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The importance of detectability to acoustic surveys of semi-demersal fish

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A major source of bias and imprecision in acoustic abundance estimates of semi-demersal fish is detectability, defined here as the proportion of the true abundance of a target species within the ensonified volume (surface to bottom) that is detected by an echosounder and included in integration. In autumn 1996 and 1997, acoustic surveys for Atlantic cod (*Gadus morhua* L.) in inshore Placentia Bay, Newfoundland, Canada, indicated mean daytime densities (e.g. 0.016 fish m^{-2} in 1997) an order of magnitude higher than at night (0.001 fish m^{-2}). A corresponding downward shift in vertical distribution at night was also observed. At the same site in 1996, *in situ* video censuses of cod from a submersible showed equivalent cod abundance by day (n=3) and night (n=1). Submersible observations indicated that at night cod were located nearer to bottom, and preferred rocky and boulder-strewn substrates and not open sandy bottoms ($p<0.001$). Acoustic densities measured from the submersible cruising 20 m above bottom, and from the surface vessel, were similar. Submersible acoustic estimates and video census indices were positively associated during daytime. The sole night-time acoustic estimate was near zero while the corresponding video index was the highest recorded. We conclude that diel change in acoustic density resulted from variations in detectability caused by cod vertical movements and habitat preferences. A broad-scale springtime inshore and offshore survey of cod in the same stock area confirmed the trend of higher acoustic density estimates during the day than at night. We advocate the inclusion of a time-dependent detectability coefficient in the scaling of acoustic backscatter to abundance for semi-demersal fish.

Key words: cod, detectability, acoustics, submersible, Newfoundland, availability.

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Introduction

The accuracy and precision of acoustic measurements of fish abundance may be affected by several factors, including vessel noise, equipment sensitivity, calibration, target strength, and species identification (MacLennan and Simmonds, 1992). Several reviews have focused on the quantification and standardization of these variables (e.g. Foote *et al.*, 1987; Rose, 1992; Mitson, 1995; Ona, 1995; Scalabrin *et al.*, 1996). A major additional source of bias stems from the inability of echosounders to detect all fish actually present. Acoustic surveys typically assume that the detection of fish is constant or varies at random within and between surveys, and hence may be a source of imprecision, but not bias. The likelihood that not all fish can be detected has been regarded as a positive characteristic of acoustic surveys because estimates of abundance will be conservative (Shotton and Bazigos, 1984). However, few experiments have tested the absolute degree of detectability or its variability within and between surveys.

We define detectability as the proportion of the true abundance of a target species within the ensonified volume (surface to bottom) that is detected by an echosounder and included in integration. The term "detectability" is drawn from sampling theory (Thompson and Seber, 1996), where it is used to denote the common problem of not being able to detect all population members within a sampling unit. Detectability better describes the problem to acoustics than

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"availability" which has been used in the acoustic literature (e.g. Godø and Wespestad, 1993), because the latter is often used in a broader sense in fisheries sciences and unavailable fish may be inside and outside the acoustic beam, or in unsurveyed areas. Detectability is specific to the detection of fish within the ensonified volume.

Detectability is determined primarily by physical properties of the acoustic beam and pulse, characteristics of the substrate, and how these relate to the distribution and behaviour of the fish. Detectability is reduced near bottom as a consequence of the acoustic shadow – or dead zone: a region immediately above the substrate in which the echoes of fish overlap with that of the bottom (Mitson, 1983; Ona and Mitson, 1996). In Ona and Mitson's (1996) terminology, echoes from fish in the dead zone may be "detected", but not "discriminated" from the bottom echo, and therefore can not be integrated. In our terminology, fish that are detectable must also be integrated. Dead zone height is set by the half pulse length and beam geometry, and increases with bottom roughness and slope (Mitson, 1983). An acoustic blind zone also exists at the water surface, and is determined by transducer depth, the blanking range, acoustic beam forming factors, and surface noise (Rose, 1992). Detectability may introduce substantial bias and imprecision to acoustic surveys of areas having rough bottoms or steep slopes and where fish are distributed in close or variable proximity to the substrate or surface.

Behavioural patterns, such as vertical movements of fish into or out of the bottom and surface blind zones, can lead to bias through temporal and spatial variation in detectability (e.g. Fréon *et al.*, 1993b; Demer and Hewitt, 1995; Michalsen *et al.*, 1996). Habitat selection for substrates of high or low detectability may also bias acoustic estimates (Fréon *et al.*, 1993a). Detectability may vary with differences in age composition and local density where these factors affect vertical distribution (Godø and Wespestad, 1993). A key problem in quantifying detectability is that the true abundance of fish present typically is not known. Comparisons of acoustic density estimates with net catches cannot be used to quantify absolute detectability because traditional net catches provide relative indices of density subject to their own biases (Godø, 1994). Submersibles may enable independent and less biased *in situ* observations of fish behaviour, distribution, and abundance, allowing estimates of absolute detectability.

Detectability is of particular importance for semi-demersal fishes such as Atlantic cod (*Gadus morhua* L.) which are frequently concentrated in close proximity to the bottom. In addition, vertical movements of bottom-dwelling fish are often complex and variable (Rose *et al.*, 1995; Michalsen *et al.*, 1996). Resultant variations in detectability may be especially acute in inshore shallow-

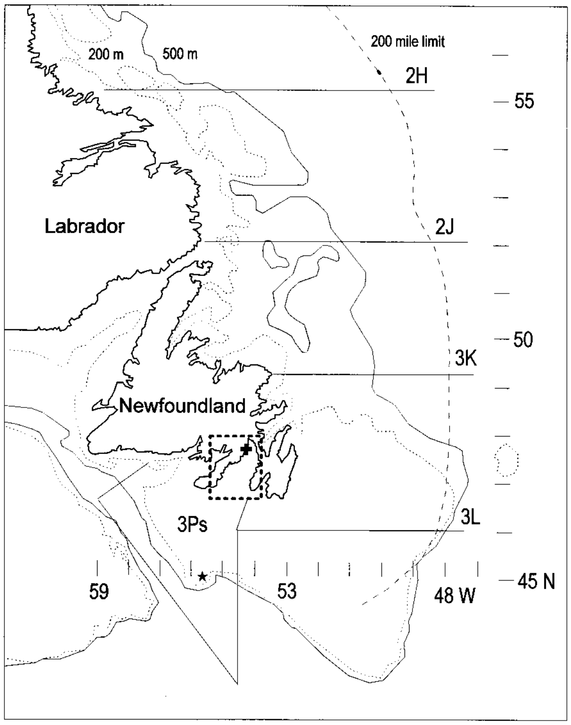

Figure 1. NAFO divisions around Newfoundland and Labrador. Placentia Bay is indicated by a dashed rectangle. The inshore study site is represented by a plus symbol (+) and the offshore transect is represented by a star (★).

water acoustic surveys, where rocky bottoms and steep bathymetry are commonplace.

