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Geographical variation in the vertical distribution of cod (*Gadus morhua* L.) and availability to survey gears

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Abstract

Vertical density distributions of cod (*Gadus morhua* L.) are expressed in terms of their free vertical range to normalize for the variation in vertical extent that is related to change of pressure with depth. Thus the relative cumulative vertical profiles obtained from different sources and from places with different bottom depth become compatible for a discussion of the relationship between the vertical distribution and other environmental conditions. Of particular interest are the environmental conditions that influence the cod's vertical distribution and thereby cause a large discrepancy between availabilities of fish to different survey gears, and how these discrepancies and conditions vary with season and location. Such information may be used to assess bias and variance in the estimation of fish abundance. Analysis of acoustic and trawl catch data from demersal fish surveys in the Barents Sea during winter and summer show that in deep waters or along the polar front a large fraction of fish are found to distribute high in the water column and acoustic surveys detect more fish than the trawl surveys. When the density distribution stretches beyond mid-water, this typically happens at the warm side along the polar front, in agreement with the data storage tag records. Acoustic samples with large loss in the acoustic bottom dead zone are

found consistently over years around the Svalbard Bank. Loss in the acoustic bottom dead zone is estimated by combining information in the vertical profiles from acoustic and tag data.

Key words

acoustic bottom dead zone, capelin, cod, data storage tag, free vertical range, pelagic living, polar cod, vertical distribution.

1. Introduction

Acoustic dead zone loss and avoidance reactions to vessel and survey gear are major factors causing uncertainty in the abundance estimates of demersal physoclistous fish based on acoustic and trawl survey data. (Harden Jones and Scholes, 1981; Ona and Godø, 1990; Aglen, 1994; Aglen, 1996; Ona and Mitson, 1996; Aglen *et al.,* 1999; Hjellvik *et al.,* 2002). The catch in a bottom trawl is partly fish in the acoustic bottom dead zone and partly fish from a zone where they could be detected by acoustics. However, the fraction of fish from each zone is not known. Moreover, these fractions vary according to the vertical distribution patterns and behaviour of the target species. Fish modify their distribution and behaviour, within their own physiological limitation, in response to different environmental conditions, which vary over different locations and seasons (Neilson and Perry, 1990; Stensholt *et al.,* 2002). Therefore availability of fish to each survey gear varies accordingly. Thus spatial and temporal variation in environmental conditions contributes to the bias and variance in abundance estimates. Understanding these processes may lead to a better survey design and analytical methods to assess and reduce this part of the variance and bias.

In this paper we analyse and discuss the similarities and discrepancies between acoustic, trawl, and data storage tag (DST) data of northeast Arctic cod (*Gadus morhua* L.) in relation to geographical location and environmental condition. A method for estimating the data loss in the acoustic bottom dead zone based on acoustic and DST data is proposed.

2. Material and methods

Environmental and physiological factors influencing vertical profiles are investigated by analysis of acoustic, trawl, and temperature data together with depth and temperature time series from data storage tags (DST).

Tags were attached to adult northeast Arctic cod (53-81 cm) released into the Barents Sea in mid March 1996. Acoustic samples, which reflect the vertical distribution of all length groups combined, trawl and temperature samples are from four series of annual scientific surveys in the Barents Sea, namely, (1) summer demersal fish surveys during July-August, 1995 to 2001 (Aglen, 1999), (2) winter demersal fish surveys during February-March, 1996 to 2002 (Mehl, 1997), (3) 0-group surveys in August-September, 1996 to 2001 (Anon 1996), and (4) the pelagic surveys in September-October, 1996 to 2001 (Anon, 2001).

For the summer and winter surveys, acoustic values are allocated, mostly according to species composition from neighboring bottom trawl, to cod (*Gadus morhua*), haddock (*melanogrammus aeglefinus*), saithe (*Pollachius virens*) and redfish (*Sebastes*), and in addition to the non-target pelagic species blue whiting (*Micromesistius poutassou*), capelin (*Mallotus villosus*), and herring (*Clupea harengus*) where their distributions overlap with the target species. The s_A-values were aggregated in blocks of 1 nm length and 10 m depth from 10 m and downward. In demersal surveys, pelagic trawl hauls are few, and are decided according to acoustic indication. For the 0-group and pelagic surveys, the prey species of adult cod, e.g. young fish, capelin, herring, and polar cod (*Boreogadus saida*), are the target species. Their acoustic samples were aggregated in blocks of 5 nm length and 5 m depth.

