Diurnal variation in acoustic densities: why do we see less in the dark?

Vidar Hjellvik, Olav Rune Godø, and Dag Tjøstheim

Abstract: Diurnal fluctuations in total integrated echo abundance and in vertical density profiles were examined using data from the Norwegian combined acoustic and bottom-trawl survey for demersal fish during winter in the Barents Sea. The total echo abundance was about 40%–50% higher at day than at night. An unknown amount of fish was lost close to the seabed in the acoustic dead zone, but the systematic changes in the near-bottom vertical density profiles did not indicate that migration in and out of the dead zone was the major reason for the large diurnal differences in echo abundance. A more plausible explanation could be that diurnal changes in fish behaviour affect the mean acoustic target strength. Based on the present study, we recommend that the time series of acoustic surveys should be re-analysed, taking the diurnal bias into account. Any comparison of the fish densities indicated by trawl and acoustic surveys will suffer if this bias is not corrected. We believe that model development utilizing this type of information is crucial for future ecosystem-based monitoring.

Résumé : Nous avons examiné les fluctuations journalières des abondances totales intégrées basées sur l'écho et des profils verticaux de densité; nous avons utilisé une combinaison de données norvégiennes provenant d'inventaires acoustiques et d'inventaires au chalut de fond de poissons démersaux durant l'hiver dans la mer de Barents. L'abondance totale déterminée à l'écho est d'environ 40–50 % plus élevée le jour que la nuit. Une quantité inconnue de poissons est perdue près du fond dans la zone acoustique morte; cependant, les changements systématiques qui se produisent dans les profils verticaux de densité près du fond n'indiquent pas que l'immigration ou l'émigration dans la zone morte est la raison majeure des importantes différences journalières dans les abondances déterminées à l'écho. Une explication plus plausible est que les changements diurnes de comportement des poissons affecte la force moyenne des cibles acoustiques. Sur la base de notre étude, nous recommandons une nouvelle analyse des séries chronologiques des inventaires acoustiques qui tienne compte des sources d'erreur journalières. Toute comparaison entre les densités de poissons déterminées par les inventaires au chalut et celles données par les inventaires acoustiques sera affectée si cette erreur n'est pas corrigée. Nous croyons que la mise au point de modèles qui utilisent ce genre d'information est essentielle pour la surveillance future à l'échelle de l'écosystème.

[Traduit par la Rédaction]

Introduction

Light is one of the strongest physical stimuli in biology, affecting both the long-term (seasonal) and short-term (diurnal) behavioural characteristics of fish. Diurnal variations in the results of bottom-trawl surveys (Casey and Myers 1998; Korsbrekke and Nakken 1999; Hjellvik et al. 2002) and acoustic surveys (Engås and Godø 1986; Michalsen et al. 1996; Stensholt et al. 2002) are well known. The causes of these variations and the relationship between them, however, are poorly understood and hence difficult to treat in survey assessments. In particular, poor knowledge of the geographic distribution and behaviour of the targeted stocks is often considered a limitation on the applicability of the acoustic survey method. This is unfortunate, since acoustic surveying is now a standard tool for mapping and assessing commer-cially exploited fish stocks (MacLennan and Simmonds 1992; Fernö and Olsen 1994). The results are often crucial for the quality of final scientific advice aimed at sustainable management. Thus, any bias reduction in survey assessments is of great importance.

The acoustic dead zones are often considered to be a primary source of bias in acoustic surveys. Fish close to the surface are normally not detectable because the downward-looking transducers on the survey vessel are located at a depth of several metres, and recordings in the near field are unreliable (e.g., MacLennan and Simmonds 1992; Aglen 1994; Demer and Hewitt 1995). Similarly, fish close to the seabed may be lost because of the inaccessibility of targets found in the bottom dead zone. The problem of the bottom dead zone has been widely discussed in the literature (Johannesson and Mitson 1983; Ona and Mitson 1996). It

V. Hjellvik[1] and O.R. Godø. Institute of Marine Research, P.O. Box 1870, Nordnes, N-5817 Bergen, Norway.
D. Tjøstheim. Department of Mathematics, University of Bergen, Johs. Brunsgt 12, N-5008 Bergen, Norway.

[1]Corresponding author (e-mail: vidarh@imr.no).

Fig. 1. Cruise tracks for 2002. Trawl stations are indicated by circles. Night transects (1800–0600) are drawn in black, day transects (0900–1500) are in red, dawn (0600–0900) and dusk (1500–1800) transects are in green. Times are local.
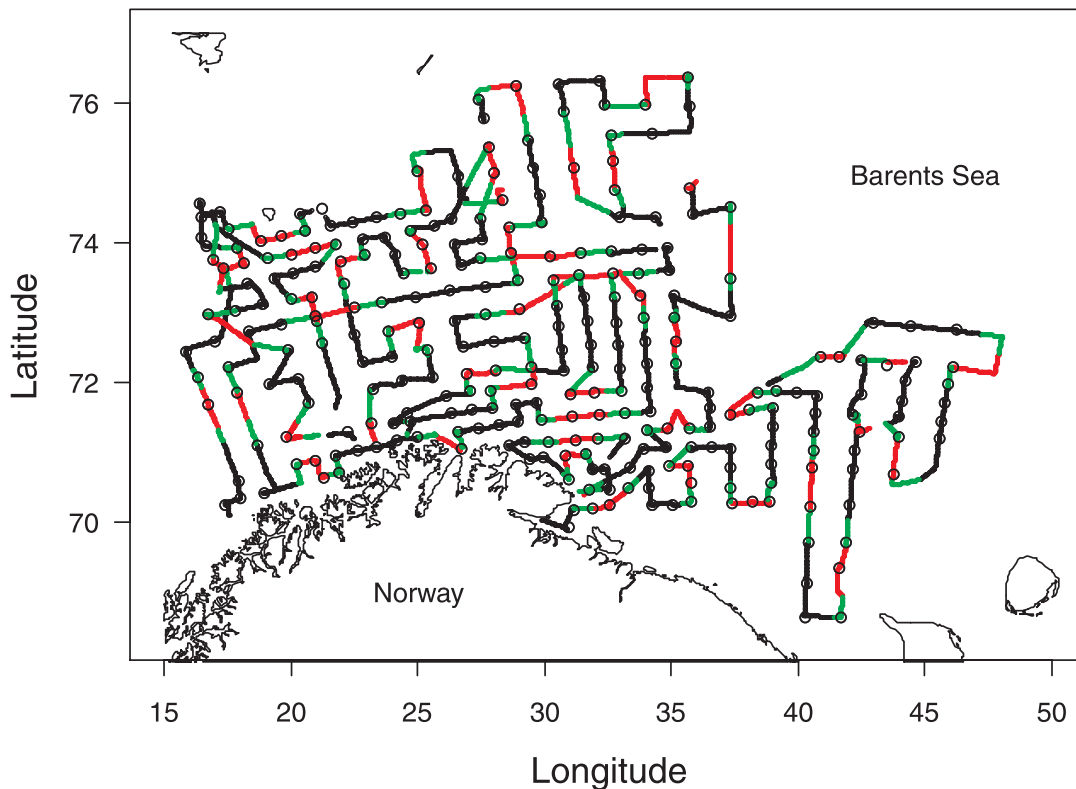
has often been suggested that unexplained variations in the ratio of trawl catches to acoustic recordings arise because an unknown amount of fish is supposed to be hidden in the bottom dead zone (Aglen 1996; Ona and Mitson 1996) or at the surface (Knudsen and Sægrov 2002). Similarly, systematic, large, diurnal variations in the total integrated echo abundance have been ascribed to diurnal migration in and out of the dead zone (e.g., Engås and Godø 1986; Aglen et al. 1999; Lawson and Rose 1999). This kind of migration is, however, not the only possible candidate for explaining diurnal variation in acoustic backscattering. Vertical fish movements higher in the water column may also affect the echo abundance through swim bladder compression and tilt-angle changes (Aglen 1994; Godø and Michalsen 2000; McQuinn and Winger 2003). Thus, assuming the total biomass is constant by day and by night, diurnal variation can be explained by at least three hypotheses: (*i*) fish hide in the bottom or surface dead zones at night; (*ii*) fish target strength (TS) varies because of diurnal variation in the tilt-angle distribution; and (*iii*) fish TS changes because of pressure-related swim bladder changes during vertical migration.

In this study, we have taken a fresh look at diurnal variation in acoustic abundance data, based on a careful and detailed statistical analysis of a large set of combined trawl and acoustic measurements. We have evaluated our results taking into account the above three hypotheses and have tried to determine their relative importance. The analysis of total integrated echo abundance is supported by a systematic investigation of diurnal variation in the acoustic vertical profiles, including a rather detailed study of the layers just

above the bottom zone. The main emphasis is on demersal fish, although pelagic fish and plankton are also examined, in so far as their density distributions are relevant to the central argument of this paper. Filtering out large acoustic values that arrive at random time points is important for our analysis. Compared with earlier investigations, it allows us to isolate and present diurnal variation in a more transparent manner, and it makes it easier to discern systematic patterns. Finally, we note that many earlier studies have been qualitative in character, and the results have thus suffered from the lack of any statistical test of significance. In this study, a randomization test is introduced to confirm the statistical significance of the main diurnal changes and also that of any effects observed during the dawn/dusk transition periods.

Materials and methods

The data

Norwegian research vessels undertake a combined acoustic and bottom-trawl survey for demersal fish in the Barents Sea during the winter of each year (Jakobsen et al. 1997; Fig. 1). We have analysed acoustic results from surveys in the period 1997–2002. The data were collected using a 38 kHz SIMRAD EK 500 echo sounder (SIMRAD, Horten, Norway) and interpreted using the Bergen Echo Integrator (BEI) (Foote et al. 1991). The data were recorded in a database with a horizontal resolution of 1 nautical mile (1 n.mi. = 1.852 km) and a vertical resolution of 10 m, referenced to the surface. In addition, near-bottom data were available in 10 bottom-referenced layers each 1 m thick. The bottom

Fig. 2. Bottom layers in a typical case (*a*) and an atypical case (*b*). In (*a*), the bottom offset is 0.3 m; in (*b*), it is 2.2 m. The solid line indicates the corrected bottom. The shaded areas show the first and tenth bottom layers in (*a*) and the third and tenth bottom layers in (*b*). The spikes are drawn manually to avoid bottom signals.
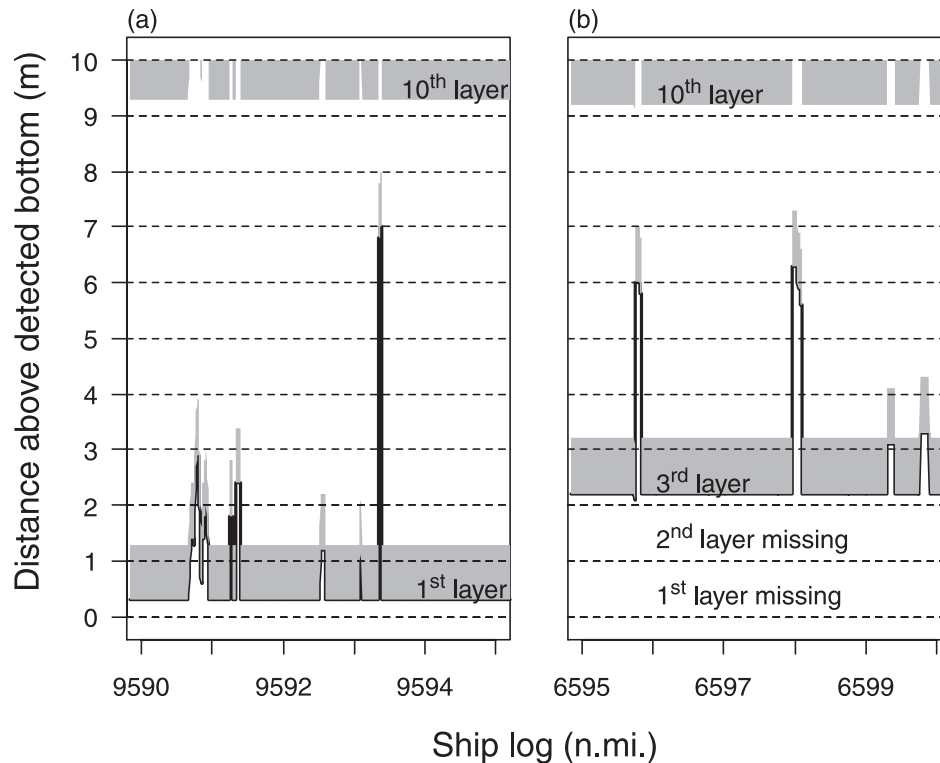
depth is variable, and the vertical distribution of physoclist fish is restricted by pressure more than by depth because of their swim bladder characteristics. Therefore, to obtain a uniform depth scale, we chose to transform the original depth-referenced layers into 30 equally thick layers for each sample, covering the surface–seabed column. For instance, if the bottom depth were 300 m or 600 m, the deepest layer would contain data from the bottom to 10 m or 20 m, respectively. The ten 1-m bottom-referenced layers were used with no such transformation in a separate analysis.