In this paper we assess the detectability of Atlantic cod to inshore acoustic surveys in Placentia Bay, Newfoundland, Canada. We use surface acoustic density estimates in conjunction with submersible-based acoustic and visual measurements to test within-survey variation in detectability. This variation is considered in relation to diel behavioural patterns of vertical movements and bottom-type preferences. We then examine the consequences of variations in detectability to the accuracy of acoustic abundance estimates.

Methods

Study area

The study took place in Placentia Bay, Newfoundland, Canada (NAFO subdivision 3Ps; Figure 1), at a study site bounded by 54°10.20′ to 54°10.70′W and 47°43.75′ to 47°43.20′N. The area was chosen for its steep slopes and variety of bottom types, in order to test our acoustic techniques under a range of conditions which are thought to affect detectability. Most of the experimental work was conducted on two transects running along the parallels 54°10.50′ (Transect 1) and 54°10.60′W

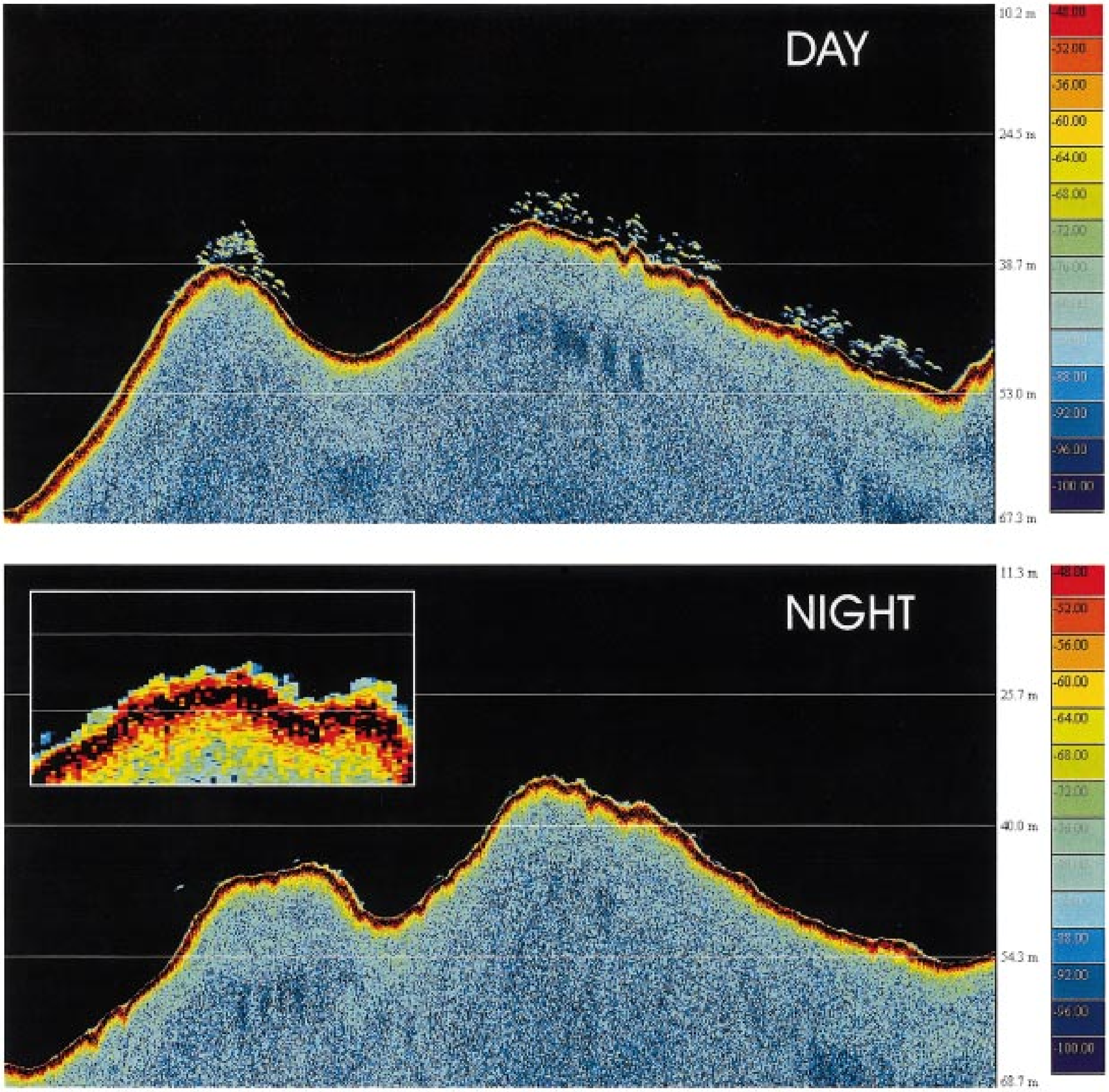

Figure 2. Representative daytime (upper panel) and night-time (lower panel) echograms from 1997. Signal consists of large single targets. In the day echogram, many cod are well off the bottom, identified by their signal shape and echo intensity. Few cod are evident at night. Inset in the night echogram is an enlargement of the second peak along the transect, from which it is apparent that fish were still present along the line.

(Transect 2), from 47°43.65′ to 47°43.30′N. Depths along these lines ranged from 35 to 80 m. A related survey was performed in the spring of 1998, covering both the inshore site and an offshore transect in 3Ps (along 45°05.00′N, from 55°34.21′ to 55°33.55′W; Figure 1).

