam and were therefore not included in the analyses.

[b]There was no statistically significant difference in shoal length by position (Welch's *t*-test, $p > 0.7$) or in shoal thickness under the vessel compared with at the trawl entrance (Welch's *t*-test, $p > 0.7$). Differences in all other measures by position were statistically significant (Welch's *t*-test, $p < 0.001$).

Previous investigation of fish behaviour during trawling has used acoustic sensors mounted on a launch or autonomous buoy with the vessel passing at close range (Ona and Godø, 1990; Gerlotto and Fréon, 1992; Suuronen *et al.*, 1997; Handegard and Tjøstheim, 2005), or internally implanted tags and receiver buoys to track the movements of individual fish (Engås *et al.*, 1991). These techniques require the cruise track to be set ahead of time, which was impractical for our investigation on board a commercial fishing vessel targeting aggregations that were highly variable in space and time. Underwater cameras were not used because of the restricted range relative to the tens of metres distance inside the trawl, and the requirement for artificial light that may affect behaviour and catchability (Gordon *et al.*, 2002; Marchesan *et al.*, 2005). Strobed images would, however, have been useful to verify the orientation and swimming direction inferred from the acoustic results.

With a sample size of 150 shoals in three hauls and a relatively homogenous size composition of fish, care should be exercised in interpreting the results too broadly. As behavioural patterns represent an interplay between sensory capacity and reaction to stimuli, differences in "state" conditions such as hunger level, reproductive stage, and perceived risk from predators (Lima and Dill, 1990; Fernö, 1993) can lead to variability in how fish respond to objects they encounter (Fernö *et al.*, 2006). The underlying state of the fish was likely similar across the hauls analysed, and cod in another state may react differently. Nevertheless, patterns in behaviour are consistent across hauls and provide new and interesting insights into behaviour, which is important when targeting cod with pelagic trawls either for commercial harvest or research sampling.

The maximum measured diving rate in the zone between the vessel and the trawl entrance was nearly 0.35 m s^{-1} (0.44 body length s^{-1}), in accord with maximum rates of 0.51 body length s^{-1} measured by Ona (1988) for cod of mean length 55.4 cm reacting to a pelagic trawl. A study of diving rates in Barents Sea cod implanted with depth-recording tags measured maximum diving rates of 0.25 m s^{-1} for fish >50 cm long (Heffernan *et al.*, 2004), but it is not known whether those dives were in reaction to an approaching fishing vessel. Handegard and Tjøstheim (2005), however, report much lower diving rates (0.02–0.06 m s^{-1}) for individual gadoids (primarily cod) of unreported size reacting to a demersal trawl. The difference in diving rates observed in relation to demersal and pelagic trawls may be attributable to differences in where in the water column noise and inaudible pressure waves are generated. Fishing with a demersal trawl generates noise and pressure at the surface (the vessel) and at the seabed (the trawl), with the result that fish in the pelagic zone experience noise and pressure propagating from both above and below. During pelagic trawling, all fishing-related stimuli are generated in the upper pelagic zone, from the surface down to the depth of the trawl.

Shallow shoals are closer to the approaching vessel and therefore experience stronger auditory and possibly visual stimuli from the vessel. In addition, the downward-angled towing warps and trawl sonar cable would have reached shallower shoals sooner following vessel passage than deeper ones. Consistent with this, shallow shoals dived at greater velocity than deeper ones. The strength of the diving reaction of *Sardinella* schools in response to a passing vessel decreases with depth (Gerlotto and Fréon, 1992), but Handegard *et al.* (2003) observed no significant relationship between depth and diving speed in scattered distributions of gadoids approached by a vessel towing a demersal trawl. The positive correlation between shoal size and diving rate may be an extension of the results of Domenici and Batty (1994), who hypothesized that fish in shoals compared with isolated individuals better orientated their swimming direction away from a perceived threat based upon the movements of their neighbours. There may also be a self-reinforcing response whereby the strength of the dive of each individual fish is reinforced by observing the diving of its neighbours, leading large shoals to dive more quickly than smaller ones.

