Effects of seismic shooting on local abundance and catch rates of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*)

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Abstract: To determine whether seismic exploration affected abundance or catch rates of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), acoustic mapping and fishing trials with trawls and longlines were conducted in the central Barents Sea 7 days before, 5 days during, and 5 days after seismic shooting with air guns. Seismic shooting severely affected fish distribution, local abundance, and catch rates in the entire investigation area of 40 × 40 nautical miles.Trawl catches of cod and haddock and longline catches of haddock declined on average by about 50% (by mass) after shooting started, which agreed with the acoustic abundance estimates; longline catches of cod were reduced by 21%. Reductions in catch rates were observed 18 nautical miles from the seismic shooting area (3 × 10 nautical miles), but the most pronounced reduction occurred within the shooting area, where trawl catches of both species and longline catches of haddock were reduced by about 70% and the longline catches of cod by 45%; a relatively greater reduction was found (in catches and acoustic estimates) for large (>60 cm) than for small fish. Abundance and catch rates did not return to preshooting levels during the 5-day period after seismic shooting ended.

Résumé : Pour déterminer si l'exploration sismique nuit à l'abondance de la morue (*Gadus morhua*) et de l'églefin (*Melanogrammus aeglefinus*) ainsi qu'au taux de capture de ces espèces, on a procédé à des travaux de cartographie acoustique et à des essais de pêche au chalut et à la palangre dans la partie centrale de la mer de Barents 7 jours avant, 5 jours durant et 5 jours après une série de tirs sismiques au canon pneumatique. Les tirs ont considérablement modifié la répartition du poisson, abaissé sa densité locale et gravement réduit le taux de capture dans l'ensemble de la région d'étude (soit un secteur mesurant 40 milles marins de côté). En moyenne, les prises de morue et d'églefin au chalut et les prises d'églefin à la palangre ont diminué d'environ 50% (en masse) après que la série de tirs ait commencé. Ces résultats concordent avec ceux des relevés acoustiques d'abondance. Les prises de morues à la palangre ont été réduites de 21%. Des baisses des taux de prise ont été observées jusqu'à 18 milles marins du secteur des tirs sismiques (un secteur de 3 × 10 milles marins), mais l'effet le plus prononcé a été observé à l'intérieur de ce secteur : les prises au chalut des deux espèces et les prises à la palangre de l'églefin ont diminué d'environ 70%, les prises de morue à la palangre d'environ 45%. La réduction est proportionnellement plus marquée dans le cas des poissons de grande taille (>60 cm) que celle des poissons de petite taille, tant dans les prises que dans les estimations par relevé acoustique. Cinq jours après la fin des tirs sismiques, l'abondance et les taux de capture ne s'étaient pas encore rétablis.
[Traduit par la Rédaction]

Introduction

Since the early 1960s, seismic shooting with air guns has been conducted on the Norwegian continental shelf to map oil and gas resources. The extent of this activity continues to increase. About 40 000 linear km were "shot" in 1974 (Anonymous 1991), and by 1993 this figure had reached about 335 000 km (Anonymous 1994). Not only has the effort increased in the traditional exploration areas in the North Sea, but exploration has also been expanded to the areas north of 62°N. As search areas expand, seismic shooting will be conducted over critically important fishing grounds, often in conflict with fisheries.

Fishermen have claimed for years that catch rates decline when a seismic vessel arrives at a fishing ground and begins to shoot, presumably because the noise from the air guns scares the fish away. Air-gun arrays produce sound in the frequency range from 20 to 150 Hz (Malme et al. 1986), which is within the auditory range of many marine species (Hawkins 1993). It has been established that the auditory sensitivity of cod (*Gadus morhua*) is best in the frequency band from 60 to 310 Hz, with a maximum at 160 Hz, where the hearing threshold has been determined to be about 80 dB re 1 μPa (Chapman and Hawkins 1973). In addition to frequency and sound level, detection threshold has also been found to be influenced by signal characteristics such as pulse duration (Blaxter et al. 1981; Hawkins 1981) and pulse rise time (Schwarz 1985). For fish to detect a sound stimulus, the stimulus must exceed the ambient noise level (about 80–90 dB re 1 μPa Hz^{-1} in open sea, Wenz 1962) by about 20 dB (Hawkins 1993). The level at which fish respond to a sound stimulus, however, may lie significantly above the detection threshold. The reaction threshold for vessel noise has been shown to be approximately 20 dB above the detection threshold (Ona, unpublished data) and agrees well with the results of experimental exposures of redfish (*Sebastes* spp.) to air guns (Skalski et al. 1992). A typical

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peak source level for a large air-gun array is 250–255 dB re 1 μPa (Greene 1985), which corresponds to 210 dB re 1 μPa·Hz^{-1} at the spectral level. The source level of the array is specified in its most powerful direction, i.e., downwards at its acoustic axis, and less energy, about 200 dB re 1 μPa·Hz^{-1}, is transmitted in the horizontal direction. Assuming a reaction threshold of 110–120 dB re 1 μPa·Hz^{-1}, the expected distance at which fish may react to this sound would be 3–10 km. The distance at which fish are capable of detecting the seismic sound, however, is about 10 times greater, i.e., 30–100 km. These rough estimates of detection and reaction distances are based on available literature on hearing in fish, together with a simple sound propagation model.

There is little documentation on how seismic shooting affects fish behaviour and catch rates. Acoustic mapping and catch trials in the North Sea indicated that fish distribution changed under the influence of seismic shooting (Dalen and Raknes 1985). Trials off the coast of California showed that hook and line catch rates for various redfish species were reduced by 50% under the influence of a single air gun (Pearson et al. 1992; Skalski et al. 1992). Analyses of catch data from longliners and trawlers before, during, and after seismic shooting in Norwegian waters showed that longline and trawl catches of cod were reduced by 55–85% during seismic shooting (Løkkeborg and Soldal 1993). However, these studies were not designed to investigate the spatial and temporal extent of the effects of seismic explorations. A controlled, full-scale experiment was therefore carried out to answer the following questions: (*i*) Does seismic shooting affect local abundance and catch rates of cod and haddock (*Melanogrammus aeglefinus*)? (*ii*) How far from the seismic shooting area can effects be demonstrated? (*iii*) For how long after seismic shooting can effects be demonstrated?

To investigate these effects, fishing trials with trawl and longline as well as acoustic mapping of fish abundance and distribution were carried out before, during, and after seismic shooting. Longlines and trawls were chosen because they are two of the most important types of gear used in the Norwegian fisheries for cod and haddock, and because of the contrast in their capture mechanisms.

Materials and methods

Study area, period, and seismic shooting

The fishing experiment and acoustic mapping were conducted from 1 to 17 May 1992, on the North Cape Bank (water depth 250–280 m) in the Barents Sea (Fig. 1). On the basis of the expected sound level from the air-gun array, absorption of sound in water, and our knowledge of fish hearing and reaction thresholds, we decided to perform fishing and acoustic mapping about 18 nautical miles (1 nautical mile (nmi) = 1.852 km) to each side of the shooting area of 3 × 10 nmi. The study area was thus about 40 × 40 nmi, with the shooting area in the centre. The trial was divided into three periods: before (7 days), during (5 days), and after (5 days) shooting.