At a location 's' and for a selected species, say cod, the theoretical s_A-value of the trawl catch (T_s) (Aglen, 1996) was compared to the observed acoustic s_A-value (A_s) along the trawl track. Let $a_s = A_s \cdot (A_s+T_s)^{-1}$; then $a_s < 0.5$ indicates a loss of acoustic value in the bottom dead zone as the bottom trawl catch exceeds the total observed acoustic s_A-value.

Since cod is a demersal physoclistous fish, i.e. with a closed swimbladder, the vertical distribution of samples from various depth ranges is expressed in terms of relative pressure reduction level (RPRL) with reference to the bottom pressure. A depth of X m is transformed to $RPRL = (B-X)(B+10)^{-1}$, where B is the bottom depth. The bottom restricted free vertical range (FVR_{bot}) is defined as a free vertical range that has its deepest end at seabed (Stensholt *et al.,* 2002). For all bottom depths, the FVR_{bot} of cod ranges from RPRL=0 to RPRL=0.5 (Harden Jones and Scholes, 1985). Thus samples from various bottom depths are normalized for variations in the extent of the free vertical range. Taking into account the fish's physiological limitation to rapid vertical movement, the FVR_{bot} is a natural yardstick suitable in a discussion, 'from the fish's point of view', of factors that influence the vertical distribution of demersal physoclists. A fish that can reach above the FVR_{bot} must be adapted to ‘pelagic living’ in the sense that its current FVR has departed from the seabed (Stensholt *et al*., 2002). Since the adaptation status is unknown, in practice a fish is identified as adapted to pelagic living when it is observed above the FVR_{bot}. For pelagic species the RPRL is sometimes calculated with reference to the deepest end of the distribution range (Stensholt *et al*., 2002).

The availability of fish to survey gears depends on the fish’s vertical density distribution, which in turn varies with geographic location. The variation is visualized by selecting samples which have total acoustic s_A-values greater than 5 and satisfy one of the following criteria:

- *More than 20% in summer survey samples (10% in winter survey samples) of the observed total s_A-value allocated to cod distributed above the FVR_{bot}, and more than 70% of the observed total s_A-value allocated to cod distributed more than 10 m above seabed.*
- *The entire distribution is within 20% of the FVR_{bot} (below RPRL = 0.1), and more than 90% of the observed total s_A-value allocated to cod is within 10 m above seabed.*

At sampling time, some cod adapted to pelagic living happens to be in the lower part of their current FVR, which overlaps with FVR_{bot}. Those cod are not counted under criterion 1, and thus the true fraction of cod adapted to pelagic living is generally higher than the observed percentage.

According to the ergodicity concept in time series analysis (Priestley, 1981) the depth distribution from time series of one tag may represent the depth distribution of several fish in the same length group migrating within the same kind of environment during the same season. For fish of the same length group, the collection over all storage tag records and the collection over the different locations of acoustic records should therefore produce the same depth distribution in the same season, except that a tag includes records from the acoustic dead zone.

The fraction, D, of adult cod in the acoustic bottom dead zone was estimated from tag and acoustic data. Let B and P be the fractions in the bottom channel above the dead zone (e.g. < 10 m above seabed) and in the pelagic channel (e.g. > 10 m above seabed), respectively. Thus,

$$D + B + P = 1.$$

Tag and acoustic data give the fractions p_t and p_a in the pelagic channel, respectively.

$$\textit{Assume: } D > 0. \textit{ If } (1 - p_a) \cdot p_a^{-1} = B \cdot P^{-1} \textit{ and } p_t = P,$$

$$\textit{then } p_a = P \cdot (B+P)^{-1} = P \cdot (1 - D)^{-1} > P = p_t.$$

When $B \cdot P^{-1}$ is estimated by $(1 - p_a) \cdot p_a^{-1}$ from acoustic data and P by p_t from tag data, then

$$D = 1 - P - P \cdot (B \cdot P^{-1}) \textit{ is estimated}$$
$$\textit{by } 1 - p_t - p_t \cdot (1 - p_a) \cdot p_a^{-1} = 1 - p_t \cdot p_a^{-1}.$$

Here p_t is the depth frequency of tagged fish in the pelagic channel (e.g. at depth > 10 m above the daily maximal depth) weighted with the squared fish length, which is theoretically proportional to the acoustic s_A-value (Foote, 1987). If tag records and acoustic samples are from water columns with similar environmental conditions, then the vector (D, B, P) is approximately the same, and p_a greater than or equal p_t. However if $p_a < p_t$, the tag records and the acoustic samples come from different vertical distributions.