Surface acoustic protocol

Over the course of 27, 28, 31 October and 1 November 1996, 17 acoustic transects were run on a north–south axis across the study site. On each of 27 September, and 2 and 7 October 1997, a 24-h survey was conducted, in which Transects 1 and 2 were both run from one to three times per hour. The timing of these three surveys were chosen to span the full range of tidal phases. Two Biosonics single beam digital DT4000 echosounders were used in this study (38 and 120 kHz; 6° half-power beam widths, pulse durations 0.4 ms, 42 kHz digital sampling rates, pulse rates 2 pings s^{-1}). Transducers were mounted on a "dead weight" body towed at a depth of 1.5 m alongside either the MV "Innovation" or

MV "Mares" (Marine Institute of Memorial University of Newfoundland research vessels, <14 m). All transect runs were performed at a constant speed of 4 knots (7.4 km h^{-1}). Calibrations were performed *in situ* with a 38 mm tungsten carbide standard target according to standard practices (Foote *et al.*, 1987). Handlines were used to collect fish at the study site to supplement acoustic interpretations and provide biological samples.

The acoustic signal consisted mostly of large and sometimes overlapping single targets (e.g. Figure 2). A 30 cm vertical offset from the detected bottom was used, equivalent to approximately one half pulse length. Background and system noise levels experienced during the surveys were less than − 100 dB. Acoustic data from the 38 kHz echosounder on each pass of an acoustic transect were integrated using FASIT software (Fisheries Assessment and Species Identification Toolkit; LeFeuvre *et al.*, 1999) to produce a mean transect areal backscatter (Sa). Mean Sa was scaled to areal density (fish m^{-2}) using mean target strengths of − 31.0 dB per fish (for 1996) and − 31.2 dB (1997). These target strengths were calculated for mean cod lengths of 56.5 cm (1996; n=39 fish sampled, s.e.=1.4) and 55.0 cm (1997; n=46, s.e.=0.9) from the relationship: $TS_{(dB)}$ at 38 kHz=20 $\log_{10}$ Length − 66 (Rose and Porter, 1996). Volumetric densities (fish m^{-3}) were also calculated for each transect over the entire water column and transect length, in bins of 1 m depth and 10 m horizontal length. Integration was referenced from the surface, so bin depth was subtracted from bottom depth to yield the height off the bottom of each volumetric integration bin.

A three-way ANOVA tested the effects of whether the transect was run during day or night, survey date, and transect on the 1997 estimates of cod density. "Day" was defined as the period from the start of nautical twilight in the morning to the end of nautical twilight in the evening.

Submersible surveys

Submersible surveys were conducted in 1996 with the Canadian Navy submersible SDL-1, supported by the HMCS "Cormorant". The SDL-1 is a free-diving submersible with a maximum operating depth of 610 m. One large (ca. 1 m diameter) forward facing viewport permits visual observations. The crew of four was comprised of two pilots and two scientists. A 120 kHz Biosonics DT4000 digital transducer was mounted on a moveable forward arm, connected through the submersible hull to the transmitter, receiver, and data storage computer. Four dives were made: one on each of 29 and 30 October (1400–2100 h), and two on 31 October (0800–1100 and 1330–1630 h). Position was determined by visually and radar-tracking a buoy attached to the submersible. The Cormorant remained approximately 0.5 nmi (ca. 900 m) from the buoy and was in constant radio contact with the SDL-1 during deployment. Once the transect starting point was attained and a run begun, the submersible's position was checked approximately every 5 min until it reached the end of the transect.

A strict protocol was observed during each submersible survey. One of Transects 1 or 2 was first run acoustically at a constant speed of 0.5 knots (0.93 km h^{-1}) and a height of 20 m off the bottom. The submersible then descended and re-ran the transect in the opposite direction as a visual line census, at a height of 2 m off the bottom (following SCUBA survey techniques for coral reef fishes: Brock, 1982; with modifications for submersible application after Zaferman, 1981). An external low-light sVHS camera with VCR recorded in a forward-facing direction continuously along the visual transect. External lighting was provided during both day and night from three 1000 W and two 500 W quartz lights. The radius of the field of view of the camera was not measured, but was judged by experienced Navy submariners to be constant since the submersible maintained a fixed height off the bottom.

Cod were the only large (>30 cm) fish observed. Small redfish (<30 cm; *Sebastes* spp.) were also present but remained down amongst rocks and boulders (and thereby in the acoustic deadzone). Cod were easily visible and identifiable at a distance of approximately 10 m in advance of the approaching submersible. There was no evidence of cod avoidance behaviour outside of the zone of observation. In general, changes in cod movement patterns were not evident unless the submersible approached within 1–2 m of the fish, by which point they had already been counted. Even at this close range, cod most often simply swam slowly out of the path of the approaching submersible.

An index of cod density was calculated by dividing the number of cod observed on the videotape of each transect by transect length. Transect length was calculated as the sum of the distances between subsequent position fixes. The height of the observed volume was set at 5 m, the approximate top of the camera's field of view. Transect width was the constant width of field of view. As a consequence of the inability to quantify this width, the video measure is expressed as a relative density index (fish m^{-1}).

Acoustic data collected from the submersible with the 120 kHz echosounder were echo-integrated to yield cod density (fish m^{-2}) using a mean target strength of − 30.0 dB, calculated for a mean length of 56.5 cm (see above) from: $TS_{(dB)}$ at 120 kHz=20 $\log_{10}$ Length − 65 (Rose and Porter, 1996). Data were integrated from the bottom (with the 30 cm vertical offset) to 5 m above bottom, for comparison to video density indices.

Cod habitat preference

The bottom type occupied by each observed cod was identified from the video record. Bottom types were defined in terms of the presence of rocks and sediment size: no cover denoted areas of sand, silt, and fine gravel; low cover areas had some rocks, but were mostly sand or gravel; high cover comprised areas with many large rocks and boulders. The time spent by the submersible over each bottom type was calculated for the visual transects. The expected number of cod in each bottom type was obtained by multiplying the total number of fish seen on the video by the proportion of total transect time spent over each substrate type. A chi-square test determined whether the observed distribution of cod differed from that expected if fish were distributed randomly relative to the proportional abundance of bottom types.