Seismic shooting was conducted from 8 May 1992 at 00:09 (GMT) until 12 May at 17:58 (GMT) from a chartered seismic vessel. The air guns were towed at a depth of 6 m. Rigging of the air-gun array (3 × 6 guns, 13 784 kPa (2000 psi), total volume 82 132 cm^3) and practical execution of the shooting assignment were performed according to normal procedures used in ordinary three-dimensional surveys for the oil industry, i.e., a shot was fired every 10 s, or every 25 m. A total of 36 seismic transects were shot, each 10 nmi long, with a distance of 125 m between adjacent transects.

Acoustic mapping

Acoustic mapping of the fish distribution was carried out with a trawler equipped with a hull-mounted 38-kHz split-beam transducer (ES38–29) and a Simrad EK500, connected to the Bergen Echo Integrator System (Knudsen 1990; Foote et al. 1991). The instruments were calibrated in accordance with standard practices (Foote et al. 1987; Nes 1991).

To obtain higher coverage in the shooting area, this area was crossed systematically to a radius of 20 nmi from the centre, with the central crossing point varied from transect to transect. In addition, the shooting area was mapped more densely by means of shorter north–south transects before and during shooting (Fig. 2A). For the data analysis, the study area was divided into five parts: the shooting area and four circular belts of 5 nmi width, with the midpoint of the shooting area as the centre. The measured acoustic quantity was the area backscattering coefficient, s_A:

$$(1) \qquad s_A = 4\pi(1852^2)\int_{z_1}^{z_2} s_v \, dz$$

which is the depth-integrated volume backscattering coefficient, s_v (Urick 1975), normalized to the absolute unit (m^2·nmi^{-2}). The average area backscattering coefficient was computed for the pelagic region (from 10 m above the bottom to the surface) and for the bottom region (from the bottom to 10 m) and totals were calculated for all areas and for each time period (before, during, and after seismic shooting), subsequently referred to as acoustic density.

To identify species and length compositions of the acoustically recorded fish, trawling was carried out at random positions with the standard bottom sampling trawl (cod-end mesh size of 40 mm) (Engås and Godø 1989). Altogether, 94 hauls were conducted (Fig. 2A). Each trawl haul lasted for 30 min at a speed of 1.5 m·s^{-1}. The measured door spread was 54 m, and the average head-line height was 3.8 m.

On the basis of the trawl catches and echograms, the acoustic registration was interpreted in accordance with the standard methods used by the Institute of Marine Research (Dalen and Nakken 1983) and split between cod–haddock and other species. The acoustic measures of area density for cod and haddock were further converted to number and mass in 5-cm groups, by computing the average target strength from the trawl catches.

Geostatistic was used to compute the variance ($\sigma_E 2$) of the acoustic abundance estimates (Petitgas and Poulard 1989; Simmonds et al. 1991; Petitgas 1993). This was expressed through the standard deviation, σ_E, normalized to the average value, $\bar{z}$:

$$(2) \qquad s_{geo} = \frac{\sigma_E}{\bar{z}}$$

Fishing trials

The stern trawler used a typical bottom fishing trawl (Alfredo No. 3), with cod-end mesh sizes of 139 and 140 mm (twin bags). Each haul lasted for 30 min at a towing speed of 1.8 m·s^{-1}. The door spread was measured at about 150 m, and the vertical opening of the trawl was 4.2 m. The total number of hauls was 60, 65, and 60 for the periods before, during, and after seismic shooting, respectively (Fig. 2B). The trawl hauls were made at four distances from the seismic shooting area: within the shooting area, and 1–3, 7–9, and 16–18 nmi from the shooting area. The directions of the hauls were varied randomly every day, and trawling was conducted day and night.

The longliner was equipped with an autoline system and Mustad Quick Snap line (7 mm) rigged with Mustad EZ-hooks (quality 39975, No. 12/0). Each longline fleet (one fleet = 15 connected longlines) consisted of about 3000 hooks and the hook spacing was

Fig. 1. Experimental area on the North Cape Bank, also showing the centrally located shooting area. Depths are in metres.

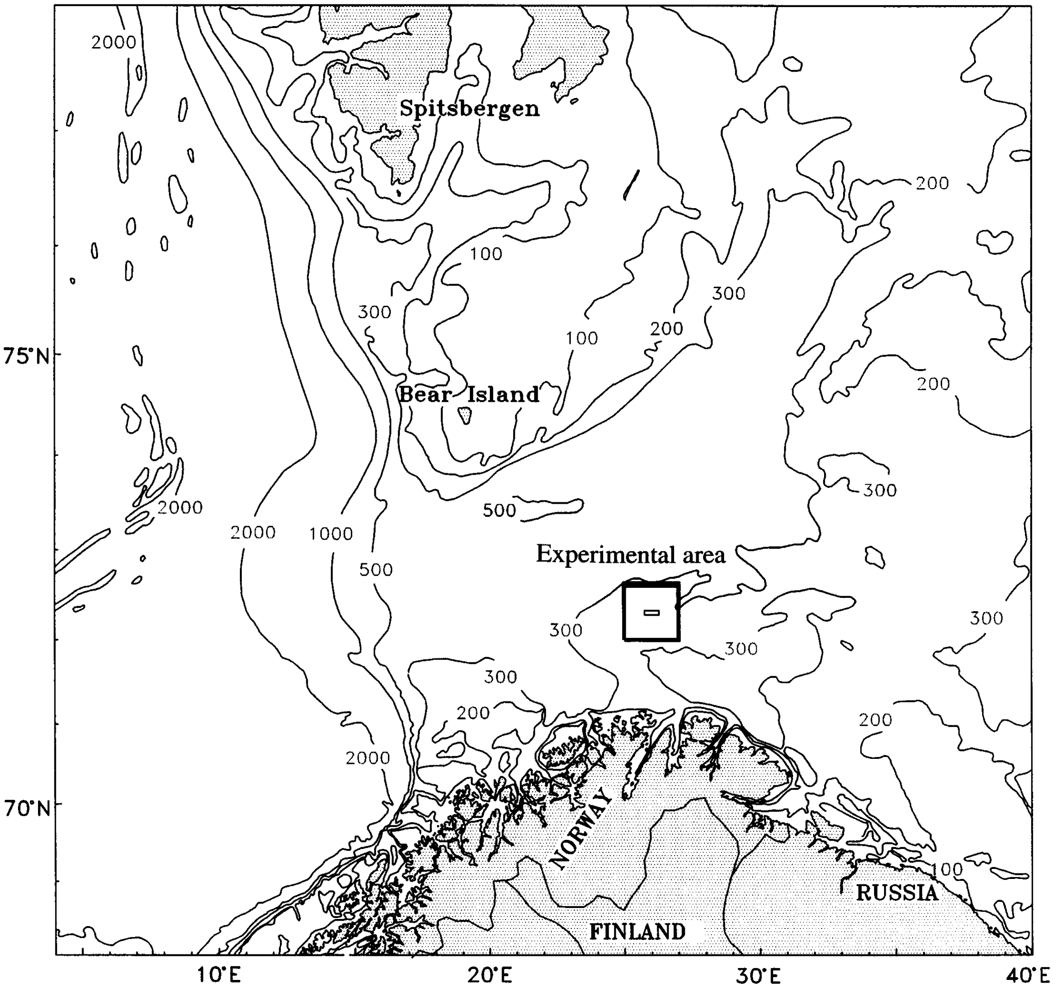


Fig. 2. Survey grid for the acoustic investigations and distribution of trawl sampling stations (solid circles) (A), and location of longline fleets (bars) and trawl hauls (open circles) (B) before shooting.