Detailed information on the near-bottom distribution is important for evaluation of the dead zone problem. To avoid interference from the bottom echo, we do not normally end the integration of fish density exactly on the detected bottom (i.e., the depth indicated by the EK500 or BI500). This depth is reduced by an offset, typically 0.5 m, giving a "corrected bottom" at which the integration ends (for details, see Ona and Mitson 1996). However, under good conditions the offset may be less than 0.5 m, and under bad conditions it may be more. The dead zone height in metres for a transducer with beam width 14.2° and pulse duration 1 ms is h_d = bottom offset + 0.375 + 0.00238d, where d is the bottom depth (Ona and Mitson 1996).

Occasionally, the bottom offset is adjusted manually by inspection of the echogram to avoid any automatic bottom detections that are obviously wrong. In the data from BEI, the first bottom-referenced 1-m layer contains data from the corrected bottom to 1 m further up. Sometimes the corrected bottom is more than 1 m above the detected bottom. We have redefined the layers so that the number i bottom-referenced 1-m layer always contains data from $i − 1 + a$ to $i + a$ metres above the detected bottom (except for manually excluded bottom spikes), where $0 \leq a < 1$ and $1 \leq i \leq 9$ (in Fig. 2*a*, $a = 0.3$ and in Fig. 2*b*, $a = 0.2$). If the bottom offset is more than 1 m in a given sample, the first layer is missing (Fig. 2*b*). Unfortunately, this applies to as much as 24% of the samples, and it typically reflects rough ground or rough weather conditions. But importantly, these samples are evenly distributed over day and night. The second layer is missing in only 2% of the cases. The tenth layer is $1 − a$ metres thick (0.7 m in Fig. 2*a* and 0.8 m in Fig. 2*b*). On average it will be 0.5 m, meaning that the echo abundance is reduced by 50% as compared with a full 1-m layer.

Classification

On a daily basis during the surveys, the backscattered acoustic energy was scrutinized mile-by-mile and allocated to species or groups of species using the BEI (Foote et al. 1991). The species and group classifications varied slightly over the years and among vessels (Table 1). The species allocation was done by experienced scientists on the vessel, using visual characteristics while scrutinizing the echograms, as well as information from catches taken at the nearest trawl stations. Typically, 200–300 catches were taken in each survey. Clearly, the classification is not exact. Several sources of error may be involved, for example, the species distribution of the trawl catches does not necessarily reflect that in the whole water column, and vertical migration of fish between day and night may lead to diurnal patterns in the classification error. Objects with target strength below a

2240

Can. J. Fish. Aquat. Sci. Vol. 61, 2004

Table 1. The species and categories to which acoustic data were allocated on the various vessels the various years.

Year	Vessel	Cod Dem	Had Dem	Red Dem	Sai Dem	Pol Dem	Blw Dem	Oth Dem	Cap Pel	Her Pel	Pla Pla
2002	GS	×	×	×	×	×	×	—	×	×	—
2002	JH	×	×	×	×	×	×	×	×	×	×
2001	GS	×	×	×	×	×	—	×	×	×	×
2001	JH	×	×	×	×	×	—	×	×	×	×
2000	GS	×	×	×	×	—	—	×	×	×	×
2000	JH	×	×	×	—	×	—	×	×	×	×
2000	VR	×	×	×	×	×	—	×	×	—	×
1999	GS	×	×	×	×	×	—	×	×	×	×
1999	JH	×	×	×	×	×	—	×	×	×	×
1998	GS	×	×	×	×	×	×	×	×	×	×
1998	JH	×	×	×	×	×	—	×	×	×	×
1998	JM	×	×	×	—	×	—	×	×	×	×
1997	GS	×	×	×	×	—	—	×	×	×	×
1997	JH	×	×	×	×	×	—	×	×	×	×
1997	JM	×	×	×	×	×	—	×	×	×	×
Abundance 100%		650	500	218	56	1545	305	868	3117	383	1120
Abundance 99%		572	394	172	12	309	245	627	843	95	882
% zero samples		7	34	43	93	84	65	66	67	83	4
% at depth >300 m		44	42	62	24	33	74	57	39	30	41

Note: The top row shows categories from left to right as follows: Cod (*Gadus morhua*), haddock (Had; *Melanogrammus aeglefinus*), redfish (Red; *Sebastes marinus*), saithe (Sai; *Pollachius virens*), polar cod (Pol; *Boreogadus saida*), blue whiting (Blw; *Micromesistius poutassou*), others (Oth), capelin (Cap; *Mallotus villosus*), herring (Her; *Clupea harengus*), plankton (Pla). The second row shows the group to which each category belongs: demersal (Dem), pelagic (Pel), and plankton (Pla). The vessels are G.O. Sars (GS), Johan Hjort (JH), and Varegg (VR). The third and fourth rows from the bottom give for each species average echo abundance multiplied by number of samples (in 1000 $m^2 \cdot n.mi.^{-2}$) when (*i*) all samples are included (Abundance 100%) and (*ii*) samples larger than the 99% quantile are excluded (Abundance 99%). The second row from the bottom gives the percentage of zero samples, and the bottom row gives the percentage of nonzero samples that is taken at depths larger than 300 m.

given threshold are generally allocated to the plankton group, which thus may also contain other small organisms (e.g., fish larvae). Small fish of the target species may also be wrongly included in the "other" group.

Large values

The distribution of marine survey data is typically skewed with a few very high values. Large values may dominate distribution statistics and thus obscure any diurnal patterns in the observations. This problem arises with the present data. A log transformation would yield approximately normally distributed echo abundance values, but when analysing vertical density profiles, it is not clear how the log transformation should be done nor how the results should be interpreted. Instead, to discern the general diurnal pattern in the total echo abundance and in the vertical density profiles, we have eliminated a small percentage of the samples with the highest echo abundance values.

Descriptive indicators

To examine the diurnal variation, we calculated the vertical density profiles and the total integrated echo for each 1-h interval. That is, we divided the samples into 24 subgroups, according to the local time t when the samples were taken. Local time was calculated as $t = t_{UTC} + longitude/15 + \Delta$, where UTC is coordinated universal time, and $\Delta = \{-0.4083 \sin[0.0172 (day - 80)] - 1.7958 \cos[0.0172 (day - 80)] + 2.4875 \sin[0.0344 (day - 80)]\}/15$, with $1 \leq day \leq 365$ being the day of the year is an approximation to the equation of

time (Smart 1977, p. 150). If sample i was taken at time t_i, it was allocated to group j if $j - 1 \leq t_i < j, j = 1, ..., 24$. For each subgroup, we calculated the average echo abundance value for each layer and analysed changes over the day in both the total echo abundance and the density profile (i.e., the vertical distribution of acoustic energy). The density profile was described by its 25%, 50%, 75%, and 90% quantiles and the mean.

Randomization

To test whether changes in total echo abundance and in the quantiles of the vertical profile were statistically significant, we performed tests by randomizing the time when the samples were taken. The simplest way to do this would be to perform the following steps m times:

(*i*) allocate a random time, t_i^* where $0 \leq t_i^* < 24$, to each sample y_i

(*ii*) allocate the samples into 24 groups as described above, using the new times t_i^* instead of the observed times t_i

(*iii*) calculate the quantiles and the mean for the vertical density profiles and the total echo abundance for each of the 24 groups

This would lead to m observations of each test statistic under the null hypothesis of time independence (i.e., no diurnal fluctuations). For each time group, p values for the observed quantiles, means, and total echo abundance and confidence bands under the null hypothesis would be calculated. However, the samples are strongly correlated in time (autocorrelated), and this is not taken into account in the

procedure outlined above, so the confidence intervals would be too narrow. An adjustment of step (i) is needed to take care of the statistical dependence. Instead of allocating a random time to each sample, we allocated a random integer time displacement for each day. For example, if the samples at day $d(i)$ were taken at $t = 0.35, …, 14.53, 15.15, …, 23.78$, and a random displacement of 9 h were drawn for this day, the new times for day $d(i)$ would be $t^* = 9.35, …, 23.53, 0.15, …, 8.78$. Thus, the local correlation structure is preserved, whereas, as an approximation, samples taken on different days were taken to be independent. This intuitive and simple (but somewhat ad hoc) procedure is clearly related to block bootstrapping (Carlstein et al. 1998). Alternatively, a bootstrap based on an autoregressive approximation could have been used.

To better detect differences among day, night, and dawn/dusk, we also grouped the data in these categories, with night defined as 0000–0600 and 1800–2400, dawn/dusk as 0600–0900 and 1500–1800, respectively, and day as 0900–1500. The standard error of, for example, the mean is much smaller for the night data than for a 1-h interval, since the night category contains 12 times as much data, and hence the confidence interval is correspondingly narrower.

Test statistics

In the above scheme, each time period of 1 hour can be tested separately to examine whether the mean, the quantiles, or the total echo abundance for the period differs from the overall average. Owing to random fluctuations, if the null hypothesis of no diurnal variation were true, one would expect, for example, the median to fall outside the 95% confidence interval in 1 of 20 periods on average. However, it is easy to construct global test statistics. We followed the ideas in Hjellvik et al. (2001, 2002) to construct two test statistics, one of which takes a possible symmetric pattern into account. In both cases, we test several null hypotheses: H_0^T, there is no diurnal pattern in the total echo abundance, and H_0^q, there is no diurnal pattern in the quantile q of the vertical density profile. In the general case, the alternative hypotheses are H_1^T and H_1^q: there is a diurnal pattern in the total echo abundance or in the quantile q, respectively. A test statistic for these tests is

$$(1) \qquad \hat{L}_1 = \sum_{j=1}^{24} (\hat{f}_j - \hat{f})$$

where $\hat{f}_j$ is the value of some quantity (e.g., total echo abundance) in time period j, $j = 1, …, 24$, and $\hat{f} = 24^{-1} \sum_{j=1}^{24} \hat{f}_j$. If H_1 is replaced by H_2: there is a diurnal pattern that is symmetric around noon, the following test statistic is appropriate:

$$(2) \qquad \hat{L}_2 = \sum_{j=1}^{12} [(\hat{f}_j - \hat{f}) + (\hat{f}_{25-j} - \hat{f})]^2$$

$$= \sum_{j=1}^{12} (\hat{f}_j + \hat{f}_{25-j} - 2\hat{f})^2$$

If H_2 is true, $\hat{L}_2$ has a higher power for revealing deviations from H_0 than $\hat{L}_1$. This is because under H_0, they have similar distributions, with $\hat{L}_2$ tending to be slightly smaller than $\hat{L}_1$, whereas under H_2, if $\hat{f}_j \approx \hat{f}_{25-j}$, then $\hat{L}_2 \approx 2\hat{L}_1$. The null distributions of $\hat{L}_1$ and $\hat{L}_2$ are estimated from the m randomized samples $\hat{L}_{i,1}^*$ and $\hat{L}_{i,2}^*$, $i = 1, …, m$, and empirical p values of the original observations $\hat{L}_1$ and $\hat{L}_2$ are calculated by relating them to the simulated null distributions.