Analysis of cod preferences for particular substrates was undertaken only for fish estimated to be within 1 m of the bottom, based on the assumption that only these fish could be selecting for bottom type. It was also noted whether the fish was in the acoustic lee of any rocks. A fish must be at least one half pulse length above the height of any rock within the footprint of the acoustic beam to be discriminated from the bottom echo (Mitson, 1983). The approximate half-power footprint of a surface DT4000 at the range of depths censused by the submersible (35–80 m) is between 3.5 and 8 m. A fish observed on video was therefore conservatively defined as being outside the "acoustic lee" of rocks if it was located either more than 10 m away from, or clearly above, any rock.

Results

Surface acoustics

In the autumn of 1996, acoustic areal density estimates of cod at the survey site were higher during the day than at night (Kolmogorov-Smirnov test statistic $Z=1.61$, $p=0.01$, Figure 3). Only four transects were performed during darkness and only two in the early morning, so a full day–night comparison is not possible. Nevertheless, this initial result led to the hypothesis of a major diel change in detectability.

Transects spanning the full daily cycle in 1997 showed acoustic areal densities increasing sharply at sunrise, remaining high but quite variable during the day, and then dropping off at sunset (Figure 3). All three experimental days in 1997 showed this pattern. The three-way

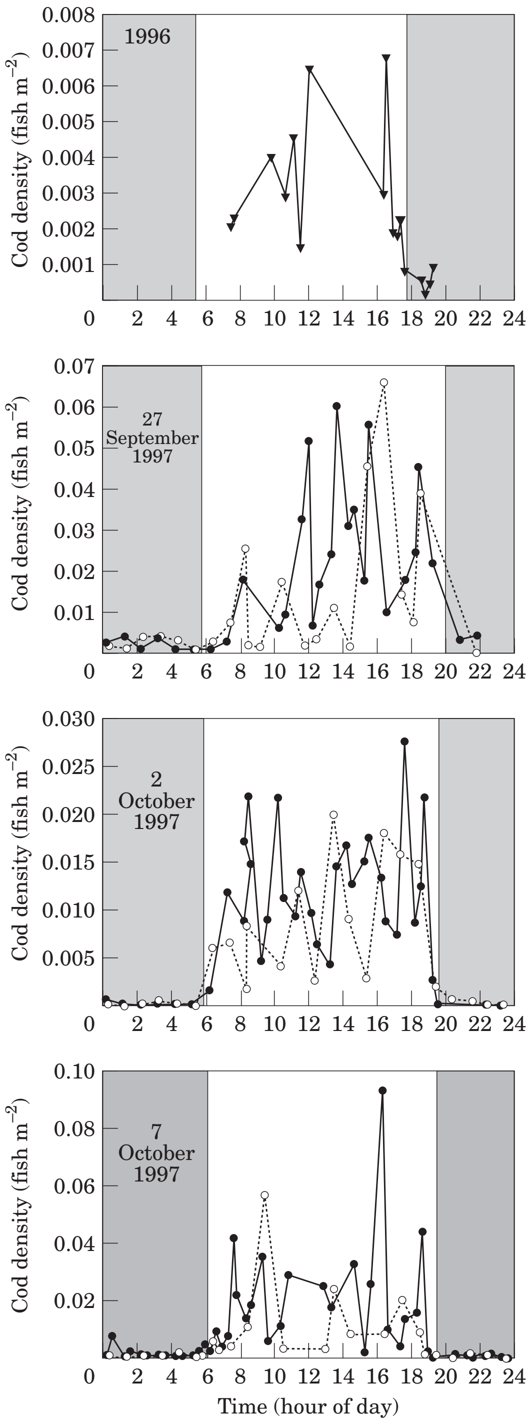

Figure 3. Acoustic cod density estimates (fish m^{-2}) from each surface run of a study transect, by hour of day (Newfoundland Standard Time NST=GMT − 3.5). Separate graphs are given for the 1996 data (27, 28, 31 October and 1 November combined) and each of the 1997 survey days (27 September, 2 and 7 October). The 1996 data give density estimates from a number of north–south transects across the study site. The 1997 survey concentrated on repeated passes of Transects 1 (closed circles) and 2 (open circles). Night-time is indicated by gray background, day by white.

Table 1. Three-way ANOVA results, examining the effects on 1997 cod acoustic density estimates of day and night, survey date (27 September, 2 or 7 October), and Transect (1 or 2). All two- and three-way interaction effects were non-significant (all p's $\geq$0.133).

Effect	Sum of Squares	d.f.	F	Significance (p)
Model	2.4×10^{-2}	11	7.7	<0.001
Day/Night	1.5×10^{-2}	1	50.4	<0.001
Survey date	1.6×10^{-3}	2	2.7	0.073
Transect	8.4×10^{-4}	1	2.8	0.096

ANOVA indicated that transect timing (day or night) was the sole significant determinant of density (p<0.001); the effects of transect and date were not significant (p's>0.05; Table 1). On each study day, average densities were at least an order of magnitude greater by day than by night (Table 2). Averaged across transects and days, the mean 1997 daytime cod density was 0.016 fish m^{-2} (mean of 119 transects, s.e.=0.001) while the mean night-time density was 0.001 fish m^{-2} (n=64, s.e.=0.0001).

A visual inspection of night-time echograms (e.g., Figure 2) indicates that although some of the cod could be detected, most were too close to the bottom to be reliably discriminated from it during echo-integration. In contrast, the majority of fish during the day were found between 0.3 and 4 m from the bottom (Figure 2), and were easily integrated.

Volumetric density estimates were higher during the day than during the night, and showed a major shift in vertical distribution. During daytime, higher cod densities were located at greater heights from the bottom and over a greater range of heights than at night (Figure 4).

Habitat preference and *in situ* behavioural observations

During both day and night, cod observed on videotape occurred primarily as solitary individuals or in small groups of two to four. Some larger aggregations of up to 50 individuals were also observed. Cod tended to be less active by night, remaining motionless or circling slowly with no sustained directionality. During the day, cod moved much more, often seeming to travel on some particular heading.

In the daytime, cod were found in all habitats with no significant preference for any bottom type (χ^2=2.1, p=0.351, n=45 fish observed; Figure 5a). At night, the observed distribution across the three substrates differed significantly from that expected (χ^2=26.3, p<0.001, n=72; Figure 5b). More fish preferred areas of high cover, and fewer areas of low cover. During the night, 43.0% (n=72) of cod observed with the video camera were outside the acoustic lee of any rocks, and no cod were estimated to be more than 1 m off the bottom. By day, 83.3% (n=66) of observed fish were outside the acoustic lee, and 12.5% were more than 1 m off bottom.