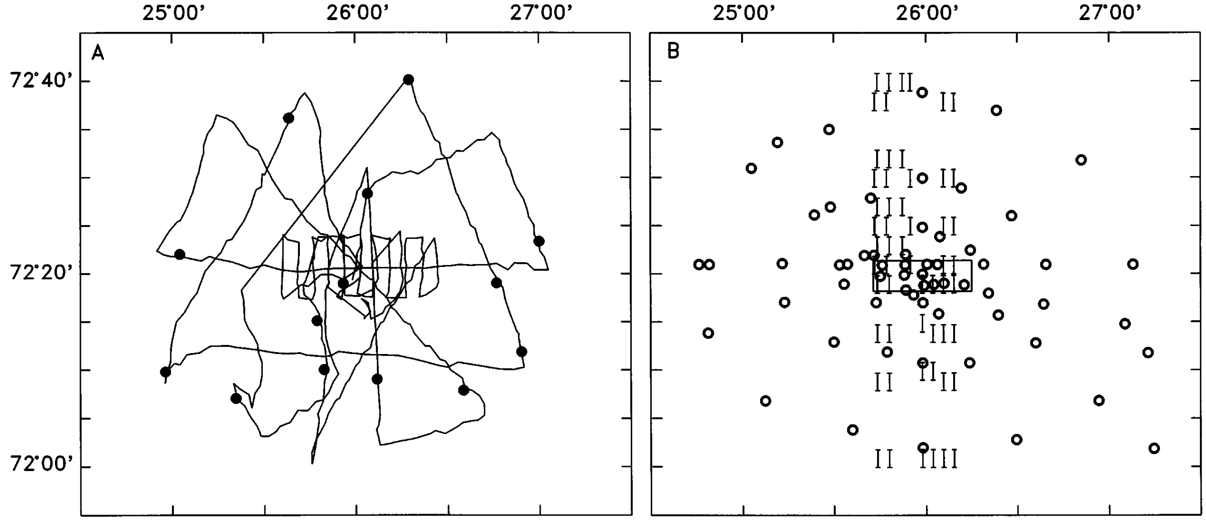


Table 1. Number of combinations of time and distance in the trawl and longline trials.

	Trawl				Longline			
	0 nmi	1–3 nmi	7–9 nmi	16–18 nmi	0 nmi	1–3 nmi	7–9 nmi	16–18 nmi
Before	12	16	16	16	7	7	7	7
During	15	16	17	17	5	5	5	5
After	12	16	16	16	5	5	4	5

1.3 m. Eight longline fleets were set and hauled each day along north–south transects at the same four distances relative to the shooting area as the trawl hauls (Fig. 2B), i.e., two fleets were set at each distance every day. These two fleets were set relatively close (0.5 nmi east–west distance) and therefore were regarded as one observation in the analysis of variance. A total of 56, 40, and 35 longline fleets were set and hauled before, during, and after shooting, respectively. The longline fleets were set between 02:00 and 08:00 (GMT) every day and soak time varied from 6 to 18 h.

Data analyses

To investigate whether seismic shooting had any effect on the catch rates of trawl and longline, the following model was used for cod and haddock:

$$y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ijk} \qquad (3)$$

where y_{ijk} is the catch in kilograms (after logarithmic transformation) per trawl haul or per longline fleet pair set at the same distance on the same day, μ is the expected catch, α_i is the distance effect, β_j is the effect of time in relation to the seismic shooting, $(\alpha\beta)_{ij}$ is the interaction between time and distance, and ε_{ijk} represents random variation. A logarithmic rather than a linear scale is used, because for marine catch data the variance is often proportional to the square of the mean (Pennington 1983; Pennington and Vølstad 1991) and a logarithmic transformation will consequently stabilize the variance (Snedecor and Cochran 1980).

The experimental design was roughly balanced (Table 1) and the model (eq. 3) adapted to application of type III sum of squares with multifactor analysis of variance (Statgraphics STSC, Inc. 1991). The approximate balance of the experimental design rendered the interpretation of factors in the analysis relatively uncomplicated. It should be emphasized that the trial area for longline fishing was a subset of that for the trawl trials (Fig. 2B).

The adequacy of the model in eq. 3 for the cod data was assessed using standard diagnostic checks of the residuals (Box et al. 1978). No lack of fit was detected, except that when the residuals were treated as a time series a slight autocorrelation was detected ($r = 0.2$). However, because the order in which the distances were sampled was varied during the experiment, this would not have a significant effect on the calculated probability levels of the model. As a final check of the time effect on catch size, time series methods (Box and Jenkins 1976) and intervention analysis (Box and Tiao 1975) were used to assess the data.

Sound monitoring

The sound level and frequency spectrum of the air-gun array and the vessels used were monitored by a hydrophone (Brüel and Kjær, type 8104) suspended at a depth of 80 m. The sound levels of the vessels were measured both during fishing operations and at their cruising speeds. The signals were logged on a digital tape recorder (Sony Dat Pro II). The vessel sounds were later analysed in 1/3-octave bands with a real-time analyzer (Brüel and Kjær, type 2143), whereas the recordings made during detonations of the air-gun array were analyzed using a frequency analyzer (Brüel and Kjær, type 2143 FFT) and a storage oscilloscope (Phillips).

Results

Effects on fish abundance and catch rates

Acoustic abundance estimates

The acoustic abundance estimates showed that the distributions of cod and haddock were reasonably uniform throughout the experimental area before shooting started (Fig. 3), with about 70% of the total abundance of cod and haddock in the pelagic region. The effects of seismic shooting on the total acoustic density of cod and haddock are shown in Fig. 4, with values combined according to distance from the shooting area. The acoustic density for the entire investigation area was reduced from an average of 129.8 to 72.0 during the shooting, i.e., by 45%. During the period following shooting, the average value was 46.2, which corresponds to a reduction from the initial situation by 64%.

A picture of the fish distribution pattern during the shooting period is given by a transect running through the shooting area in an east–west direction on 9 May (Fig. 5), with the lowest density within the shooting area, or 5 nmi on each side of the centre, with gradually increasing density further out on each side. In the period after shooting, a further reduction in the total density occurred, followed by a gradual smoothing of the horizontal distribution.