Fish appeared at the trawl entrance more quickly than predicted by the trawl's speed through water. It appears that fish initially swam away from the vessel and towards the approaching trawl at a velocity of 0.6 m s^{-1} (0.8 body lengths s^{-1}). This is below maximum sustainable swimming speeds measured for smaller (46–70 cm) cod at lower water temperatures (Winger *et al.*, 2000), indicating that fish should not have been fatigued by swimming in the interval between passing beneath the vessel and arriving at the trawl entrance.

Once they reached the trawl, cod showed no sign of accumulating in front of the entrance. Comparisons between shoals passing into and below the trawl revealed no difference in the rate at which they passed the footrope, and there were no elongated acoustic records suggesting that fish held position inside or ahead of the trawl entrance. This contrasts with observations of behaviour immediately ahead of demersal trawls, where fish have been observed to accumulate in front of the footrope under light conditions and swim in the direction of trawling until they become fatigued and are overtaken by the trawl (Main and Sangster, 1981; Wardle, 1993; Engås, 1994). This response in demersal trawls is believed to result from an "optomotor response" (Harden Jones, 1963) to visual stimuli from the mud cloud created by the trawl doors, sweeps, and groundgear, contrast between the trawl meshes and the stationary background of the seabed, and highly visible components of the trawl such as closely spaced meshes, the groundgear, and trawl floats or kites attached to the headrope. Demersal trawls also create significant noise as the trawl doors, sweeps, and groundgear scrape along the seabed, although the soundfield created is likely too complex for fish to orientate themselves to the individual components of a trawl (Glass and Wardle, 1989).

The forward section of the pelagic trawl used in this experiment presents a less visible or hydrodynamically solid structure than a demersal trawl, with gaps of up to 8 m between the ropes that create the forward meshes and a calculated solidity ratio some one order of magnitude less. The lack of groundgear at the footrope or kites and floats at the headrope reduces the apparent thickness of the outline of the trawl entrance, and if it is fished off the seabed, a pelagic trawl will not create sandclouds or contrast against the stationary background of the seabed. It can also be expected to generate much less noise as it moves through the water without bottom contact, reducing the auditory stimuli to the fish.

With an absolute maximum visual range of 40 m (Guthrie and Muntz, 1986; Wootton, 1998), a fish positioned at the centre of the 45×60 m trawl entrance might just make out the edges of the trawl, but it would see >99% of the area around it as unobstructed open water. Glass and Wardle (1989) recorded that, under very low light conditions ($<10^{-6}$ lux), haddock no longer displayed an ordered reaction to an approaching demersal trawl, leading them to conclude that vision is the primary sense used to react in orderly fashion to an approaching trawl. Conditions at the entrance of a pelagic trawl may be similar even in light conditions, because of the lack of strong visual components.

Distribution patterns of fish entering the trawl suggest that cod were being herded horizontally towards the centre of the trawl entrance, but the passages were concentrated well beneath the vertical centre. This could indicate that fish were being herded horizontally, but still diving as they entered the trawl. Handegard and Tjøstheim (2009) measured a strong influence from the trawl warps on the diving behaviour of individual cod during demersal trawling. During our experiments, the trawl warps and sonar cable angled downwards from the vessel to the trawl entrance and would have provided a stimulus for fish to be herded downwards, whereas the bridles and wings angled in horizontally from both sides and would have herded fish towards the horizontal centre of the trawl entrance.

Mixed catches of cod, haddock, and saithe enter a demersal trawl in the horizontal centre but in the region closest to the footrope (Engås and Ona, 1990; Ona, 1999), whereas we observed the centre of gravity of pelagic trawl entrances to be 8 m above the footrope. Fish being captured by a demersal trawl may cue to the seabed or simply be forced to stop diving as they reach it, staying concentrated in front of the lowest regions of the trawl entrance. There is no such lower barrier or visual cue beneath the footrope in the pelagic zone.