Comparison of acoustic density estimates to submersible video density index

Four full submersible surveys included both video and acoustic transects with positional information. The three daytime acoustic density estimates made from the submersible (0.003, 0.012, and 0.013 fish m^{-2}) fell within the range of daytime estimates made from the surface (Figure 3). The daytime acoustic density measures were positively associated with the video density index (Figure 6). By contrast, the night-time submersible acoustic transect had a density of nearly zero, while the corresponding video density index was the highest recorded during the study (Figure 6).

Table 2. Mean acoustic estimates (standard error in parentheses) of cod density (fish m^{-2}), by survey date in 1997, transect, and day vs. night. For each date, average densities were calculated separately for day and night from all passes over each transect (n).

Survey date	Transect 1 Day	Transect 2 Day	Transect 1 Night	Transect 2 Night
September 27	0.024 (0.004) n=21	0.016 (0.005) n=15	0.0015 (0.0005) n=8	0.0019 (0.0006) n=7
October 2	0.012 (0.001) n=29	0.009 (0.002) n=15	0.0002 (0.0001) n=8	0.0003 (0.0001) n=10
October 7	0.020 (0.004) n=25	0.011 (0.004) n=14	0.0014 (0.0004) n=20	0.0008 (0.0002) n=11

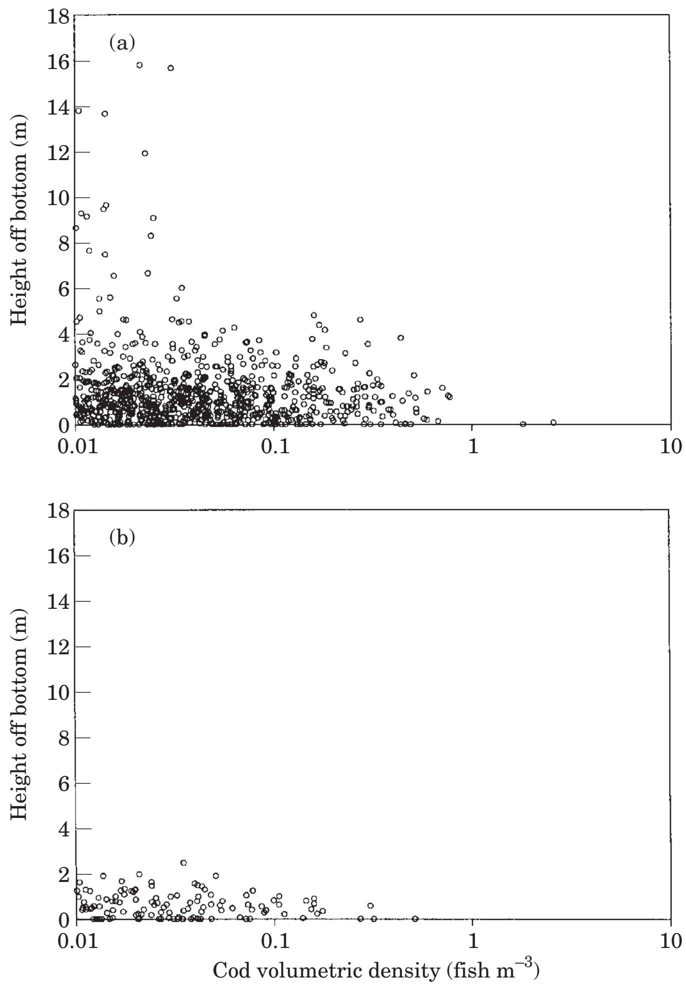

Figure 4. Surface volumetric density estimates of cod (fish m^{-3}) during (a) the day and (b) night, calculated from bins of 1 m depth and 10 m horizontal length, plotted against bin height off the bottom (m) on the y-axis. Note that to make the data set more manageable, only densities exceeding 0.01 fish m^{-3} are plotted. Trends of density with height off bottom for densities less than 0.01 fish m^{-3} are similar to those shown, during both day and night.

Discussion

Impact of cod behaviour on detectability

Our data indicate that behaviourally-mediated variations in detectability caused cod acoustic density estimates to vary by an order of magnitude over the diel cycle, independent of any change in true cod density. Surface acoustic and submersible visual observations indicated that during the day cod moved off the bottom and were not associated with any particular substrate. During daytime, cod were thus detectable to our echosounders and integrated into estimates of density. In contrast, at night fish retired to the bottom and preferred substrates where they were hidden in the acoustic lee of high rock cover. Hence, we conclude that cod behavioural patterns of vertical movement and habitat preferences reduced the detectability of fish to the acoustic survey on a diel basis, generating the observed trend in acoustic densities. Our study provides direct evidence of the effects of behaviour on detectability. Previous studies have provided only indirect evidence by documenting changes in acoustic density estimates, and attributing these changes to the target organism's behaviour (Godø and Wespestad, 1993; Demer and Hewitt, 1995; Michalsen *et al.*, 1996). In the Barents Sea, for example, diurnal and semi-diurnal vertical movements of haddock, redfish, and cod that have been inferred from acoustic data, are thought to have strong impacts on acoustic and bottom-trawl surveys (Aglen *et al.*, 1999).

The study of detectability has been hampered by uncertainties as to whether apparent changes in acoustic density arose from variations in detectability or from