The abundance computations by mass showed an initial abundance of about 33 000 t of cod and 6000 t of haddock distributed within the investigation area, or 31 t of fish/nmi^2. Apportionment of the total mass by area was performed in proportion to the acoustic density measurements for the same area and period; within the shooting area there were thus 834 t of cod and haddock before shooting, of which 85% were cod. Expressed in terms of mass for the entire area, the quantity of cod was reduced from 33 000 t before shooting to 16 500 t during shooting, and further to 9700 t after shooting (Fig. 6). The quantity of haddock for the same area was reduced from 6000 to 3200 t during shooting and to 3100 t after shooting.

In terms of vertical distribution, the relative reduction was slightly larger in the pelagic part of the water column than in the bottom channel, at 47 and 39% reductions, respectively. For both cod and haddock, large fish were significantly more affected than small fish (data not shown; see Engås et al. 1993).

Trawls

In the trawl catches more than 90% of the average catch was cod. The catches of cod were significantly higher before shooting began than during or after shooting, at all distances from the shooting area ($p < 0.001$) (Fig. 7A). The reduction was largest within the shooting area, where the average catch of cod decreased by 69%, from 556 kg before shooting to 173 kg during shooting. In hauls taken outside the central area, the reduction was 45–50% relative to that before shooting. The catch did not increase during the 5 days surveyed after shooting stopped.

Catches of haddock also were significantly ($p < 0.001$) less during and after shooting than before shooting began. Within the shooting area, catches during shooting fell by 68% relative to those before shooting (Fig. 7B). At other distances the catches were also significantly lower during and after shooting. Here the reductions during shooting relative to those

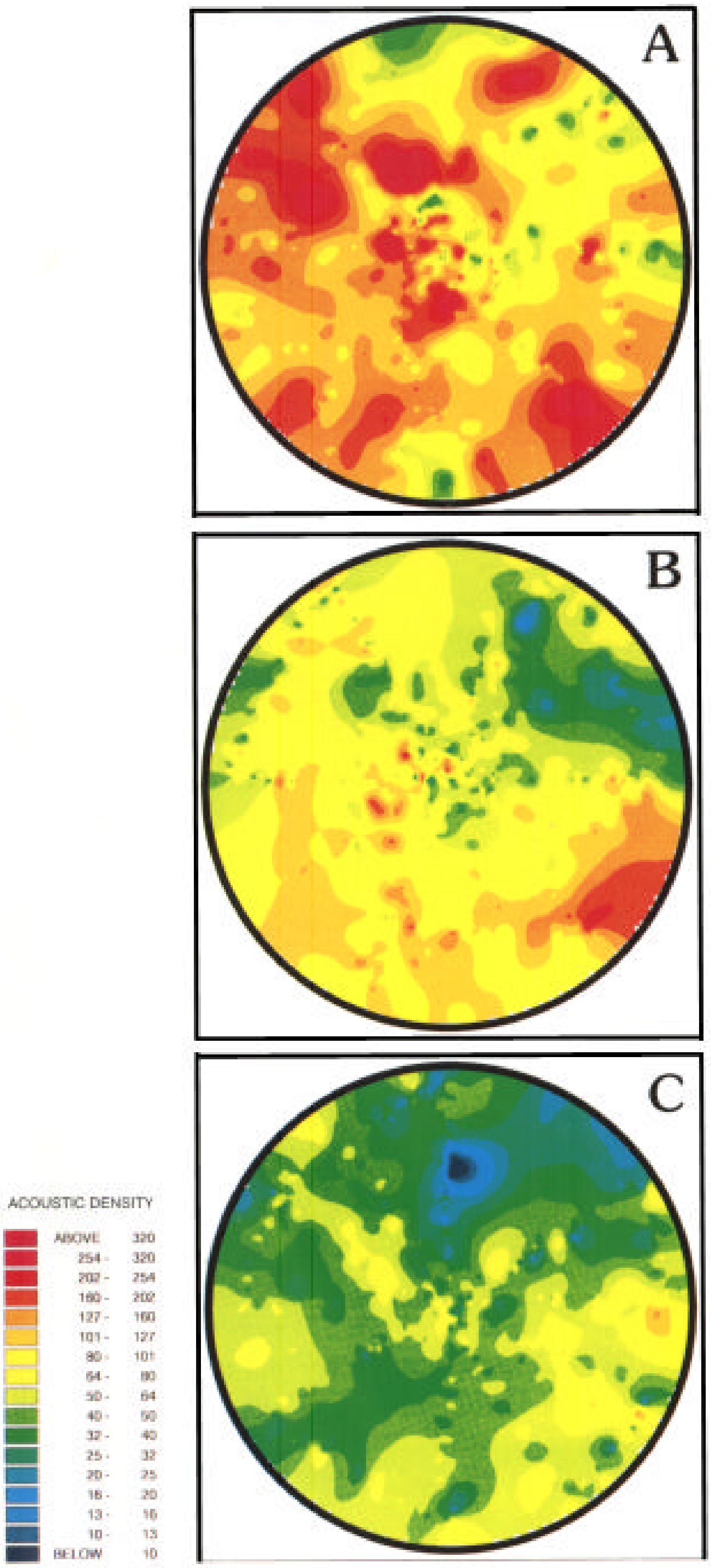

A
B
C
ACOUSTIC DENSITY
ABOVE 320
254 - 320
202 - 254
160 - 202
127 - 160
101 - 127
80 - 101
64 - 80
50 - 64
40 - 50
32 - 40
25 - 32
20 - 25
16 - 20
13 - 16
10 - 13
BELOW 10

Fig. 3. Horizontal distribution of cod and haddock in absolute units of acoustic density ($m^2 \cdot nmi^{-2}$) before (A), during (B), and after seismic shooting (C). The region displayed has a diameter of 40 nmi, with its centre at 72°20′N, 26°00′E.

Fig. 4. Total acoustic density ($+s_{geo}$) of cod and haddock before (solid), during (striped), and after (grey) shooting, by distance from the shooting region.

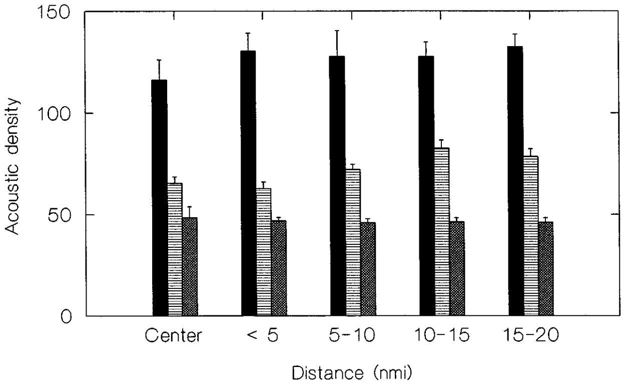


Fig. 5. Total acoustic density of cod and haddock, with 1-nmi resolution, measured along a straight transect running through the centre of the area in an east–west direction during shooting on 9 May.