Results

The impact of large values

The nautical area scattering coefficient (NASC) for the data ranges from 0 to over 70 000 $m^2 \cdot n.mi.^{-2}$ (square metres per square nautical mile). The amplitude distribution is rather skewed, with a very high proportion of the total echo abundance deriving from relatively few samples (Table 2). For example, for the demersal category, 13% of the total echo abundance of the demersal category comes from 39 (about 0.1%) of the samples. For the pelagic species, more than 51% of the total echo abundance is from less than 0.5% of the samples. Although a diurnal pattern is seen for the quantiles of the density profiles (Fig. 3a), the picture is unclear, mainly because of some large concentrations of pelagic fish encountered around midnight and in the periods 0800–0900 and 1800–1900. There is also a large concentration near the bottom between 1400 and 1600. In particular, for the total echo abundance values in the top part of the figure, no clear pattern emerges because of the unpredictable timing of large echo abundance values. If a more limited comparison of the total night versus total day echo abundance were attempted, based on one survey for instance, the results would again be subject to a few occurrences of extreme concentrations of fish. As the timing of these will in general vary from one year to another, no stable pattern can be expected.

In fact, all the samples with large echo abundance values in the time interval 2300–0200 were recorded by one vessel during 3 successive days (Fig. 4). If these samples were removed, the high pelagic concentrations in the time intervals 2300–2400, 0000–0100, and 0100–0200 would disappear (Fig. 3a). This illustrates how sensitive the analysis is to large values. When the 2% of samples that have the largest values are removed (Fig. 3b), a very smooth and clear pattern emerges. The 774 samples thus eliminated were evenly distributed between day and night, for both the number of samples and the echo abundance values (Table 3). We consider this filtering of the data to be absolutely essential for a meaningful interpretation of the results.

The diurnal pattern

The general diurnal pattern of the total echo abundance is clear (Fig. 3b): the total daytime echo abundance value is about 40% higher than the total nighttime value; the fish are generally more concentrated towards the bottom in daytime; there appears to be a dawn/dusk effect previously unnoticed in the literature, it seems, when the fish are highest in the water column; and the percentage in the bottom segment is somewhat greater during the night.

2242

Can. J. Fish. Aquat. Sci. Vol. 61, 2004

Table 2. Distribution of echo abundance for the years 1997–2002 for various species and groups.

Echo abundance	Cod	Demersal	Pelagic	All groups
−1	1.000 (38 636)	1.000 (38 636)	1.000 (38 636)	1.000 (38 636)
0	1.000 (35 841)	1.000 (37 664)	1.000 (15 958)	1.000 (38 596)
1	0.998 (32 754)	1.000 (36 389)	1.000 (13 966)	1.000 (38 358)
2	0.992 (30 155)	1.000 (35 399)	0.999 (12 812)	1.000 (38 054)
4	0.972 (25 895)	0.998 (33 900)	0.998 (11 362)	1.000 (37 450)
8	0.914 (19 455)	0.995 (31 400)	0.995 (9 405)	0.999 (36 369)
16	0.781 (11 994)	0.983 (27 244)	0.987 (7 171)	0.996 (34 150)
32	0.558 (5 608)	0.945 (20 609)	0.974 (5 079)	0.982 (29 094)
64	0.294 (1 721)	0.855 (12 506)	0.953 (3 509)	0.936 (20 500)
128	0.117 (375)	0.721 (6 318)	0.924 (2 373)	0.841 (11 386)
256	0.037 (67)	0.574 (2 901)	0.878 (1 485)	0.720 (5 489)
512	0.008 (8)	0.410 (981)	0.821 (921)	0.592 (2 340)
1 024	0.002 (1)	0.307 (343)	0.753 (589)	0.493 (1 079)
2 048	0.000 (0)	0.247 (167)	0.657 (355)	0.411 (567)
4 096	0.000 (0)	0.188 (79)	0.518 (188)	0.317 (282)
8 192	0.000 (0)	0.132 (39)	0.331 (72)	0.213 (122)
16 384	0.000 (0)	0.059 (12)	0.180 (23)	0.105 (36)
32 768	0.000 (0)	0.000 (0)	0.058 (4)	0.024 (4)
65 536	0.000 (0)	0.000 (0)	0.019 (1)	0.008 (1)
Average	16.819	107.209	90.593	226.778
Median	8.125	35.573	0.000	69.922
q_{98}	96.478	578.761	660.991	1 444.023
q_{99}	129.365	927.679	1 822.518	3 141.895

Note: Data are the fraction of total echo abundance contained in samples with echo abundance higher than the value in the leftmost column ($m^2 \cdot n.mi.^{-2}$). In parentheses, the number of samples with echo abundance higher than the value in the leftmost column is shown. The last four rows show the average and median echo abundance and the 98% and 99% quantiles. Species and groups are as follows: Cod (*Gadus morhua*); Demersal species (cod, haddock (*Melanogrammus aeglefinus*), redfish (*Sebastes marinus*), saithe (*Pollachius virens*), blue whiting (*Micromesistius poutassou*), others); Pelagic species (capelin (*Mallotus villosus*), herring (*Clupea harengus*)); and All groups (demersal, pelagic, plankton).

When plankton, capelin (*Mallotus villosus*), and herring (*Clupea harengus*) data were removed, the diurnal pattern was the same, but as expected all quantiles were closer to the bottom (Fig. 5a). In deep water, the demersal fish generally had a more pelagic distribution (the quantiles were situated higher in the water column), and the diurnal changes in the density profile were more pronounced (Fig. 5b). It was sufficient to remove the 1% largest samples to eliminate the irregularities that corrupted the pattern for the demersal fish. However, the removed samples appeared to be less uniformly distributed by time of day, as compared with the case where all species were included (Table 3). In fact, the daytime echo abundance samples we removed were more than twice as large and about twice as many as those removed from the nighttime records. But 39% of the echo abundance within the 1% largest samples was concentrated to 62 samples taken between 1200 and 1800 on 1 day by one vessel. Therefore, the large concentrations of fish might still be randomly distributed over the whole day. If the vessel had arrived 12 h later, there would probably have been a corresponding overweight of nighttime number and echo abundance in the removed samples. Similar arguments can be applied to the dominance of large night recordings for nondemersal fish.

Cod (*Gadus morhua*), the target species in the Barents Sea survey, showed a different pattern (Fig. 6a) compared with the complete demersal species group. The pattern in total echo abundance was similar, with 46% higher daytime values, whereas the mean depth of the cod was constant over

the 24 h. Generally, the curves do not have the same dip around noon as in Fig. 5. In contrast, plankton density profiles do show this dip at midday (Fig. 6b), but the total echo abundance is more constant around the clock, with a slight reduction in daytime.

A summary of the total echo abundance and density profiles for the various species shows similar patterns for all of the demersal fish, although blue whiting (*Micromesistius poutassou*) and the "other" category have a slightly more pelagic distribution than cod, haddock (*Melanogrammus aeglefinus*), redfish (*Sebastes marinus*), and polar cod (*Boreogadus saida*) (Fig. 7). Capelin, herring, and plankton are found higher in the water column than any of the other species.

The demersal group shows good consistency between years, especially regarding total echo abundance, which is about 50% higher in daytime (Fig. 7). 1998 is an exception, however, with a rather low daytime echo abundance value. This temporal stability of the diurnal pattern can easily be missed if large values are not eliminated.

Testing for significance

As a typical illustration, the diurnal patterns seen on Fig. 5b are highly significant, for both the total echo abundance and the quantiles of the vertical density profiles (Fig. 8 and Table 4). The observed values clearly exceed the randomized 95% confidence intervals for the respective quantities under the null hypothesis of no diurnal fluctua-

Fig. 3. Vertical density profiles for all species and all years joined together. (*a*) All samples are included. (*b*) Values larger than the 98% quantile are excluded. The area of each segment of a profile is proportional to the average echo abundance over all samples taken in the actual time interval and the actual fraction of the water column. Small circles indicate the 25%, 75%, and 90% quantiles of the profiles; large circles indicate medians; and squares indicate means. The horizontal dotted line indicates the average of the means. The number of samples (*n*) and average echo abundance (nautical area scattering coefficient, NASC) in each time interval are given at the top. The length of the solid bars at the top is proportional to the average echo abundance. The horizontal solid lines in (*b*) indicate the average echo abundance at night, dawn/dusk, and day. The corresponding numbers on the right of (*b*) are the night average and the factors this must be multiplied with to get dawn/dusk and day averages. The number at the bottom of a profile indicates the percentage of the total echo abundance that is contained in the segment closest to bottom.
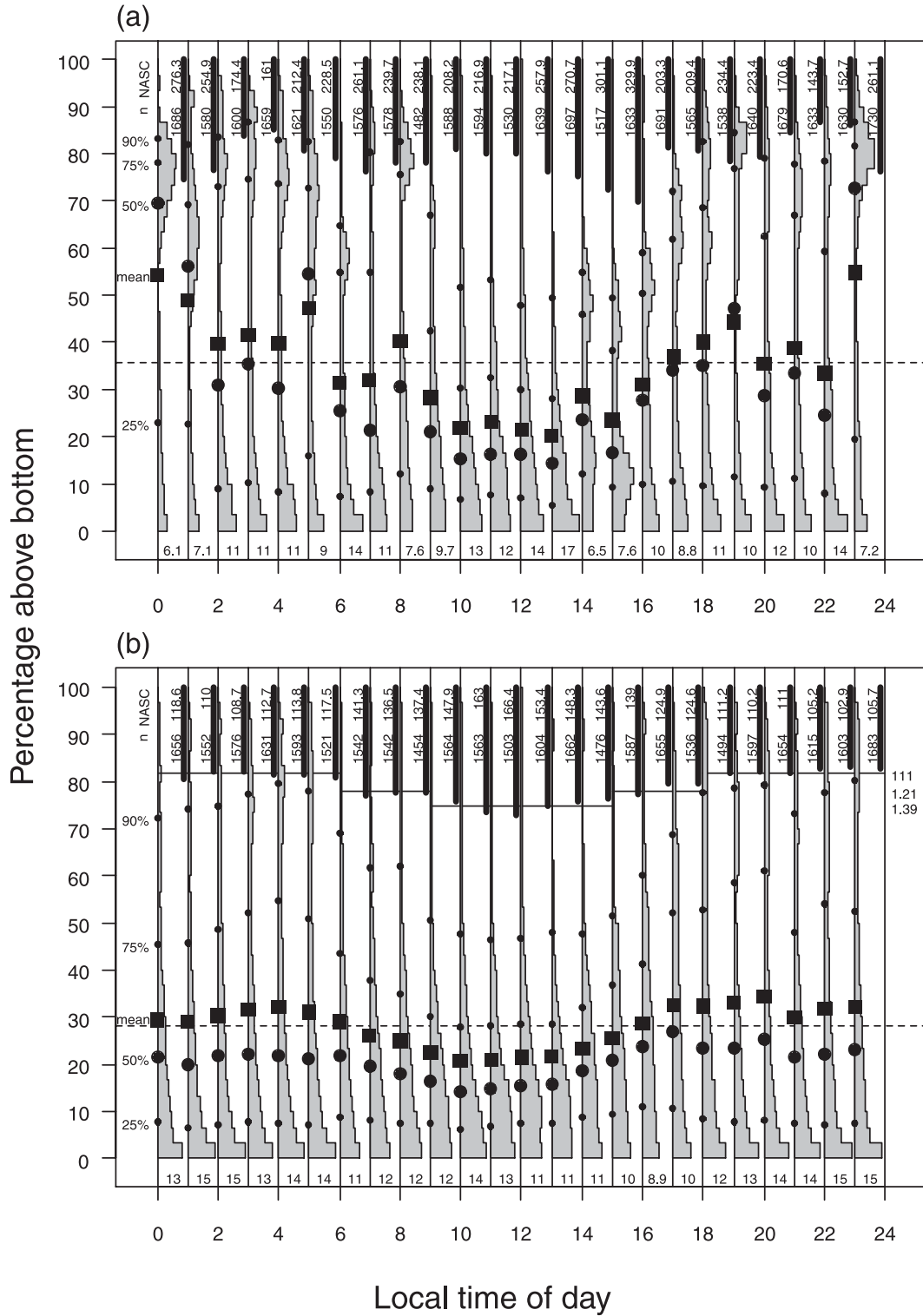
2244