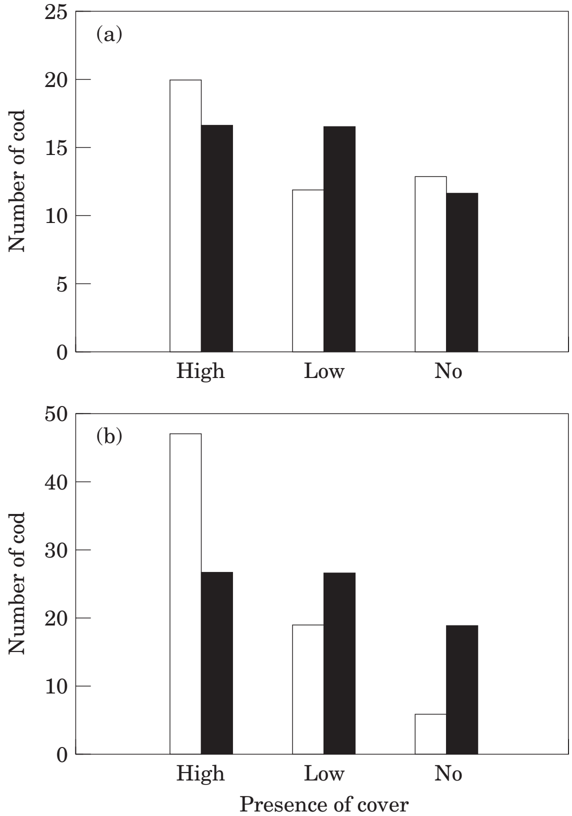

Figure 5. Comparison during (a) the day and (b) night of the observed number of cod in bottom types of high, low, and no cover, to that expected if the fish were randomly distributed relative to the proportional abundance of each bottom type in the study site. In the day, no difference was evident ($\chi^2=2.1$, $p=0.351$, $n=45$ fish observed). At night, the observed and expected numbers in each bottom type differed significantly ($\chi^2=26.3$, $p<0.001$, $n=72$). □, Observed; ■, expected.

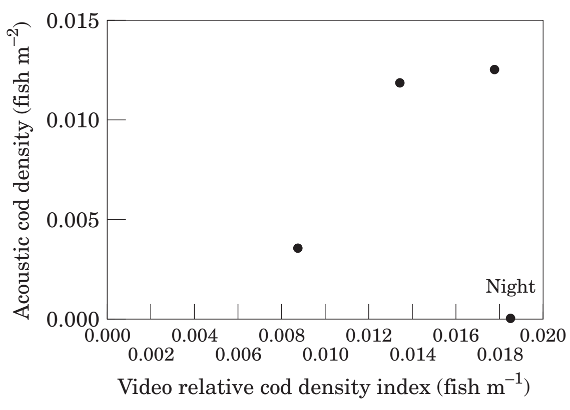

Figure 6. Acoustic density estimates of cod (fish m^{-2}) plotted against corresponding relative density indices (fish m^{-1}) from video censuses. Three submersible surveys were made during the day, and one at night.

horizontal dispersion of fish (Shotton and Bazigos, 1984). In our study, acoustic measures varied by an order of magnitude, yet direct visual observation from the submersible indicated no difference in the number of fish observed by day and by night. The low acoustic density measured at night with the submersible was in fact matched with the highest recorded video density index. Moreover, visual inspection of night-time echograms suggests that fish were present along the acoustic line, but so close to the substrate that their echoes overlapped with those of the bottom and were excluded from echo-integration. Finally, our surface acoustic data demonstrate a vertical shift in density, with higher volumetric density estimates during the day at greater heights off the bottom than at night. All of these lines of evidence suggest a vertical rather than horizontal movement of cod, and that true density did not differ between day and night.

General applicability

A consistent pattern of high acoustic densities during the day and low at night was observed at our study site in two successive years. Nevertheless, it remained uncertain how typical this result was of other regions and times of year. In the spring of 1998, an inshore and offshore acoustic cod survey was conducted in the same NAFO subdivision in which we carried out our study (3Ps). This survey included a transect which was run east–west across our study site during the day, and which showed a mean cod density of 0.214 fish m^{-2} (s.d.=0.130; n=7 passes). In comparison, three night-time passes of the same transect gave a mean estimate of 0.004 fish m^{-2} (s.d.=0.003). A day–night comparison of density estimates from an offshore transect of this survey (Figure 1) indicated a mean daytime density of 0.054 fish m^{-2} (n=2 passes) and <0.001 fish m^{-2} at night (one pass). Furthermore, bottom-trawl catchability in 3Ps has been shown to be higher for cod during the night than during the day (Casey and Myers, 1998), which is consistent with our acoustic results because trawl catchability increases with proximity of cod to the bottom (Michalsen *et al.*, 1996). An upwards movement of cod from the bottom during the daytime may therefore be typical of this stock.

In contrast to our results, the general understanding of the vertical migratory behaviour of Atlantic cod is that fish move upwards in the water column at night and return to near bottom during the day. Such behaviour has been observed acoustically or inferred from variation in trawl catches on the Nova Scotian fishing banks (Beamish, 1966), in the Gulf of St Lawrence (Clay and Castonguay, 1996), in northern Newfoundland waters (Rose and Porter, 1996), as well as in the Northeast Atlantic (Engås and Soldal, 1996). However, variation in and deviations from this general pattern have also been reported (e.g. Rose *et al*., 1995; Casey and Myers, 1998). It should be noted that the scales of the vertical movements detected in earlier acoustic studies are typically much greater (tens of metres) than the approximately 1–5 m movements observed in our study. This plasticity of cod vertical migratory behaviour underscores the importance of behavioural variability as a key and variable source of bias in acoustic and trawl surveys, and thereby the importance of understanding the behaviour of fishes subject to such surveys.

Validation of acoustic density estimates

Our submersible visual indices of density are thought to be relatively free from bias, and therefore present a reasonable basis for the validation of acoustic density estimates. Bias in visual census arises predominantly from avoidance reactions and an inability to adequately enumerate cryptic species (Dolloff *et al*., 1996). Within the limits of our field of view, cod seldom avoided the submersible. Studies of juvenile cod in Placentia Bay also using the SDL-1 submersible similarly observed little avoidance behaviour (Gregory and Anderson, 1997). Cod coloration relative to substrate appearance, and the large size of cod observed, make it unlikely that any individuals were missed due to crypsis.

A full assessment and calibration of daytime acoustic densities cannot be attempted because our submersible video index data are too few and not absolute. However, bias in daytime acoustic densities might be indicated by non-equivalent increments in acoustic density and the video index, irrespective of scaling. Our daytime acoustic density estimates increase with the video index in generally equivalent increments. Furthermore, the ratio of video indices to acoustic density estimates was very close to 2:1 (Figure 6). Though unmeasured, the width of the video camera's field of view was judged to be approximately 2 m. As such, if submersible video and acoustic density estimates are compared both in units of fish m^{-2}, a ratio of nearly 1:1 is evident. These lines of evidence are consistent with the notion of no bias in the acoustic estimates. We acknowledge that additional data would be required to fully support this conclusion, and that we can not rule out the possibility that systematic bias might exist in either or both measures despite the fact that they increase in proportion to one another. Although previous studies have attempted to combine submersible with acoustic survey estimates (Zaferman, 1981; Starr *et al*., 1996), the present study represents to the best of our knowledge the first attempt at validating acoustic techniques through the use of submersible visual census.