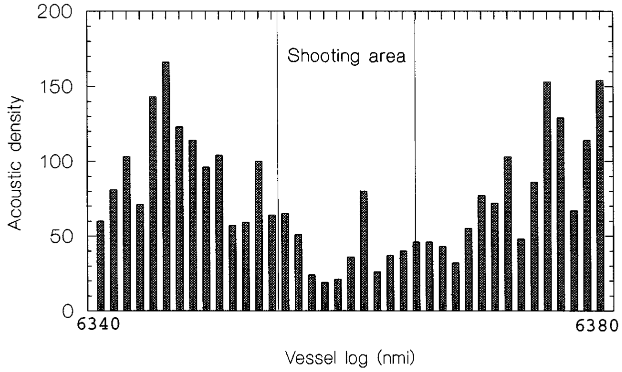


Fig. 6. Total quantity ($+s_{geo}$) of cod and haddock by mass before (solid), during (striped), and after (grey) shooting.

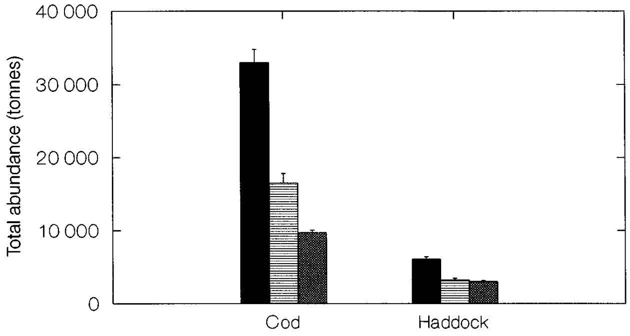
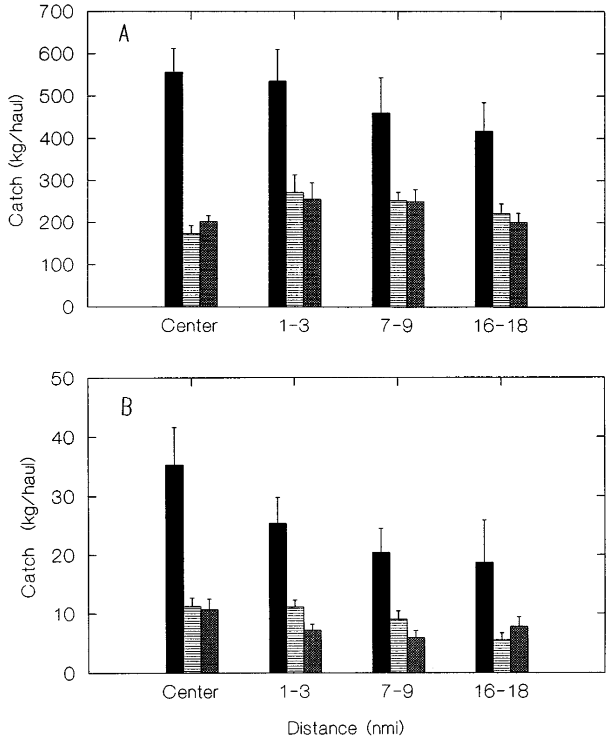


Fig. 7. Average trawl catch rates (+SE) of cod (A) and haddock (B) before (solid), during (striped), and after (grey) shooting, by distance from the shooting area.



before shooting were 56, 56, and 71%, respectively, at 1–3, 7–9, and 16–18 nmi. There was no increase in catch rates after shooting ceased.

Figure 8 shows the time series of catch rates for cod and haddock by trawl, where the catches are shown as a deviation from the overall average for the entire trial period. There was a significant variation in catch quantity from haul to haul throughout the trial period, but it is nevertheless clear that the catch rates of both cod and haddock fell immediately after shooting started. The low level was maintained throughout the whole shooting period (hauls 63–130) and also in the days after shooting had ceased. Both time series and intervention analysis confirmed that there was a 50% drop in catch after shooting began and no significant increase after shooting stopped. The time-by-distance interaction was not statistically significant for catch rates of either cod ($p = 0.118$) or haddock ($p = 0.559$) (see Appendix F in Engås et al. 1993).

Longlines

The most important species in the longline catches was cod, but the proportion of haddock was greater than in the trawl catches, especially in the preshooting period (about 25% by mass). As for trawling, the statistical model showed a decrease ($p < 0.001$) in longline catch rates for cod when shooting started. In the central experimental area the catch rate declined by 45% when shooting began, but outside of this area the reduction was less (16 and 25%, respectively, at 1–3 and 7–9 nmi), with no reduction at the furthest position (Fig. 9A). There was a tendency for the longline catches of cod to increase after the conclusion of shooting, except for the furthest position where the catch rate declined.

Fig. 8. Trawl catch rates of cod (A) and haddock (B) in chronolgical order without regard to distance from shooting area. The catches are shown relative to the average (horizontal line) over the entire trial period.

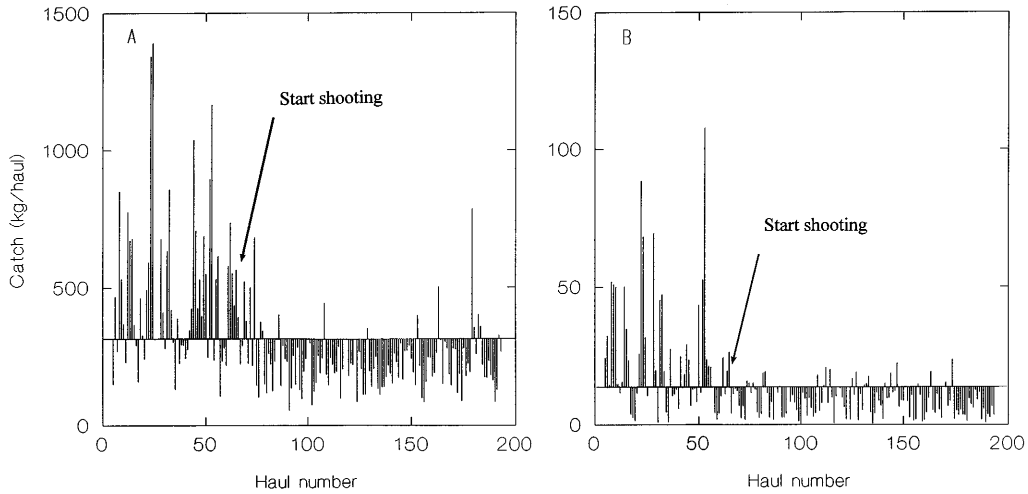
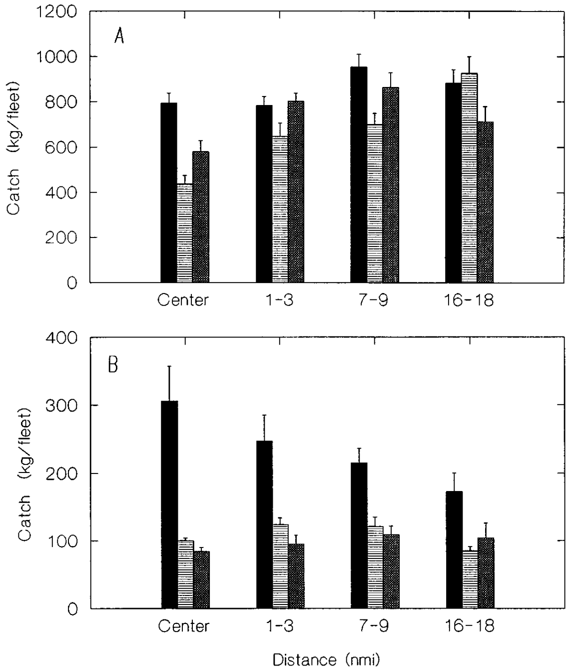