Can. J. Fish. Aquat. Sci. Vol. 61, 2004

Fig. 4. Total echo abundance (nautical area scattering coefficient, NASC) plotted as a function of local time. Samples taken at the same day are connected with lines. The horizontal dotted line indicates the 98% quantile. Open circles indicate samples taken at 3 successive days by one vessel.
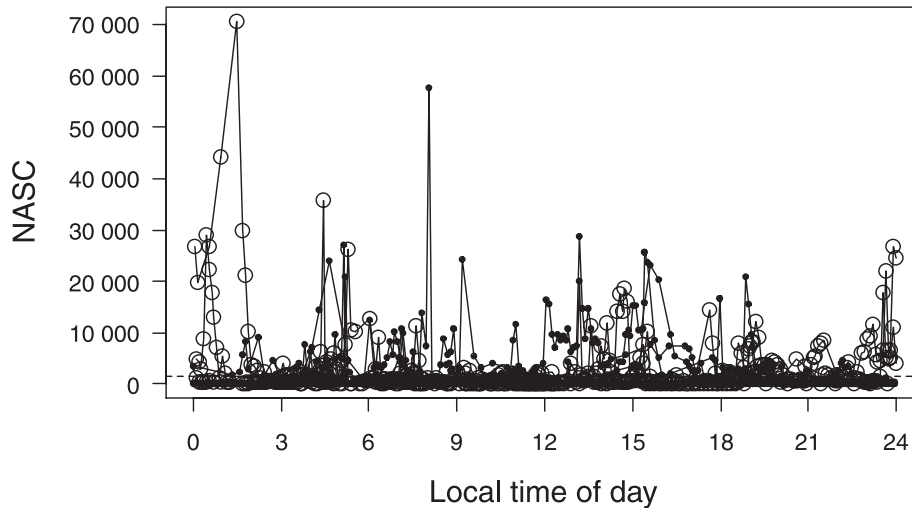

Table 3. Distribution of the samples larger than the 98% (q_{98}) and 99% (q_{99}) quantiles on day (here defined as 0600–1800) and night (1800–2400, 0000–0600) for all species and demersal species.

Category	Quant	Day		Night		% of total*
		n	Sum	n	Sum	
All species, q_{99}	3141.8	199	1 594 049	188	1 550 629	35.9
All species, q_{98}	1444.0	403	2 012 288	371	1 941 287	45.1
Demersal, q_{99}	927.6	255	919 391	132	393 523	31.7
Demersal, q_{98}	578.7	466	1 068 700	307	518 694	38.3

Note: Quant denotes the echo abundance at the actual quantile, n is the number of samples higher than this value, and Sum is the echo abundance summed over these samples.

*Data are the percentage that the echo abundance of the large samples contributes to the total echo abundance.

tions. When the data were allocated to three groups instead of 24 one-hour groups, the confidence intervals were generally narrower because of more observations being in each group. Also, note that the confidence intervals for the dawn/dusk group were narrower than those of the day group, even though the number of observations is about the same. This occurs because the dawn/dusk group is composed of two subgroups, separated in time by 6 hours, while the day group covers a continuous time interval. The lower correlation of the dawn/dusk group is therefore expected.

The results based on the test statistics in eqs. 1 and 2 are given for all species, demersal species, cod, and plankton (Table 4). The diurnal variation was generally most significant in deep waters, and the symmetry-based tests (eq. 2) gave, in most cases, lower p values than the general tests (eq. 1). For cod, the results for the 25% quantile and the median were the most significant (as would be expected from Fig. 6).

Discussion

Acoustic surveys in the Barents Sea show a substantial reduction in the acoustic biomass of all fish categories during the nighttime compared with daytime. In contrast, the plankton category has a relatively constant biomass around the clock, with only a small reduction in daytime. All species or

groups of species displayed substantial diurnal vertical migration, although cod showed less variation of the mean depth. Below, we discuss the observed diurnal patterns in distribution and density and evaluate the three hypotheses that were stated in the Introduction.

Diurnal variation

The diurnal pattern of behaviour is a general feature of marine species (Engås and Godø 1986; Neilson and Perry 1990; Abe et al. 1999). Light is normally considered to be the primary trigger of this pattern, but species interactions through predator–prey relationships may provide a causal connection between successive trophic layers of the ecosystem. The variation in light level at high latitudes is dramatically different from that in the tropics. The feeding and survival strategies of species probably vary accordingly. Further, diurnal variations will also relate to area-specific physical and biological features. For example, the opposite diurnal pattern in echo abundance has been observed for pelagic species in the Baltic (Orlowski 2000). Lawson and Rose (1999), using acoustics combined with observations from an underwater vessel for a period of a few days, found daytime densities of Atlantic cod to be an order of magnitude higher than nighttime densities in Placentia Bay, Newfoundland, Canada, at depths of 35–80 m inshore. The reason was that at night, cod were located nearer to the bottom, and