As cod entered the trawl, their rate of passage decreased to less than the trawl's speed through water, indicating that they changed orientation and began swimming in the direction of tow. The calculated swimming speed was slow, but it increased with distance into the trawl, from 0.2 m s^{-1} (0.4 body length s^{-1}) over the first 100 m to 0.5 m s^{-1} (0.6 body length s^{-1}) from 100 to 130 m into the trawl. This is well within sustainable swimming speeds and suggests that the fish were not in a state of panic. A reduction in water flow inside the trawl would have resulted in decreased passage rates, but investigations using the same trawl on a later cruise measured no reduction in flow between the trawl entrance and inside the extension (unpublished data). Swimming in the direction of the tow is a more likely explanation and is consistent with observations of Atlantic herring (*Clupea harengus*) and walleye pollock (*Theragra chalcogramma*) in the extension of pelagic trawls (Suuronen and Millar, 1992; Pikitch *et al.*, 2002; Rose, 2004) and of cod, haddock, and whiting (*Merlangius merlangus*) in the extension of a demersal trawl (Krag *et al.*, 2009). A strong reaction to visual stimulus of the separator frame in the latter study was proposed as the stimulus for the swimming behaviour observed.

Assuming that fish can detect the meshes visually once they are inside the trawl, swimming in the direction of tow might be explained by a weak optomotor response serving to decrease the relative speed at which the meshes travel past them. As the solidity ratio increases with distance inside the trawl, making the trawl panels increasingly visible, the optomotor response may strengthen and lead to the observed increase in swimming velocity.

Shoals compressed vertically as the taper of the trawl led to a decrease in both height and width with distance aft from the entrance. Average shoal thickness halved between the trawl entrance and 100 m into the trawl, then halved again between 100 and 130 m into the trawl. It was not possible to measure shoal width with the instruments available, but the horizontal taper of the trawl likely led to compression of shoals in that dimension too. With no statistically significant change in shoal length and assuming that shoal width did not increase, the packing density of fish must have increased at least twofold in the first 100 m and twofold again in the next 30 m.

Accompanying the increased packing density, shoals came increasingly closer to the bottom panel of the trawl. By 100 m aft of the footrope, the lower portions of the shoals were on average just 1 m above the bottom panel, and by 130 m, the clearance had reduced to <0.5 m. Clearance below the top panel of the trawl was ten times greater. The low position of cod in the trawl entrance is consistent with previous observations, and work with separator and raised fishing line demersal trawls (Main and Sangster, 1985; Beutel *et al*., 2008), and the continued position near the bottom panel 100 and 130 m into the trawl, shows that cod remained low in the trawl as they were carried towards the extension and codend.

Conclusions and implications for commercial pelagic trawling for cod

Catch results demonstrated that commercially viable quantities of adult cod could be harvested in the Barents Sea with the trawl used in the trials. However, the trawl's construction and fishing strategy do not seem to have been optimized to the distribution and behaviour of the fish we observed. Better catch rates would likely have been achieved by placing the trawl even lower in the water column, to compensate for diving during the interval between passage of the vessel and the arrival of the trawl.

The top panel of the trawl appears to have played a minor role in retaining cod, which were concentrated well below the vertical centre. The use of larger meshes in constructing the top panel would reduce towing resistance and fuel consumption during the trawling operation. Further work is necessary to determine how large meshes can be used effectively, and how far back the sections of large meshes can be extended without a loss of targeted cod. As the cod did not appear to swim to exhaustion before entering the trawl, it may be possible to maintain high catch rates while trawling at reduced speeds, providing additional fuel savings.

The strong preference cod exhibited towards the lower portion of the trawl could be used to design trawls capable of separating the catch by species. Other species may exhibit a different preference for position inside the trawl; haddock, for instance, rise and attempt to escape through the top panel and side panels of demersal trawls (Main and Sangster, 1981). It may be possible too to improve selectivity by placing escape windows in the portion of the trawl where non-target species are present, but targeted species are not. Further development in this area will require the collection of additional data on both cod and co-occurring species.

Together, these results suggest that pelagic trawling may offer an opportunity to reduce the environmental impact of fishing for cod by harvesting commercially sustainable quantities of fish with no seabed contact, reduced fuel consumption with large-mesh trawls, and the potential for improved species selectivity. The frequent lack of cod in the pelagic zone and the greater cost and complexity in handling and fishing with pelagic trawls make it unlikely that they will replace demersal trawls in the Barents Sea fishery, but combining demersal and pelagic trawling should be feasible, and any portion of fishing effort that can be shifted from demersal to pelagic trawling will likely yield environmental benefit.

Supplementary material

Specifications of the acoustic instruments are provided in the *ICESJMS* online version of the manuscript.

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