Fig. 9. Average longline catch rates (+SE) of cod (A) and haddock (B) before (solid), during (striped), and after (grey) shooting, by distance from the shooting area.



The catch reduction for haddock averaged about 50% over the entire area during shooting ($p < 0.001$). There was a reduction in catches out to the edge of the area, but the decrease was greatest in the central area where the catch rates declined by 67% (Fig. 9B). In contrast to the results for cod, there was no sign of an increase in catch after shooting had ceased.

The longline catches of cod were distinctly reduced from the moment the seismic shooting began (Fig. 10A). However, there were large variations in catch rates between longline fleets. It should be remembered that the longline fleets at all distances from the shooting area are included in Fig. 10A and, as mentioned earlier, there was no reduction in catch at the border of the experimental area. This will contribute to greater variability than in the equivalent figure for the trawl catches. It might appear that there was a distinctly negative trend in the longline catch rates for haddock before shooting started (Fig. 10B). However, the variability in catch was relatively large in this period. When shooting began, the variability in catch rates was much less, and catch rates stabilized at a low level. The time-by-distance interaction was found to be significant for longline catches of cod ($p < 0.001$), but not for haddock ($p = 0.592$).

Effects on small and large fish

When shooting started the length distributions changed, particularly in the central area. The sharpest change for cod occurred for fish larger than 60 cm, which nearly disappeared in both gears (Fig. 11, data for longline not shown). For haddock, in the trawl catches the reduction in the different size groups was more even, whereas for longlines the reduction was greater for large fish (Fig. 12).

The average mass per fish from each haul was related to distance and time using the model in eq. 3. Before shooting began, the size of cod was relatively uniform over the entire investigation area (Fig. 13). After the shooting began, masses fell significantly ($p < 0.001$) in the shooting area and in nearby areas. The changes in average mass of fish caught gradually decreased with increasing distance from the shooting area, and at the furthest position there was no significant change. Both main effects and interaction effects were significant ($p < 0.01$). After shooting operations had ceased, there was a tendency for the length distribution to return to preshooting levels. For individual mass of haddock neither the main effects nor the interaction effects were found to be significant.

Radiated noise measurements

The maximum peak value of the recorded seismic shots was measured to be 248.7 dB re 1 μPa at 1 m. A variation in peak value of about 3 dB from shot to shot was observed. The measurement point was roughly 65° off the acoustic axis and the recordings, corrected for directivity, indicate a source level of

Fig. 10. Longline catch rates of cod (A) and haddock (B) in chronological order without regard to distance from shooting area. The two longline fleets taken at the same distance each day are regarded as a single unit. The catches are shown relative to the average (horizontal line) over the entire trial period.

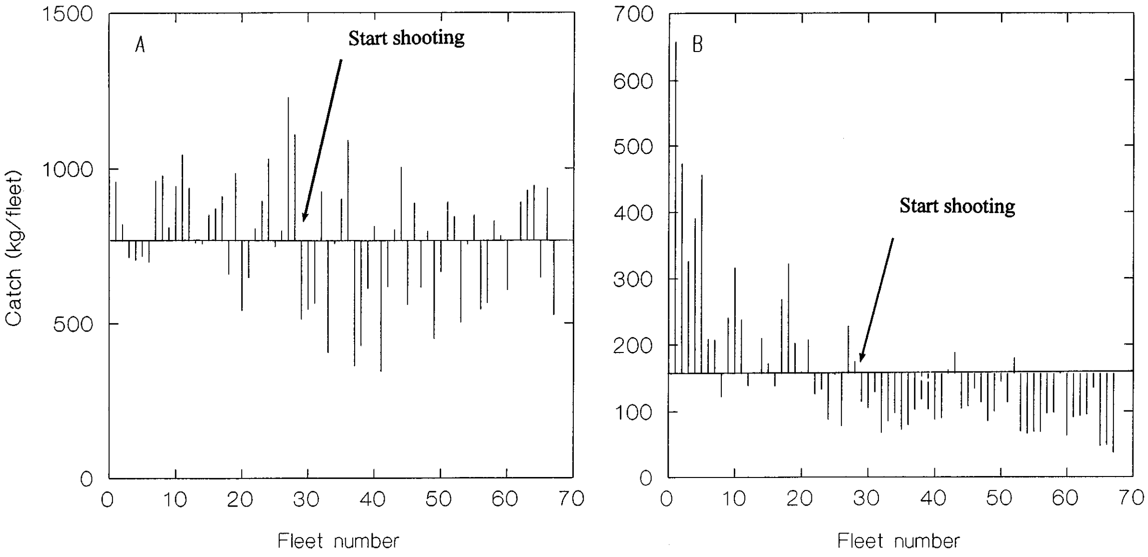
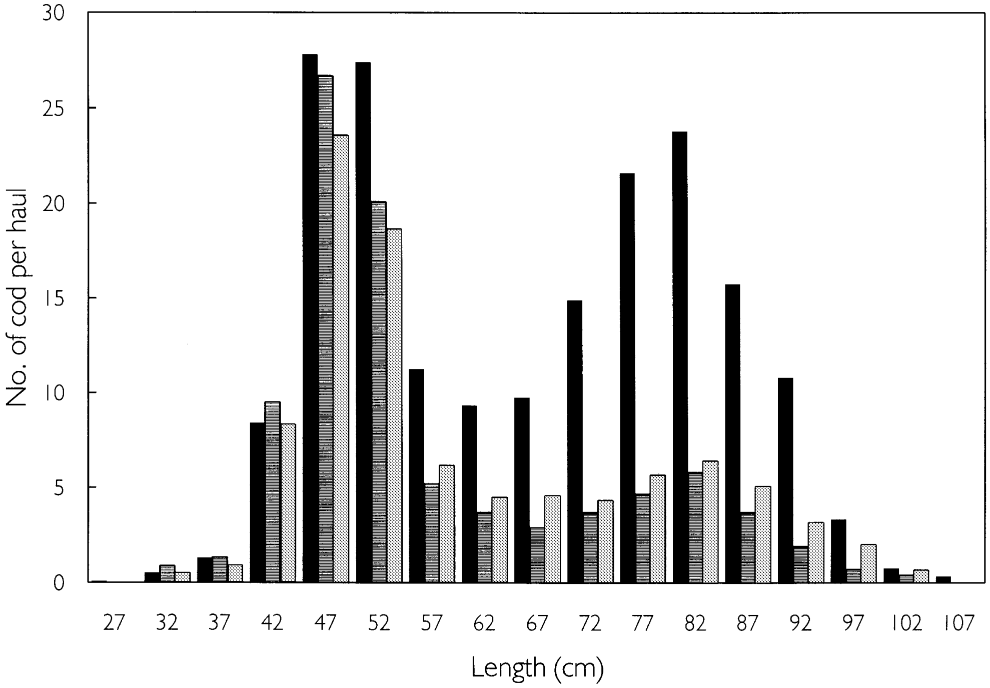


Fig. 11. Length distribution of cod in trawl hauls within the shooting area before (solid), during (striped), and after (grey) shooting.