Fig. 5. Vertical density profiles for all species except plankton, capelin (*Mallotus villosus*), and herring (*Clupea harengus*) and all years joined together. Samples larger than the 99% quantile are excluded. (*a*) Samples taken at all bottom depths. (*b*) Samples taken at bottom depths larger than 300 m. The area of each segment of a profile is proportional to the average echo abundance over all samples taken in the actual time interval and the actual fraction of the water column. Small circles indicate the 25%, 75%, and 90% quantiles of the profiles; large circles indicate medians; and squares indicate means. The horizontal dotted line indicates the average of the means. The number of samples (*n*) and average echo abundance (nautical area scattering coefficient, NASC) in each time interval are given at top. The length of the solid bars at the top is proportional to the average echo abundance. The horizontal solid lines indicate the average echo abundance at night, dawn/dusk, and day. The corresponding numbers on the far right of the figure are the night average and the factors this must be multiplied with to get dawn/dusk and day averages. The number at the bottom of a profile indicates the percentage of the total echo abundance that is contained in the segment closest to bottom.
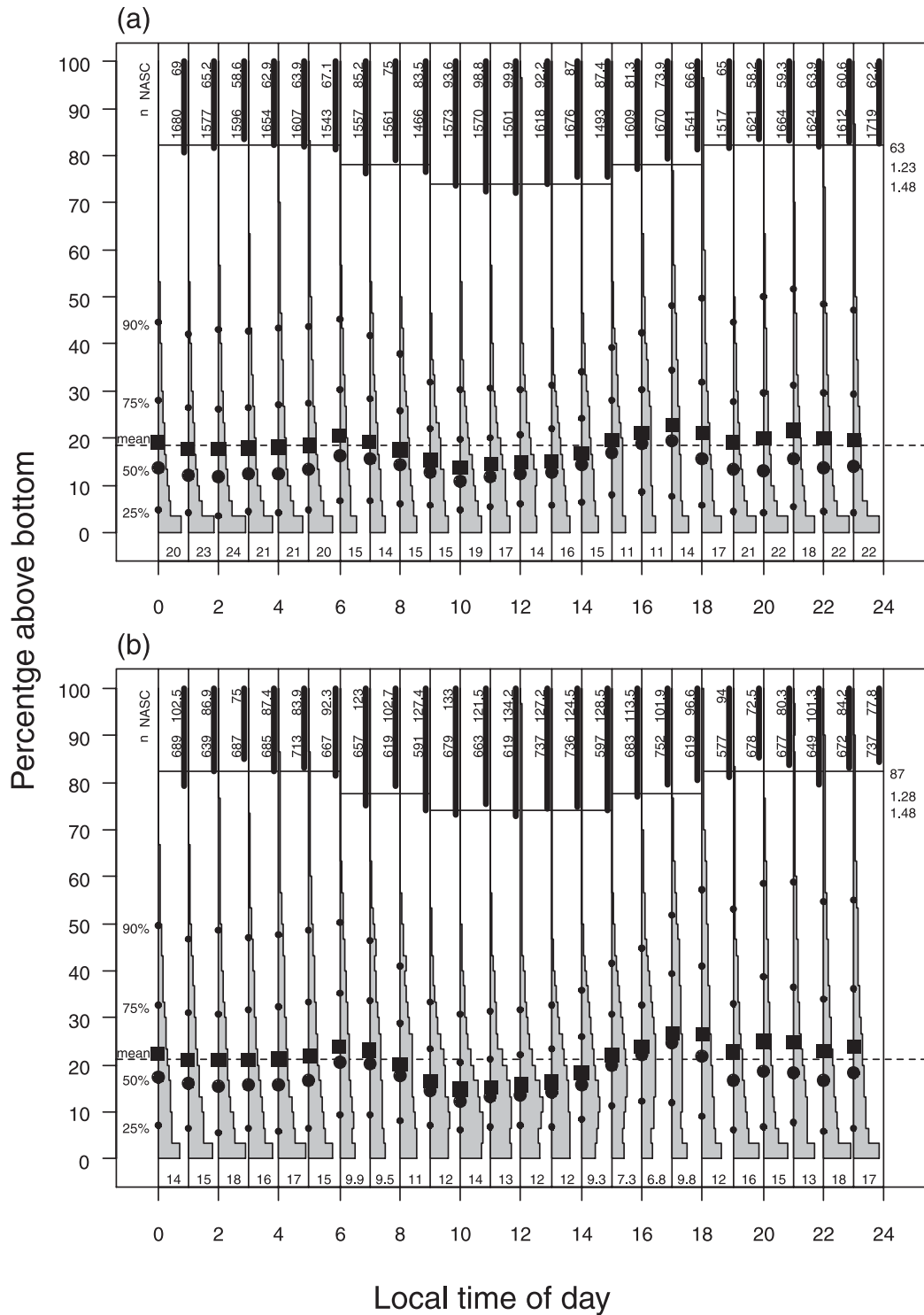
Fig. 6. Vertical density profiles all years joined together for (*a*) cod (*Gadus morhua*) only, all samples included; and for (*b*) plankton only, samples larger than the 99% quantile excluded. The area of each segment a profile is proportional to the average echo abundance over all samples taken in the actual time interval and the actual fraction of the water column. Small circles indicate the 25%, 75%, and 90% quantiles of the profiles; large circles indicate medians; and squares indicate means. The horizontal dotted line indicates the average of the means. The number of samples (*n*) and average echo abundance (nautical area scattering coefficient, NASC) in each time interval are given at top. The length of the solid bars at the top is proportional to the average echo abundance. The horizontal solid lines indicate the average echo abundance at night, dawn/dusk, and day. The corresponding numbers on the far right of the figure are the night average and the factors this must be multiplied with to get dawn/dusk and day averages. The number at the bottom of a profile indicates the percentage of the total echo abundance that is contained in the segment closest to bottom.
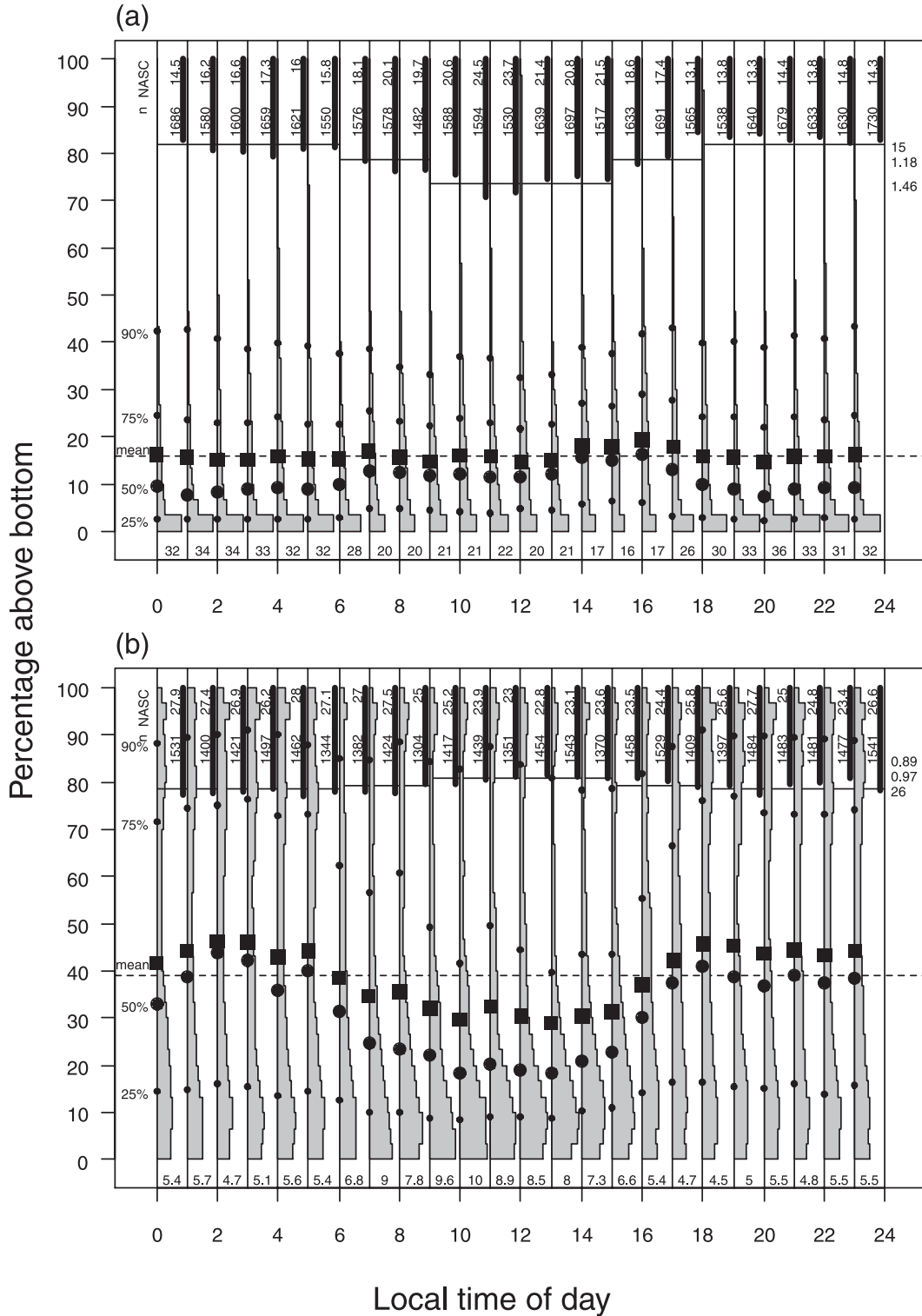
Fig. 7. Total echo abundance (upper bars) and 25%, 50%, 75%, and 90% quantiles of density profiles for the demersal category each year and for each species all years. The data are grouped in night (N, 1800–0600), dawn/dusk (U, 0600–0900 and 1500–1800), and day (D, 0900–1500) instead of in 24 one-hour intervals. The total echo abundance bars are scaled so that the night echo abundance bar is equal for all groups. Horizontal dotted lines are drawn at 100% and 150% of night echo abundance. The percentage of the samples used for each group is given in the bottom line. The species are as follows: demersal (dem), cod (*Gadus morhua*), haddock (had; *Melanogrammus aeglefinus*), redfish (red; *Sebastes marinus*), polar cod (pol; *Boreogadus saida*), blue whiting (blw; *Micromesistius poutassou*), others (oth), capelin (cap; *Mallotus villosus*), herring (her; *Clupea harengus*), and plankton (pla).
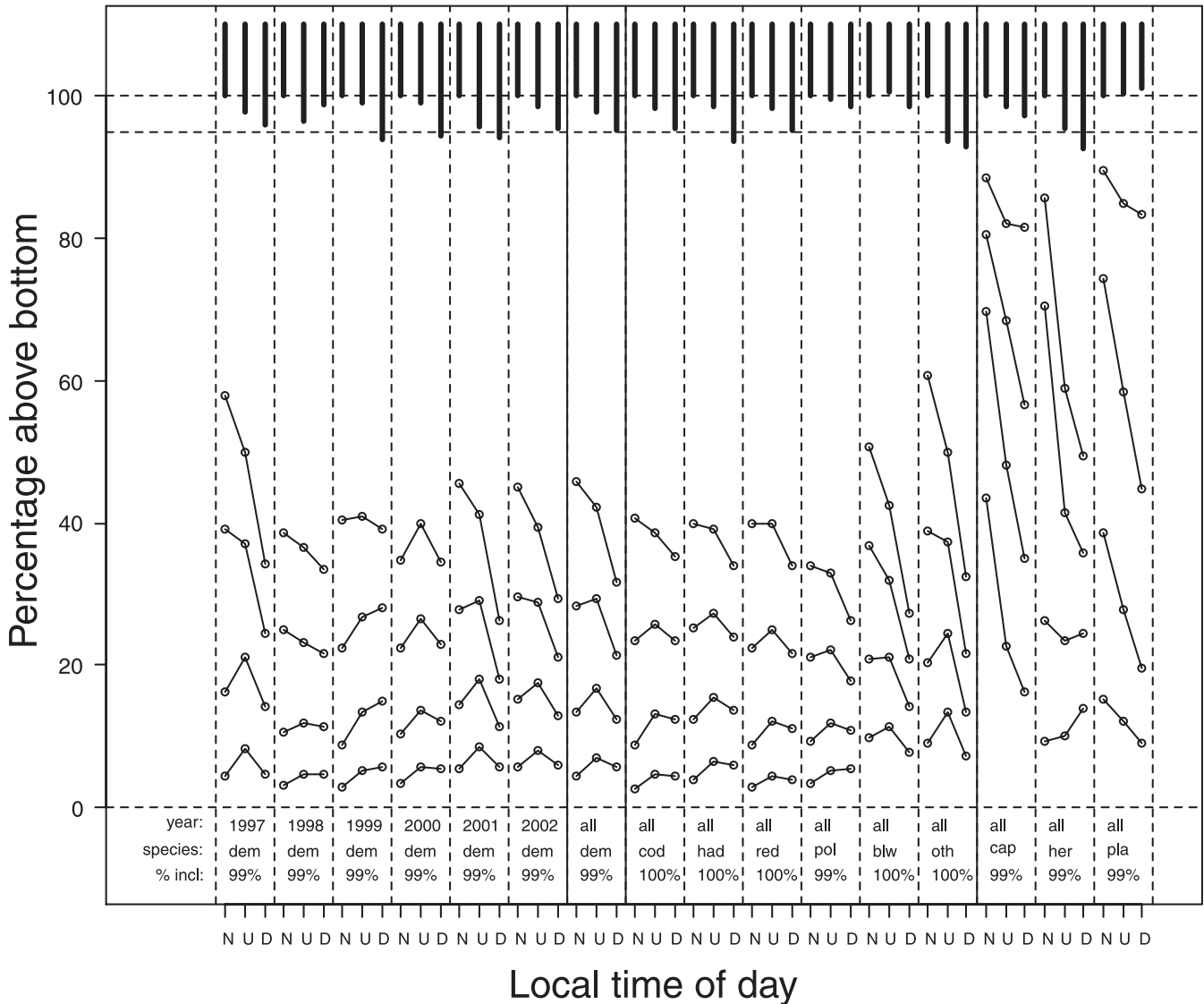

they preferred rocky or boulder-strewn substrates to open sandy ground. Thus, the near-bottom cod were undetectable by acoustic methods.

After excluding the largest recordings, there is a highly significant trend (at the 1% level) in our data, with the echo abundance observed in daytime being higher than at night ($p < 0.001$ for cod and for the demersal category). This is a common phenomenon in acoustic surveys of fish stocks (Engås and Godø 1986; Michalsen et al. 1996; Huse and Korneliussen 2000), and as such it is analogous to the diurnal pattern of bottom-trawl survey recordings (Casey and Myers 1998; Korsbrekke and Nakken 1999; Hjellvik et al. 2001). If data from the two types of surveys are being com-

bined to support the quantitative evaluation of a stock (e.g., Karp and Walters 1994; Jakobsen et al. 1997), a wrong interpretation can result if the diurnal variations are not appropriately incorporated in the analysis.