The classification of tag observations as ‘pelagic channel’ or ‘bottom channel’ including the dead zone gives a smaller number of borderline cases, and consequently a smaller number of mistakes, than classification as ‘dead zone’ or ‘(just) above dead zone’, especially in tags with low depth resolution. However, both classifications depend on the daily maximum depth being a reasonable estimate of the bottom depth.

Day and night are defined by the sun’s crossing the height circle 5° below the horizon. Since the storage tags do not record geographic location, their recorded Greenwich Mean Time (GMT) hours were converted to day and night hours in the Barents Sea (Table 1) at the 1996 winter and summer survey sampling positions.

3. Results

3.1 Geographic variation of loss in the acoustic bottom dead zone

Acoustic samples from winter and summer surveys satisfying criterion (1), with total s_A-value > 5, are mainly found along the warm side of the polar front (Map 1a, 1d, 2a, 2e). Summer samples satisfying criterion (2) are found consistently mainly around the Svalbard Bank (Map 2b). The Svalbard Bank is not covered in winter surveys, but winter samples satisfying criterion (2) are mainly found around the southern coast of the

Barents Sea and along the southwest steep edge of Svalbard Bank. Most summer and winter samples, with total s_A-value <5, show fish distribution closer to seabed, but some samples in areas of depth greater than 200 m satisfy criterion (1).

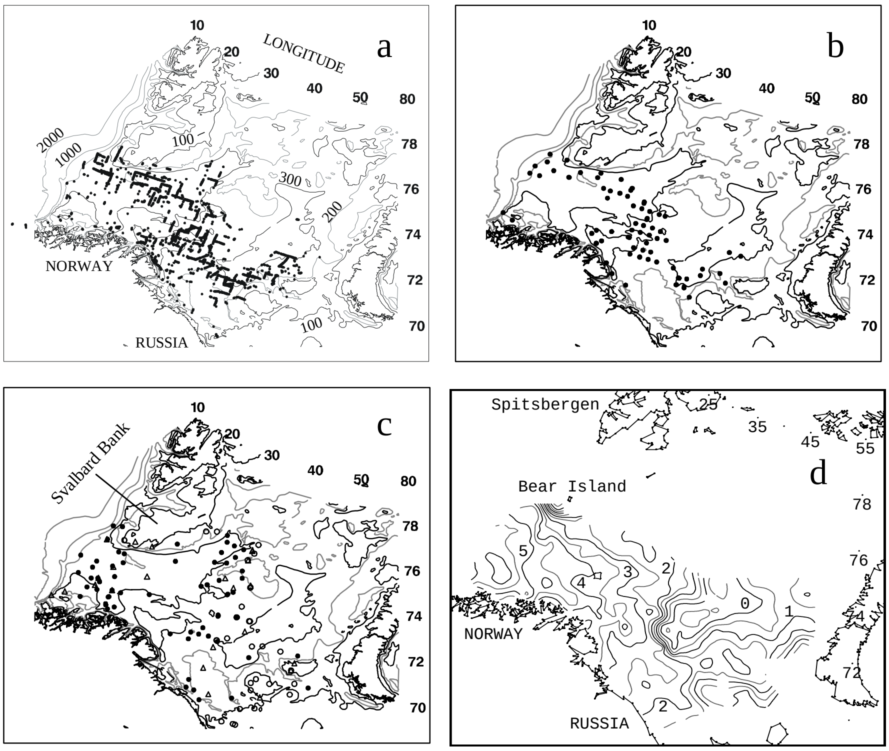
Stations with co-located acoustic and trawl samples, which satisfy criterion (1) and have a_s > 0.5, cluster along the warm side of the polar front with depth deeper than 200 m (Map 1b, 2c). Stations that satisfy criterion (2) and have a_s < 0.5 as well as stations that have total loss in the acoustic bottom dead zone (acoustic s_A-value equal to 0, but large trawl catch) mostly cluster at the Svalbard Bank and coastal areas in summer (Map 2d), but show no clear pattern in winter (Map 1c). Large or total loss in the acoustic bottom dead zone is more common in summer surveys than in winter surveys. Although in summer and autumn both acoustic and tag data show that a significant proportion of cod is found above FVR_{bot} (Figure 1a, 2b, 2c, 2e, 2f, Table 1), a significant proportion of cod is also found in the acoustic bottom dead zone, as verified by trawl data. During the winter survey most cod distribute within FVR_{bot} (Figure 1b), but at the same time above the acoustic bottom dead zone. Results above are supported by the vertical profiles from DSTs (Figure 2; Table 1 and 2). Thus one should expect acoustic stock estimates to be more reliable in winter than in summer.