253 dB re 1 μPa at 1 m, ±3 dB. This was somewhat higher than expected from this air-gun array, namely 250 dB re 1 μPa at 1 m. Most of the energy in the seismic shots was confined to the band 10–150 Hz (Fig. 14).

The spectral level of the sound from the air guns was about 120 dB above the measured ambient noise level and about 60 dB above the noise level from the fishing vessels. Detailed spectra of recorded ambient noise and all participating vessels at cruising and operating speeds were reported by Engås et al. (1993).

Discussion

Effects on fish abundance and catch rates

The acoustic survey and the fishing trials showed that seismic shooting with air guns affected fish distribution and caused trawl and longline catch rates of cod and haddock to fall. This effect of seismic activity was demonstrated within the region in which shooting occurred and also in surrounding areas, and the effect appeared immediately after seismic shooting started and continued after it ended.

Fig. 12. Length distribution of haddock in longline catches within the shooting area before (solid), during (striped), and after (grey) shooting.

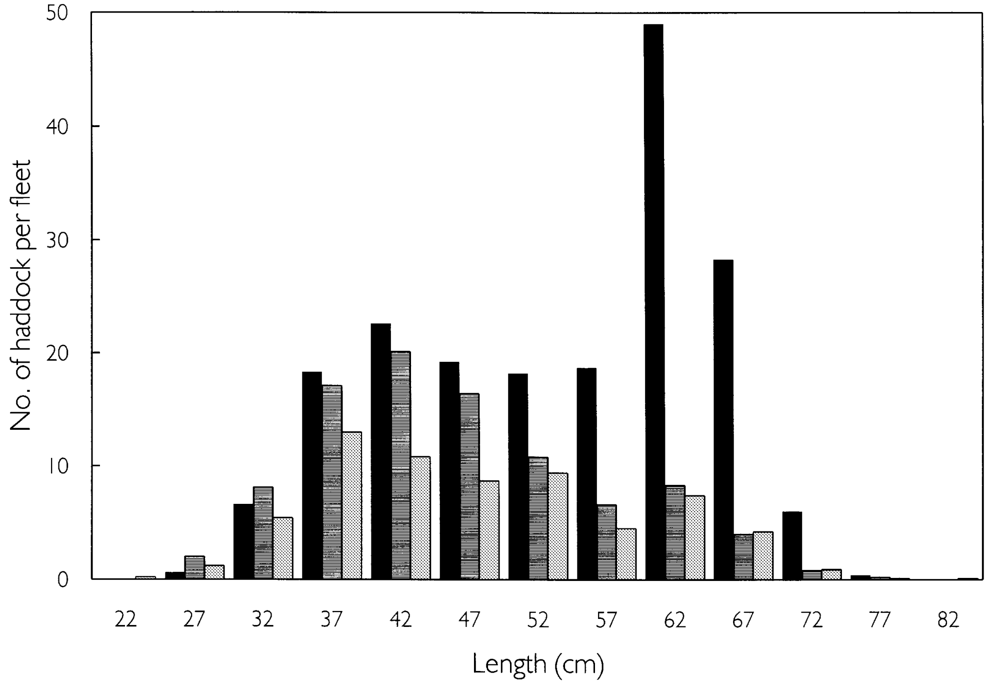


Fig. 13. Mean individual masses of cod (solid lines) and haddock (broken lines) in trawl hauls before, during, and after shooting, by distance from the shooting area.

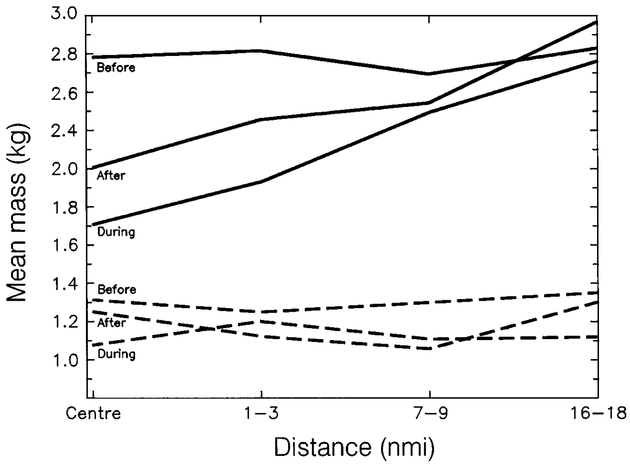
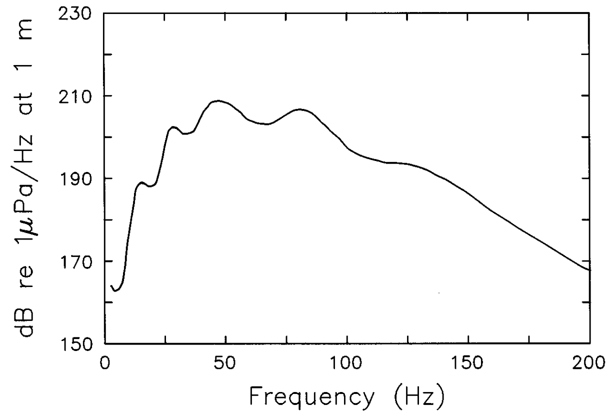


Fig. 14. Measured frequency spectrum for a single shot from the air-gun array.



While statistical tests on the main effects (time and distance) of seismic shooting on catch rates of cod and haddock generally were significant (in six of eight cases), the interaction term (time by distance) was not significant (in three of four cases) (Engås et al. 1993). Within the investigated area the change in fish distribution happened so rapidly after the shooting started that the sampling frequency used with trawls and longlines could not reveal real changes in the horizontal distribution of fish with time. The main reason for a nonsignificant interaction term, however, is that the study area was too small to see the effects diminish with distance, and that the duration of the experiment was insufficient to see catch rebound with time.

The most pronounced indicators of the effects of seismic shooting are therefore the rapid drop in catches immediately after seismic shooting started (Figs. 8A, 8B) and the local drop in fish density across the central area, as measured on some of the acoustic transects during seismic shooting (Fig. 5). It is unlikely that a natural rapid shift in horizontal distribution coincided with the seismic shooting, and the results are thus most likely explained by the hypothesis that fish are scared by the sound generated by the air guns and migrate out of the area.