For our data, there is a high consistency over the years and amongst the fish species and groups studied; there are systematically lower night than day values and intermediate dawn/dusk values. Based on the observed consistency in echo abundance, it is tempting to assume that the diurnal variation of fish density must have a common explanation. Admittedly, this pattern is rather weak for polar cod and blue whiting, but for both of those species there are few non-zero samples. It should be noted that our findings are at odds

2248

Can. J. Fish. Aquat. Sci. Vol. 61, 2004

Fig. 8. Randomized 95% confidence bands (shaded areas) for the total echo abundance and the 25%, 50%, 75%, and 90% quantiles of Fig. 5*b*. Data are based on 1000 randomizations. The right part of the figure shows the results when the data were distributed on three groups (i.e., night (N, 1800–0600), dawn/dusk (U, 0600–0900 and 1500–1800), and day (D, 0900–1500)) instead of on 24 one-hour groups.
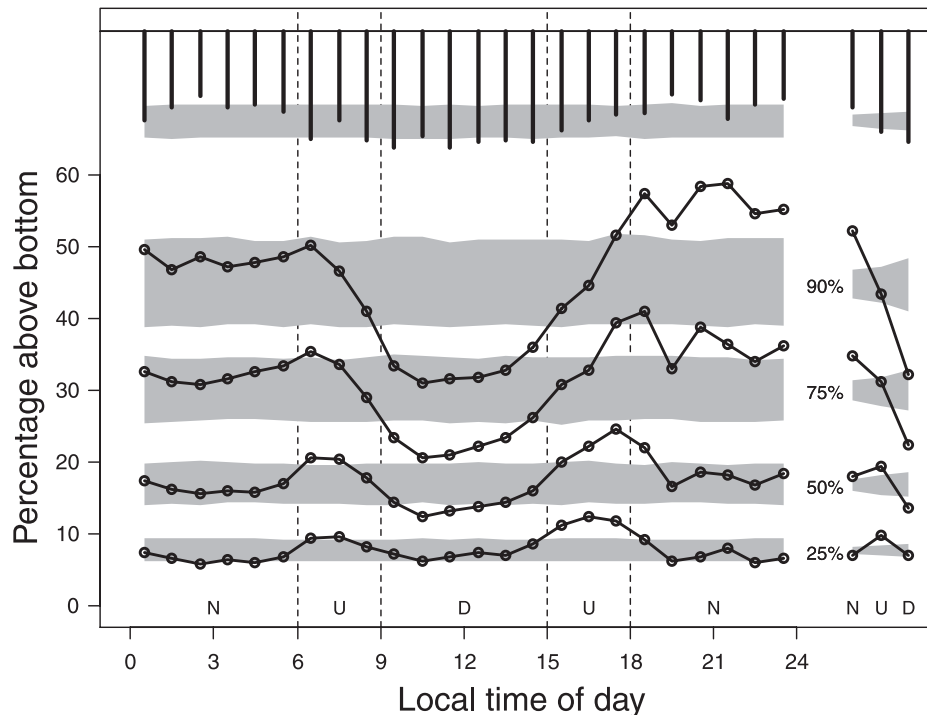
with the results of Aglen et al. (1999), who, in a much more limited 10-day experiment, observed the lowest echo abundance (virtually zero) during the dawn/dusk periods.

The plankton group follows a different pattern, with slightly less echo abundance during the day than at night. However, this is not unexpected, since most plankton is not susceptible to diurnal variation through tilt angle and swim bladder changes. This applies even though in our case the plankton is indeed a complex group of species, which may to some extent include small fish, since it includes all targets not identified as belonging to the fish groups.

As with the variation of echo abundance, there is a high degree of consistency in all species and groups with respect to vertical migration. For all groups, the biomass distribution is more widespread during the night. The slightly delayed descent of the demersal group compared with the near-surface plankton group might reflect a delay in reaction time to light with increasing depth. The hourly quantiles of the fish density are generally highest at dawn/dusk and lowest around noon, independent of their vertical distribution, but there are some exceptions. Monitoring cod fitted with data storage tags has demonstrated that individual cod may perform an extensive vertical migration without any diurnal pattern (Godø and Michalsen 2000). This is consistent with the weak diurnal pattern we observed for cod.

The patterns in total echo abundance and vertical distribution profiles of cod, haddock, redfish, and polar cod appear similar. The 25% and 90% quantiles are further apart at night than during the day, indicating a diurnal migration dynamics where the fish disperse in the water column during darkness and concentrate more in daytime. In contrast, blue

whiting and the "other" group display stronger diurnal oscillations, moving towards the bottom in daytime and ascending and spreading out in the water column at night and are thus behaving more like the pelagic fish and plankton.

Based on combined observations from acoustics and pelagic trawling over 10 days, Aglen et al. (1999) suggested that patterns in the vertical migration of gadoids depend on fish size. Hjellvik et al. (2001) also demonstrated that the diurnal variation of bottom-trawl catches of small cod and haddock generally exceeded those of larger fish. As small fish (e.g., age 1 and 2 cod and haddock) feed on plankton (Mehl and Sunnanå 1991), it is expected that they might have behavioural characteristics similar to pelagic fish and plankton. Unfortunately, our acoustic data on the cod group are not easily resolved between large and small individuals. The smallest gadoids may occasionally be difficult to allocate to species in the interpretation of the acoustic signals because of their low backscattering strength and the fact that they are often underrepresented in the catches (Godø and Walsh 1992). Therefore, one cannot rule out the possibility that some of the small cod and haddock may have been wrongly included in the "other" group.

Why do we see less in the dark?

Three factors of potential importance to the diurnal variability have already been introduced: (*i*) fish are inaccessible to acoustics if located in the bottom or surface dead zones; (*ii*) fish TS depends on the tilt-angle distribution; and (*iii*) fish TS changes because of pressure effects on the swim bladder during vertical migration. In this paper, we give no further consideration to the surface zone, since the available

Table 4. Results from randomization tests of the null hypothesis of no diurnal variation against the alternative hypotheses H_1 and H_2.

| Species	Depth		q_{25}	q_{50}	q_{75}	q_{90}	Mean	Total
Empirical p values								
All	>300	H_1	0	0	0	0	0	0
		H_2	0	0	0	0	0	0
	>0	H_1	0.001	0	0	0	0	0
		H_2	0.002	0	0	0	0	0
Demersal	>300	H_1	0	0	0	0	0	
		H_2	0	0	0	0	0	0
	>0	H_1	0	0	0	0	0	0
		H_2	0	0	0	0	0	0
Cod	>300	H_1	0	0	0.230	0	0.033	0.006
		H_2	0	0	0.066	0	0.009	0.001
	>0	H_1	0	0	0.208	0.020	0.053	0
		H_2	0	0	0.230	0.006	0.092	0
Plankton	>0	H_1	0	0	0	0	0	0.822
		H_2	0	0	0	0	0	0.452
$\hat{L}_i / \max \hat{L}_i^*$								
All	>300	H_1	1.90	1.94	2.44	2.65	2.49	1.58
		H_2	1.77	1.64	2.76	2.90	2.35	2.06
	>0	H_1	—	1.73	3.74	3.77	3.25	1.86
		H_2	—	2.18	4.83	5.02	3.82	2.27
Demersal	>300	H_1	2.42	1.52	2.44	2.98	2.51	1.27
		H_2	2.48	1.69	3.08	3.90	2.84	1.35
	>0	H_1	2.89	1.94	2.25	3.22	2.28	2.88
		H_2	2.84	2.35	2.63	3.83	2.93	3.58
Cod	>300	H_1	1.52	1.32	—	1.08	—	—
		H_2	1.80	1.15	—	1.29	—	—
	>0	H_1	1.66	1.77	—	—	—	1.94
		H_2	1.82	2.41	—	—	—	2.12
Plankton	>0	H_1	1.79	2.66	2.94	1.76	3.21	—
		H_2	2.86	3.40	3.33	2.30	3.69	—

Note: H_1: there is some diurnal variation: H_2: there is a symmetric diurnal variation. H_1 and H_2 are tested using the test statistics $\hat{L}_1$ and $\hat{L}_2$, respectively. See eqs. 1 and 2 for definitions of $\hat{L}_1$ and $\hat{L}_2$, respectively. The results are based on 1000 replicates. In the lower half of the table, the ratios $\hat{L}_1 / \max \hat{L}_1^*$ and $\hat{L}_2 / \max \hat{L}_2^*$ are given for H_1 and H_2, respectively. The term $\max \hat{L}_i^*$, $i = 1,2$ is the maximum value of $\hat{L}_i^*$ for the randomized samples. This is only given for cases with zero p values.

vertical profiles indicate that only plankton is likely to be much affected, although it is uncertain in which direction. Naturally, the hypotheses are not mutually exclusive. The observed pattern can be the result of a combination of all of the three options, although for pelagic fish the dead zone option is hardly a viable alternative.

The day–night variation in records of demersal fish biomass has often been explained by losses in the bottom dead zone (Aglen 1996; Aglen et al. 1999). In our case, this implies a higher concentration and loss of fish in the bottom dead zone during the night. Studying the vertical profiles for demersal fish in more detail (Fig. 9), we can see that a substantial amount of fish (48% of the total) has to dive into the dead zone at night to equal the daytime results. This comes in addition to the amount that already is in the dead zone during daytime. The percentage in the deepest layer is slightly higher at night than at day (Fig 9a), and the same holds for the 10 m closest to bottom (Fig 9b). The thickness of the dead zone with 0.5 m bottom offset is, for a transducer with beam width 14.2° and pulse duration 1 ms, about 0.875 + 0.00283d, where d is bottom depth (Ona and Mitson 1996). That is, for 85% of the samples, the dead zone is between 1 and 2 m thick. The exponential increase with proximity to the bottom observed in the lowermost layers certainly suggests that there is much more fish in the dead zone than just above it, but in fact the exponential increase is stronger at day than at night (at day the echo abundance in the deepest layer is 2.4 times that in the second deepest; at night the ratio is 2.2, and at dusk/dawn it is 2.1 (Fig. 9b)). The profiles give little or no indication that the nighttime density in the dead zone by itself would be sufficient to explain the large discrepancies in nighttime and daytime echo abundance. At the very least, it would have to be combined with other effects. Also, it is interesting to note that the concentration in the dead zone seems to be minimum at dawn/dusk (Fig. 9). This is consistent with the general appearance of the vertical profiles in Fig. 5, but contrary to the results from the data of Aglen et al. (1999), who, for that particular data set, suggested that at dusk and dawn nearly all the fish seem to be hidden in the dead zone. Finally, if fish were go-

2250

Can. J. Fish. Aquat. Sci. Vol. 61, 2004

Fig. 9. (*a*) Density profiles for the data on which Fig. 5 is based, grouped in night (1800–0600), dawn/dusk (0600–0900 and 1500–1800), and day (0900–1500). The numbers to the right of the bins indicate the cumulative percentage of the total observed echo abundance. The numbers at the bottom indicate the percentage that must be added to the total observed echo abundance to reach the day level of total echo abundance. (*b*) The same data are shown for the 10 m closest to bottom.
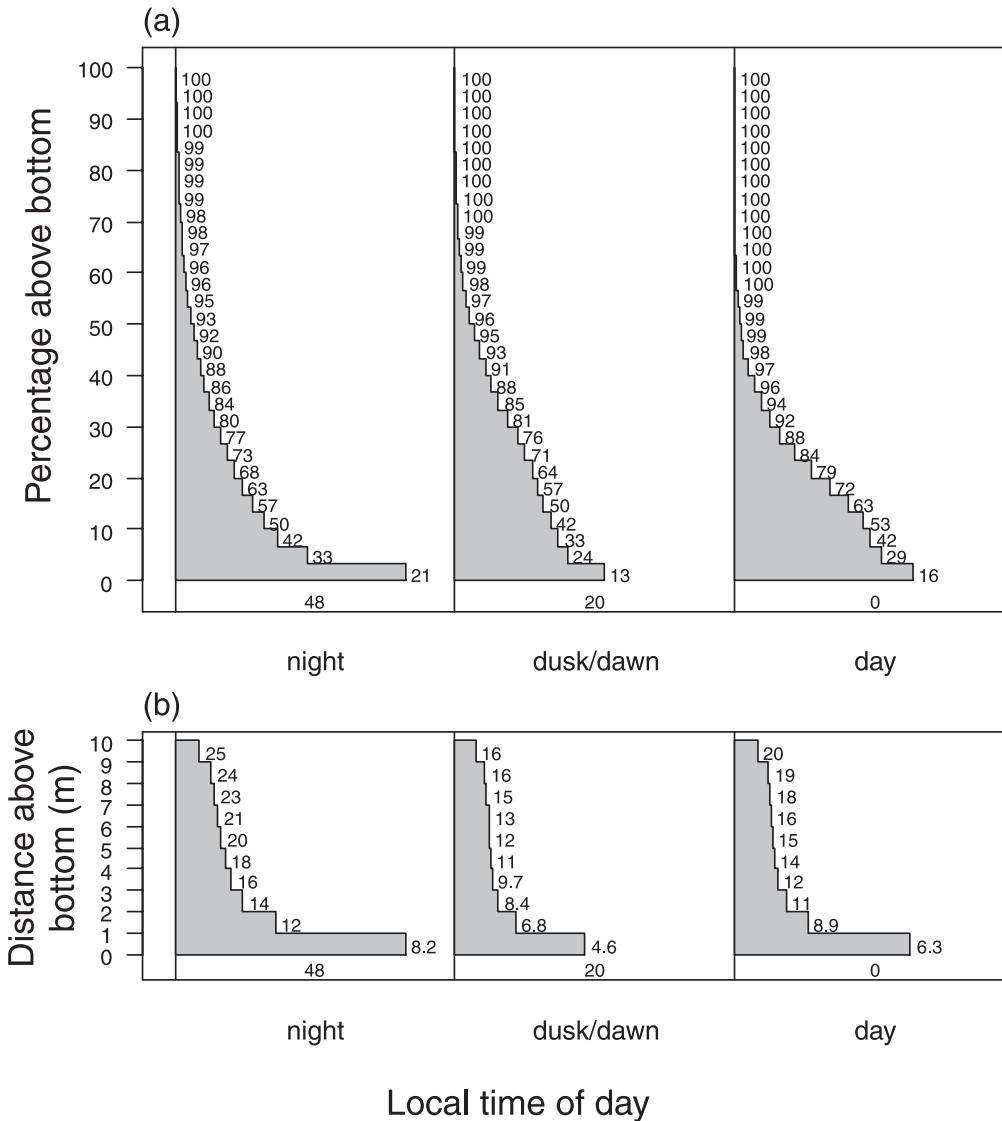
ing into and out of the dead zone at dusk and dawn, one would expect a higher density just above the dead zone at these times, whereas the opposite is the case.