Acoustic abundance estimates

Our results suggest that behaviourally-mediated, systematic variation in detectability can be the major source of bias in acoustic density estimates. In our study, mean detectability was over an order of magnitude (10 dB) lower at night than during the day. It is unlikely that any other source of error would be of that magnitude, be it from target strength, calibration, or species identification. Accordingly, we suggest that a detectability coefficient (D) should be incorporated into the scaling of acoustic backscatter to abundance, following:

$$\text{Abundance} = [(A \times Sa)/\sigma]/D(t) \tag{1}$$

where A = survey area; Sa = mean acoustic backscatter per unit cross-sectional area; σ = mean acoustic cross section of one fish; and D(t) = detectability coefficient as a function of time.

Detectability should be defined as a function of time of day (and thereby of diel behavioural patterns), or of other parameters which affect detectability. In the absence of reliable information explaining systematic variation in detectability, a mean survey detectability coefficient could be employed. Acoustic surveys of Antarctic krill biomass have employed such a time-dependent detectability function to correct for the diel migration of the target species above the acoustic observation window (Demer and Hewitt, 1995). Analogous catchability coefficients have also been suggested for trawl survey analyses (Godø, 1994).

The central problem in estimating the detectability coefficient is that there is no simple means of assessing true fish density. Comparisons of density estimates from acoustic to other fishery surveys are problematic because the latter suffer from their own biases. Visual censuses from submersibles might provide the least biased estimates possible of true density, and hence of detectability. Unfortunately, submersibles are not commonly available for acoustic surveys. In our case, a lack of sufficient submersible time precluded an absolute estimate of detectability.

Although the quantification of absolute detectability is at present very difficult, every effort nonetheless should be made to assess detectability on a relative scale. Models of relative detectability may help constrain bias arising from variations within and between surveys. Such models can be based on experimental measurements of cod density made over a range of factors that may influence detectability. For example, a model could be fit to experimental density estimates plotted by time of day, where the peak of the model curve is defined as the maximum relative detectability, and is set to unity (Figure 7). Subsequent acoustic densities would be scaled by a measure of detectability which would be a function of the time of day at which the estimate was made. In our experiment, night-time acoustic density estimates were near zero. For such data, a binary step-function of detectability is suitable, where daytime detectability is defined as one and night-time as

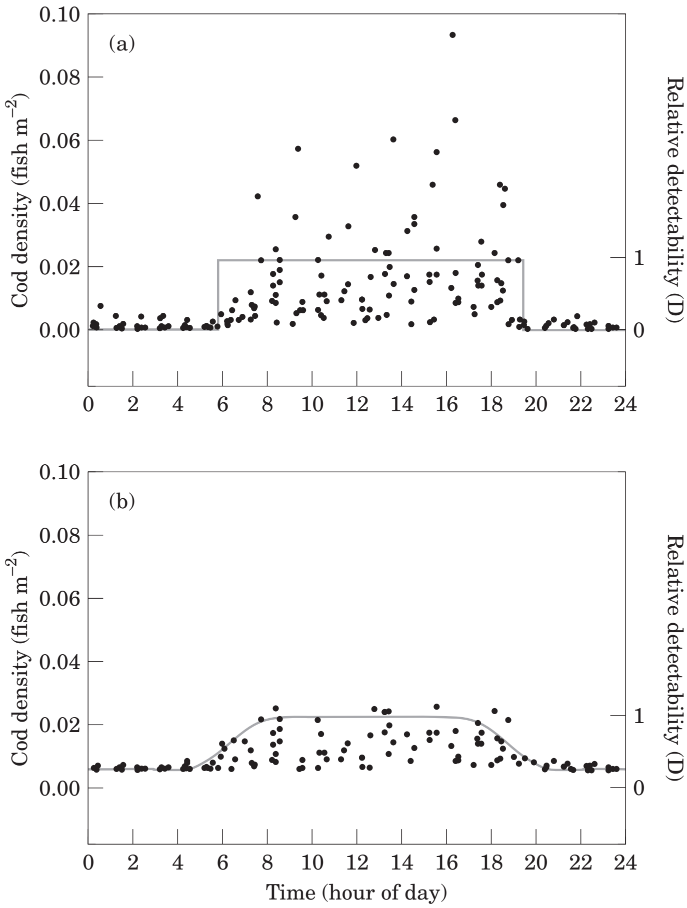

Figure 7. (a) Surface acoustic density estimates from all 1997 days and transects, plotted against the time of day at which the estimate was made (NST). A binary step-function of relative detectability is shown in gray, with detectability (D) indicated on the right-hand y-axis. Relative detectability is set to one by day and zero at night. (b) Hypothetical acoustic density data in which density changes on a diel basis more gradually, and never decreases to zero. A relative detectability curve has been fit to the data and is plotted by the right-hand y-axis. The curve's peak is defined as the maximum relative detectability and is set to unity.

approaching zero (Figure 7a). In our study area, acoustic surveys therefore should be performed during daylight hours only, and detectability should be assumed to be unity at this time. In other survey circumstances, however, acoustic densities may not decrease to zero at any time, and a curve might be fit to density data to describe detectability (e.g. Figure 7b). In the hypothetical data of Figure 7b, low night-time densities could be corrected by a detectability coefficient extracted from the model curve to remove bias, and 24-h surveys could be undertaken.

A related method was proposed by Godø and Wespestad (1993) to accommodate variations in detectability (their "availability") between surveys resulting from interannual changes in stock size and age composition, local density, and vertical and areal distributional dynamics. These authors suggested that all factors that potentially affect detectability be monitored during the actual survey, and incorporated into survey analysis. This approach has the advantage of using data from the survey itself. The use of survey data to correct for variation in detectability has been successfully employed in the case of Antarctic krill diel migrations into the surface blindzone (Demer and Hewitt, 1995). However, the use of survey data does not allow for the separation of the effects of covarying factors which is permitted by the repeated experimental transect approach we advocate. A *post hoc* non-experimental examination of detectability also may result in inefficient use of survey effort that might be expended at times when detectability later proved to have been below working limits.