Fishing effort within the experimental area could have had only a minimal effect on the observed catch reductions. The largest effort was made within the shooting area, where total catches were about 20 t of cod and 4.5 t of haddock. The total quantity available within the shooting area, determined acoustically, was about 834 t. Fishing therefore removed only 3% of the initial stock. A fish-out effect would also have caused a gradual change in abundance and catch rates, as opposed to the sudden reductions observed immediately following the start of seismic shooting.

Reductions in catch rates caused by seismic activity have also been demonstrated in other studies. Løkkeberg and Soldal (1993) investigated catch data obtained from commercial vessels that happened to be operating on fishing grounds where seismic explorations were being conducted and found a 55–80% reduction in longline catches of cod and a reduction of 80–85% in the by-catch of cod in shrimp trawling. For fishing with vertical lines, catches of various redfish species declined by 50% during discharges of a single air gun (Skalski et al. 1992).

In this study, differences were found between trawls and longlines in terms of the degree of reduction in catches of cod and its spatial and temporal extent. During seismic shooting, the masses of cod taken by trawl fell by 69% within the area where the seismic vessel was operating, and a total catch reduction of about 45% was observed throughout the survey area. For longline fishing, however, the catch rates for cod fell by 44% in the seismic shooting area, but the influence on catch rate gradually diminished towards the border of the survey area, where no significant change in the catch rates was observed after shooting started. After shooting ended, there was a tendency for the longline catches of cod to increase.

The differences in the results for trawl and longline catches of cod may be due to the different catch mechanisms of these gears. Longlines have a definite point of gear saturation limited by the number of baited hooks (Skud 1978), and a linear relationship between catch rate and fish abundance cannot be assumed. If a nonlinear relationship applies, the consequence of estimating fish abundance from longline catch rates is that changes in fish abundance are consistently underestimated, especially when abundance is high (Siegler 1993). The decrease in fish abundance owing to seismic activity may therefore have been more pronounced than was reflected in the longline catch rates. However, in our study only about 20% of the hooks had caught a fish, and gear saturation alone can hardly explain why the longline catches did not reflect a 50% reduction in cod abundance at the border of the survey area, as measured by trawl and acoustics.

Catch per unit effort in longline fishing may be affected by competition between species (Skud 1978; Siegler 1993). In the period after shooting, the catch rates for haddock were much lower than in the preshooting period, and the longline may have become more efficient in catching cod. Furthermore, the seismic shooting caused the fish to migrate out of the area, and the movement of fish may have increased the rate of encounters with the baited hooks.

On the other hand, if we assume that the longline catch per unit effort data on cod in this experiment correctly reflect real changes in abundance, the trawl and acoustic measures must have been biased. The trawl itself and the trawling operation both generate noise (MacLennan and Hawkins 1977). Fish that have been subjected to sound from air guns may be more sensitive to sound and show a stronger avoidance reaction to trawling than unaffected fish, causing trawl catchability to decrease in areas already affected by seismic activity. The observed decrease in abundance, as reflected by the trawl catches, may thus have been overestimated. However, the trawl data were in agreement with the acoustic density estimates, and the changes in abundance seem therefore to be more accurately reflected by the trawl data than the longline data. The longline catch per unit effort, particularly for cod, may be biased through a combination of the effects of gear saturation, changes in interspecific competition for bait, and increases in fish movement induced by sound emission.

Our study was also designed to investigate the spatial and temporal range of the effects of seismic explorations. The size of the experimental area was chosen to include distances beyond those within which fish reactions and catch reductions were expected to be demonstrated. On the basis of our knowledge of fish hearing and reaction thresholds, it was assumed that fish would be able to detect the sounds emitted by the air-gun array at the border of the experimental area, but no reaction was expected further out than 5–6 nmi from the shooting area. However, catch reductions beyond this distance were demonstrated for both trawls and longlines. In our calculations we assumed that the reaction threshold exceeded the detection threshold by about 20 dB, but the results indicated a smaller difference between the detection and reaction thresholds for air-gun noise. Alternatively, the threshold of detection of air-gun noise may be lower than the auditory thresholds reported in the literature (see Chapman and Hawkins 1973; Hawkins 1993).

The catch rates did not return to preshooting levels during the 5-day period after shooting ended. Trawl catches of cod and haddock and longline catches of haddock showed no increase after shooting ended. The longline catches of cod approached the preshooting level during this 5-day period, but the catch rates in the shooting area and at the border of the experimental area were still below preshooting levels. The length–frequency distribution in the area also approached, but did not return to, its initial pattern. The results thus indicated that trawl catches do not normalize during the first 5 days after seismic shooting ends, whereas there is a tendency for longline catches to approach preshooting levels. The investigation therefore demonstrated that the effects of seismic shooting lasted for at least 5 days.

Effects on small and large fish

We found that the reductions in the acoustic estimates and in the longline and trawl catches were more pronounced for large than for small fish. An increase in longline catches of small cod was even observed after seismic shooting started (see Engås et al. 1993). The higher catch rate of small cod by longline may be due to less competition for available bait at lower fish density (Løkkeberg and Bjordal 1992). Small individuals may be more successful in taking the bait available when the larger individuals have avoided the area.

The stronger response of larger fish to air-gun discharges may be explained by size-dependent swimming capacity. Assuming that fish within the shooting area responded to the sound emissions by swimming at their maximum sustained speed, then a 30-cm cod (maximum sustained swimming speed = 0.6 $m \cdot s^{-1}$ (Wardle 1977)) would have been able to swim 28 nmi and reach the border of the survey area during the first 24 h after shooting started. However, as the fish were responding to continuously discharging air guns and swimming through a gradient of exponentially decreasing sound levels, habituation may have occurred. Thus, fish may have terminated their avoidance reaction at different distances from the central area depending on their size and swimming speed. Alternatively, the fish may have responded to the air-gun discharges by increasing their swimming speed beyond the sustained speeds, leading to exhaustion. Avoiding the sound source by prolonged swimming speeds (He 1993) may thus have produced a response pattern of alternating intervals of swimming and resting until habituation terminated the response at different distances for fish of different sizes.

Another explanation for this difference may be based on improved hearing ability with increasing size for species with a swim bladder owing to reradiation of sound from the swim bladder, although such a relationship has not been documented. Larger fish also have lower resonance frequencies than small fish, and may therefore be more sensitive to sound of lower frequencies. However, this is not a likely explanation for a stronger response to air-gun discharges in larger fish because the resonance frequency for a 1 m long cod is about 600 Hz (Hawkins 1977; Løvik and Hovem 1979), while most of the energy spectrum of the air gun is below 150 Hz. At frequencies above 600 Hz, the energy is significantly lower, and there is little reason to believe that resonance phenomena can cause the differences in behaviour we observed between large and small fish.

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