An all-out dead zone explanation also conflicts with the fact that many studies report higher trawl catches by day than by night (Engås and Soldal 1992; Hjellvik et al. 2001, 2002). This may partly be explained by a higher catchability in daytime because of more effective herding. However, any difference in herding efficiency must be substantial indeed to compensate for the 48% of fish that are supposed to enter the dead zone at night (Fig. 9). Finally, a much stronger concentration of fish in the dead zone during the night should result in a higher proportion of large trawl catches associated with low acoustic densities at night. However, this is not the case (Fig. 10).

Aglen et al. (1999) and Stensholt et al. (2002), for instance, suggest that large and small demersal fish behave differently, with large fish moving up from the bottom (i.e., out

of the dead zone) into the water column during the day, and small fish doing so during the night. If large fish also tended to disperse in the water column while they were off the bottom less than small fish, this might explain the observed patterns. As we do not know the length distribution of the fish in the acoustic data, this hypothesis is not easy to check directly. However, we can get a rough idea by analysing the eastern and western parts of the survey area separately, since the abundance of small fish is relatively larger in the eastern part. Setting the limit at 35°E, the root mean square length of demersal fish in the trawl catches is about 28 and 22 cm in the western and eastern parts, respectively. However, evaluation of differences in distribution and densities from these two areas gives no univocal response supporting a major impact of the small–large fish hypothesis.

The third option is to explain diurnal variation in total echo abundance by the pressure-related swim bladder volume changes. We note that fish that undertake substantial di-

Fig. 10. Catches of demersal fish taken at trawl stations with small demersal echo abundance as a function of local time of day. A NASC (nautical area scattering coefficient) value of 1 $m^2 \cdot n.mi.^{-2}$ corresponds to a fish density of about 200 cod with a mean length of 50 cm·n.mi.$^{-2}$. Stations with $0 \leq NASC \leq 5$ are represented by solid cirlces; stations with $5 < NASC \leq 10$ are represented by open circles.
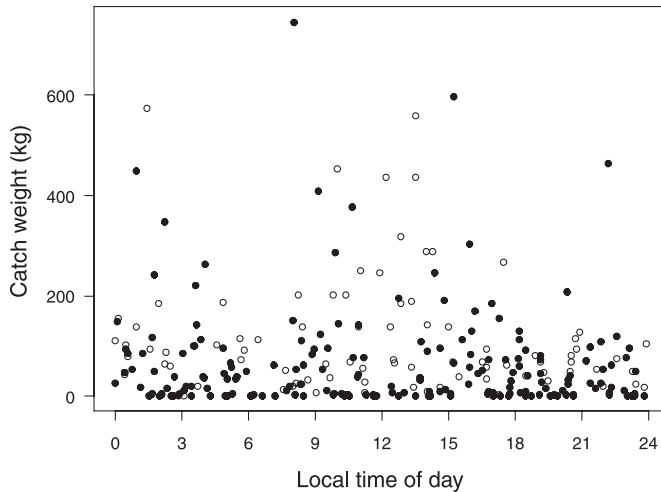
urnal vertical migrations may not be able to compensate their buoyancy by gas secretion and excretion. Thus, the fish will be negatively buoyant in the deepest parts of their depth range (see Arnold and Greer Walker 1992; Godø and Michalsen 2000). If one assumes a constant tilt-angle distribution at all times, this would in our case imply lower daytime than nighttime echo abundance values, which contrasts the actual observations. However, a negatively buoyant fish might be forced to swim at an acoustically favourable angle to maintain its position in the water column. Thus, it is difficult to estimate the combined direct and indirect effect of swim bladder volume changes. However, since the major species disperse in the water column at night and concentrate during the day, with little change in their mean depth, we think that the swim bladder effect is of minor importance.

Having discussed options (*i*) and (*iii*) as causes for diurnal variation in echo abundance, we now come to option (*ii*): diurnal variation in acoustic target strength because of light-controlled behavioural change. There is some evidence of this effect, mainly from fish in captivity. The fish is certainly a directive acoustic target, and the tilt angle of the body is an important determinant of the reflected energy (Nakken and Olsen 1977). A less organised behaviour at night, resulting in a more variable tilt angle, will cause a substantial reduction in echo abundance, as has been shown in model experiments (MacLennan and Simmonds 1992; McClatchie et al. 1996; Huse and Korneliussen 2000). McClatchie et al. (1996) examined the relationship between the standard deviation of the tilt-angle distribution and the average target strength. When the standard deviation increased from 5 to 15 degrees, they found that the average target strength decreased by about 2–3 dB. This corresponds to about 37%–50% reduction in echo abundance.

Cod is a visual feeder (Anthony 1981), and it is thus likely that nighttime behaviour is more relaxed and less directed. In a food search experiment reported by Løkkeborg

and Fernö (1999), cod exhibited a diurnal activity rhythm, with higher swimming speeds and a larger range during the day than at night. Lawson and Rose (1999) reported energetic and directed swimming by cod in the daytime, while at night the fish remained motionless or circled slowly with no sustained directionality. Studies of captive cod have shown how that sort of behavioural change from day to night is associated with a reduction in the mean TS (E. Ona, Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway, personal communication). While we do not rule out that the dead zone alternative plays a role, we think that of the options discussed above, this last effect (which we call the TS–TA (target strength – tilt angle) link) is the heaviest contributor to the observed diurnal variation in echo abundance. The TS–TA link also provides a simple explanation of the gradual increase of total echo abundance during the dawn period as the fish gradually respond to increased light intensity by adopting a more uniform tilt-angle distribution and the corresponding decrease of echo abundance during the dusk period. Moreover, if we look at capelin, for which any dead zone effect is considered negligible (Fig. 11), it is interesting to note that the diurnal total echo abundance profile is about the same as that of demersal fish. It is hard to reconcile these facts with an all-out dead zone explanation. In contrast, for plankton (whose tilt angle is irrelevant at 38 kHz), the total echo abundance is about the same at all times. Finally, it is interesting to note that the TS–TA link may help to explain the minor but recurring peak in the quantiles at dawn and dusk, observed for all fish groups. With light as the controlling factor, the fish will organise themselves and their target strength will increase progressively with depth. Assuming the TS–TA link is dominant, the result will be higher echo abundance in shallow water first, with associated peaks in the quantiles, as we have observed. If this conclusion holds, the dawn/dusk effects may partially be artefacts of varying target strength.

Consequences and future research

The observed variation in acoustic backscattering has serious implications for the consistency of results from acoustic surveys and is an important consideration for the calibration of trawl catches against acoustic measurements. It is essential to understand the mechanisms behind the observed variation, and the validation of our hypothesis is thus an important task for future research. This could be done by further investigations on fish held in captivity under controlled conditions, and similar techniques might be used for in situ observations (e.g., Huse and Ona 1996). Based on such results, diurnal-modulated TS models can be developed (McClatchie et al. 1996).

The above discussion assumes that the number of fish in the dead zone is correlated with that just above the dead zone and that the fish in the dead zone do not greatly outnumber those above the dead zone. The observed correlation between acoustic recordings and trawl catches, roughly 0.5 on the log scale (Hjellvik et al. 2003), indicates that this assumption is to some extent justified. However, to decide the exact contribution of the bottom dead zone to the variation in echo abundance, studies should be done with autonomous underwater vehicles (Fernandes et al. 2000a, 2000b; Patel et al. 2004) or other means of placing the transducer close to