In conclusion, detectability may be a major source of bias in acoustic surveys for semi-demersal fish. Patterns of variation in detectability may be complex as a result of the plasticity of fish behaviour. It is of note that analogous bias exists in trawl surveys. Incorporation of a relative and time-dependent detectability coefficient into the calculation of acoustic abundance estimates would reduce bias arising from systematic variation in detectability, and thereby enhance the reliability of acoustic estimates within and between surveys. Even then, acoustic estimates must be explicitly recognized as being relative indices, unless survey detectability can be quantified absolutely or shown to approach unity.

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References

Aglen, A., Engås, A., Huse, I., Michalsen, K., and Stensholt, B. K. 1999. How vertical distribution may affect survey results. ICES Journal of Marine Science, 56: 345–360 (this issue).

Beamish, F. W. H. 1966. Vertical migration by demersal fish in the Northwest Atlantic. Journal of the Fisheries Research Board of Canada, 23: 109–139.

Brock, R. E. 1982. A critique of the visual census method for assessing coral reef fish populations. Bulletin of Marine Science, 32: 269–276.

Casey, J. M., and Myers, R. A. 1998. Diel variation in trawl catchability: is it as clear as day and night? Canadian Journal of Fisheries and Aquatic Sciences, 55: 2329–2340.

Clay, A., and Castonguay, M. 1996. In situ target strengths of Atlantic cod (*Gadus morhua*) and Atlantic mackerel (*Scomber scombrus*) in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, 53: 87–98.

Demer, D. A., and Hewitt, R. P. 1995. Bias in acoustic biomass estimates of *Euphasia superba* due to diel vertical migration. Deep-Sea Research I, 42: 455–475.

Dolloff, A., Kershner, J., and Thurow, R. 1996. Underwater observation. *In* Fisheries Techniques, 2nd edition, pp. 533–554. Ed. by B. R. Murphy and D. W. Willis. American Fisheries Society, Bethesda, Maryland. 732 pp.

Engås, A., and Soldal, A. V. 1996. Diurnal variations in bottom trawl catch rates of cod and haddock and their influence on abundance indices. ICES Journal of Marine Science, 49: 89–95.

Foote, K. G., Knudsen, H. P., Vestnes, G., MacLennan, D. N., and Simmonds, E. J. 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Cooperative Research Report, 144, 57 pp.

Fréon, P., Gerlotto, F., and Misund, O. A. 1993a. Consequences of fish behaviour for stock assessment. ICES Marine Science Symposium, 196: 190–195.

Fréon, P., Soria, M., Mullon, C., and Gerlotto, F. 1993b. Diurnal variation in fish density estimate during acoustic surveys in relation to spatial distribution and avoidance reaction. Aquatic Living Resources, 6: 221–234.

Godø, O. R. 1994. Factors affecting the reliability of groundfish abundance estimates from bottom trawl surveys. *In* Marine fish behaviour in capture and abundance estimation, pp. 166–199. Ed. by A. Fernö and S. Olsen. Fishing News Books, London. 221 pp.

Godø, O. R., and Wespestad, V. G. 1993. Monitoring changes in abundance of gadoids with varying availability to trawl and acoustic surveys. ICES Journal of Marine Science, 50: 39–51.

Gregory, R. S., and Anderson, J. T. 1997. Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. Marine Ecology Progress Series, 146: 9–20.

LeFeuvre, P., Rose, G. A., Gosine, R., Hale, R., Pearson, W., and Khan, R. 1999. Acoustic species identification in the Northwest Atlantic using digital image processing. Fisheries Research (in press).

MacLennan, D. N., and Simmonds, E. J. 1992. Fisheries Acoustics. Chapman and Hall, London. 325 pp.

Michalsen, K., Godø, O. R., and Fernö, A. 1996. Diel variation in the catchability of gadoids and its influence on the reliability of abundance indices. ICES Journal of Marine Science, 53: 389–395.

Mitson, R. B. 1983. Acoustic detection and estimation of fish near the sea-bed and surface. FAO Fisheries Report, 300: 27–34.

Mitson, R. B. 1995. Underwater noise of research vessels: review and recommendations. ICES Cooperative Research Report, 209, 61 pp.

Ona, E. 1995. Report of the study group on target strength methodology. ICES CM 1995/B:3, 120 pp.

Ona, E., and Mitson, R. B. 1996. Acoustic sampling and signal processing near the seabed: the deadzone revisited. ICES Journal of Marine Science, 53: 677–690.

Rose, G. A. 1992. A review of problems and new directions in the application of fisheries acoustics on the Canadian East Coast. Fisheries Research, 14: 105–128.

Rose, G. A., deYoung, B., and Colbourne, E. B. 1995. Cod (*Gadus morhua* L.) migration speeds and transport relative to currents on the north-east Newfoundland Shelf. ICES Journal of Marine Science, 52: 903–913.

Rose, G. A., and Porter, D. R. 1996. Target-strength studies on Atlantic cod (*Gadus morhua*) in Newfoundland waters. ICES Journal of Marine Science, 53: 259–265.

Scalabrin, C., Diner, N., Weill, A., Hillion, A., and Mouchot, M.-C. 1996. Narrowband acoustic identification of monospecific fish shoals. ICES Journal of Marine Science, 53: 181–188.

Shotton, R., and Bazigos, G. P. 1984. Techniques and considerations in the design of acoustic surveys. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 184: 34–57.

Starr, R. M., Fox, D. S., Hixon, M. A., Tissot, B. N., Johnson, G. E., and Barss, W. H. 1996. Comparison of submersible-survey and hydroacoustic-survey estimates of fish density on a rocky bank. Fishery Bulletin, 9: 113–123.

Thompson, S. K., and Seber, G. A. 1996. Adaptive Sampling. John Wiley and Sons, Inc, Toronto. 265 pp.

Zaferman, M. L. 1981. Methods of instrumental assessment of the bottom fish abundance. *In* Meeting on hydroacoustical methods for the estimation of marine fish populations, 25–29 June 1979. II: Contributed papers, discussion, and comments, pp. 895–906. Ed. by J. B. Suomala. The Charles Stark Draper Laboratory, Inc., Cambridge, Mass., USA. 964 pp.