2252

Can. J. Fish. Aquat. Sci. Vol. 61, 2004

Fig. 11. Density profiles for capelin (*Mallotus villosus*), grouped in night (1800–0600), dawn/dusk (0600–0900 and 1500–1800), and day (0900–1500). The numbers to the right of the bins indicate the cumulative percentage of the total observed echo abundance. The numbers at bottom indicate the percentage that must be added to the total observed echo abundance to reach the day level of total echo abundance. Samples larger than the 99% quantile have been removed.
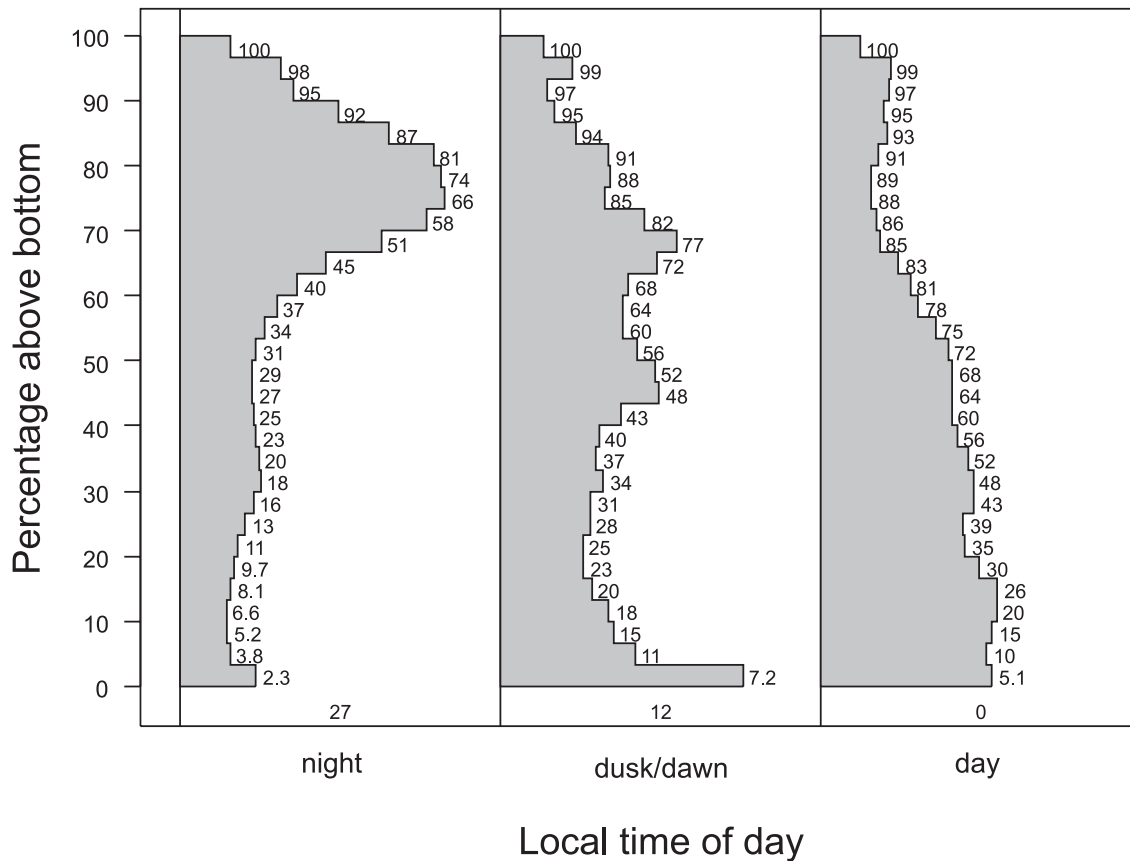
the bottom. Such studies, including the tracking of individual fish (Handegard et al. 2003), will elucidate the dynamics of echo abundance close to the bottom. Preliminary evidence does not suggest differences in vertical diving velocity as a response to trawling in nighttime and daytime, but these results are limited to tracking of individual fish (Handegard 2004). Also, if combined with photographic techniques (Lawson and Rose 1999), more information on the species composition in the bottom zone could be obtained if one could ensure representative observations without avoidance. This would substantially assist our interpretation of the acoustic signals, which can be difficult, especially for small gadoids that are often underrepresented in trawl catches (Godø and Walsh 1992). Since higher-frequency echo sounders are more sensitive to changes in tilt angle, one would expect a larger day–night difference in total echo abundance at high frequencies if the difference is due to a greater variation of the tilt angle at night. Thus, if several transducers with different operating frequencies were used during the survey, a frequency-response analysis could improve our understanding of these phenomena.

Trawl catches in the Barents Sea vary systematically between day and night (Engås and Soldal 1992; Hjellvik et al. 2001, 2002), with lower catch rates at night. A meaningful comparison of the trawl and acoustic survey techniques and

a thorough investigation of the observed variation in trawl catchability should be done, taking the inherent temporal variability of both techniques into account. Statistical compensation models can certainly improve this comparison. However, further studies of the kind suggested above will facilitate the development of combined models that incorporate knowledge of fish behaviour. Developments along these lines will be important for future field-monitoring programmes aimed at ecosystem health rather than at single-stock dynamics. For that purpose, a quantitative understanding of fish behavioural dynamics as well as species interactions in time and space will be crucial for the reliability of such programmes.

The answers to complex problems are often found in the interaction among several factors. Studies of such problems, in our case acoustic back scattering variability, often concentrate on single factors as evaluated from small-scale, short-term experiments. Such approaches may be seriously biased by the conditions during observation and may not necessarily give a representative picture applicable for a complete survey. In this paper, we have developed statistical approaches for utilizing data collected from the whole survey and during several years. We think that this gives not only a more representative and comprehensive picture of the problems, but should also be an important provider of priorities for further research.

Acknowledgments

References

Abe, K., Iida, K., and Maukai, T. 1999. Diurnal changes in area backscattering coefficient during the acoustic surveys of walleye pollock. Nippon Suisan Gakkaishi, **65**: 252–259.

Aglen, A. 1994. Sources of error in estimation of fish abundance. *In* Marine fish behaviour in capture and abundance estimation. *Edited by* A. Fernö and S. Olsen. Fishing News Books, Oxford. pp. 107–133.

Aglen, A. 1996. Impact of fish distribution and species composition on the relationship between acoustic and swept-area estimates of fish density. ICES J. Mar. Sci. **53**: 501–506.

Aglen, A., Engås, A., Huse, I., Michalsen, K., and Stensholt, B. 1999. How vertical fish distribution may affect surveys results. ICES J. Mar. Sci. **56**: 345–360.

Anthony, P.D. 1981. Visual contrast thresholds in the cod (*Gadus morhua* L). J. Fish Biol. **19**: 87–103.

Arnold, G.P., and Greer Walker, M. 1992. Vertical movements of cod (*Gadus morhua* L.) in the open sea and the hydrostatic function of the swim bladder. ICES J Mar. Sci. **49**: 357–372.

Carlstein, E., Do, K.A., Hall, P., Hesterberg, T., and Künsch, H.R. 1998. Matched-block bootstrap for dependent data. Bernoulli, **4**: 305–328.

Casey, J.M., and Myers, R. 1998. Diel variation in trawl catchability: is it as clear as day and night? Can. J. Fish. Aquat. Sci. **55**: 2329–2340.

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

Engås, A., and Godø, O.R. 1986. Influence of trawl geometry and vertical distribution of fish on sampling with bottom trawl. J. Northw. Atl. Fish. Sci. **7**: 35–42.

Engås, A., and Soldal, A.V. 1992. Diurnal variations in bottom trawl catch rates of cod and haddock and their influence on abundance indices. ICES J. Mar. Sci. **49**: 89–95.

Fernandes, P.G, Brierley, A.S, Simmonds, E.J.,Millard, N.W., McPhail, S.D., Armstrong, F., Stevenson, P., and Squires, M. 2000*a*. Oceanography: fish do not avoid survey vessels. Nature (London), **404**: 35–36.

Fernandes, P.G, Brierley, A.S, Simmonds, E.J.,Millard, N.W., McPhail, S.D., Armstrong, F., Stevenson, P., and Squires, M. 2000*b*. Addendum: fish do not avoid survey vessels. Nature (London), **407**: 152.

Fernö, A., and Olsen, S. 1994. Marine fish behaviour in capture and abundance estimation. Fishing News Books, Oxford.

Foote, K.G., Knudsen, P., Korneliussen, R.J., Nordbø, P.E., and Røang, K.S.O. 1991. Postprocessing system for echo sounder data. JASA, **90**: 37–47.

Godø, O.R., and Michalsen, K. 2000. Migratory behaviour of northeast Arctic cod, studied by use of data storage tags. Fish. Res. **48**: 127–140.

Godø, O.R., and Walsh, S.J. 1992. Escapement of fish during bottom trawl sampling — implications for resource assessment. Fish. Res. **13**: 281–292.

Handegard, N.O. 2004. Cod reaction to an approaching bottom trawling vessel investigated using acoustic split-beam tracking. Ph.D. thesis, Department of Mathematics, University of Bergen, Norway.

Handegard, N.O., Michalsen, K., and Tjøstheim, D. 2003. Avoidance behaviour in cod (*Gadus morhua*) to a bottom-trawling vessel. Aquat. Living Resour. **16**: 265–270.

Hjellvik, V., Godø, O.R., and Tjøstheim, D. 2001. Modelling diurnal variation of marine populations. Biometrics, **57**: 189–196.

Hjellvik, V., Godø, O.R., and Tjøstheim, D. 2002. Diurnal variation in bottom trawl catches: does it pay to adjust? Can. J. Fish. Aquat. Sci. **59**: 33–48.

Hjellvik, V., Michalsen, K., Aglen, A., and Nakken, O. 2003. An attempt at estimating the effective fishing height of the bottom trawl using acoustic survey recordings. ICES J. Mar. Sci., **60**: 967–979.

Huse, I., and Korneliussen, R.J. 2000. Diel variation in acoustic density measurements of overwintering herring (*Clupea harengus* L.). ICES J. Mar. Sci. **57**: 903–910.

Huse, I., and Ona, E. 1996. Tilt angle distribution and swimming speed of overwintering Norwegian spring-spawning herring. ICES J. Mar. Sci. **53**: 863–873.

Jakobsen, T., Korsbrekke, K., Mehl, S., and Nakken, O. 1997. Norwegian combined acoustic and bottom trawl surveys for demersal fish in the Barents sea during winter. ICES C.M. 1997/Y:17.

Johannesson, K.A., and Mitson, R.B. 1983. Fisheries acoustics. A practical manual for aquatic biomass estimation. Food and Agriculture Organization (UN), Rome. FAO Fish. Tech. Pap. No. 240.

Karp, W.A., and Walters, G.E. 1994. Survey assessment of semipelagic Gadoids: The example of Walleye Pollock, *Theragra chalcogramma*, in the Eastern Bering Sea. Mar. Fish. Rev. **56**: 8–22.

Knudsen, F.R., and Sægrov, H. 2002. Benefits from horizontal beaming during acoustic survey: application to three Norwegian lakes. Fish. Res. **56**: 205–211.

Korsbrekke, K., and Nakken, O. 1999. Length and species dependent diurnal variation in catch rates in the Norwegian Barents Sea bottom trawl surveys. ICES J. Mar. Sci. **56**: 284–291.

Lawson, G.L., and Rose, G.A. 1999. The importance of detectability to acoustic surveys of semi-demersal fish. ICES J. Mar. Sci. **56**: 370–380.

Løkkeborg, S., and Fernö, A. 1999. Diet activity pattern and food search behaviour in cod, *Gadus morhua*. Environ. Biol. Fishes, **54**: 345–353.

MacLennan, D.N., and Simmonds, E.J. 1992. Fisheries acoustics. Chapman & Hall, London; McGraw-Hill, New York. Fish and Fisheries Series No. 5.

McClatchie, S., Alsop, J., Ye, Z., and Coombs, R.F. 1996. Consequence of swim bladder model choice and fish orientation to target strength of three New Zealand fish species. ICES J. Mar. Sci. **53**: 847–862.

McQuinn, I.H., and Winger, P.D. 2003. Tilt angle and target strength: target tracking of Atlantic cod (*Gadus morhua*) during trawling. ICES J. Mar. Sci. **60**: 575–583.

Mehl, S., and Sunnanå, K. 1991. Changes in growth of Northeast Arctic cod in relation to food consumption in 1984–1988. ICES Mar. Sci. Symp. **193**: 109–112.

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 J. Mar. Sci. **53**: 389–395.

2254

Can. J. Fish. Aquat. Sci. Vol. 61, 2004

Nakken, O., and Olsen, K. 1977. Target strength measurements of fish. Rapp. P.-V. Reun. Cons. Int. Explor. Mer, **170**: 52–69.

Neilson, J.D., and Perry, R.I. 1990. Diel vertical migrations of marine fishes: an obligate or facultative process? Adv. Mar. Biol. **26**: 115–168.

Ona, E., and Mitson, R.B. 1996. Acoustic sampling and signal processing near the seabed: the dead zone revisited. ICES J. Mar. Sci. **53**: 677–690.

Orlowski, A. 2000. Diel dynamics of acoustic measurements of Baltic fish. ICES J. Mar. Sci. **57**: 1196–1205.

Patel, R., Handegard, N.O., and Godø, O.R. 2004. Behaviour of herring (*Clupea harrengus* L.) to an approaching autonomous unverwater vehicle. ICES J. Mar. Sci. **61**: 1044–1049.

Smart, W.M. 1977. Textbook on spherical astronomy. Cambridge University Press, Cambridge, UK.

Stensholt, B.K., Aglen, A., Mehl, S., and Stensholt, E. 2002. Vertical density distributions of fish: a balance between environmental and physiological limitation. ICES J. Mar. Sci. **59**: 679–710.