3.2 An estimate of the acoustic bottom dead zone loss

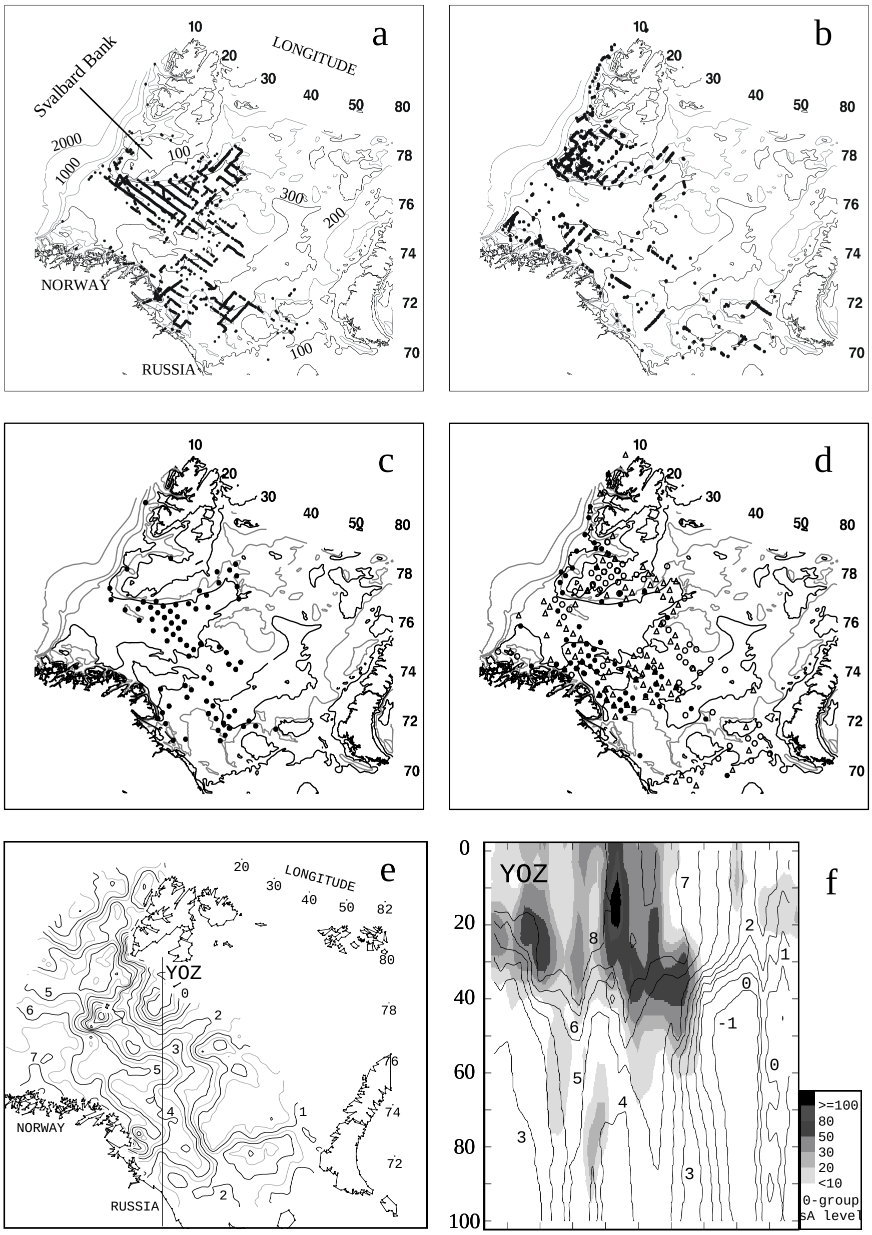
Acoustic bottom dead zone loss is estimated on the basis of six tagged cod and acoustic samples from winter 1997. In winter, tagged cod have daily maximal depths mainly > 200m and the weighted frequency is p_t = 42.9 % (43.5 % without weighting). Acoustic s_A-values for bottom depth > 200 m give p_a = 63.3% (Stensholt *et al.,* 2002). Estimated loss is $D = 1 - p_t p_a^{-1} = 1 – 429(633^{-1}) = 32.2\%$. For comparison, 28.9% of the depth observations in the tags are within 2 m above the daily maximal depth (34% at night and 18.7% at day). A 2 m zone is chosen because the depth resolution in the tag records is between 1.3 m and 2 m. With bottom depth ‘d’ meters, the estimated effective height lost due to the dead zone is 0.875 + 0.004d (Aglen, 1996).

Table 1. For each month is shown the number of observations of cod above one bottom restricted free vertical range (FVR_{bot}), using daily maximal depth as bottom depth. Total (number of) tags; P = number of tags with at least one depth recorded above the FVR_{bot}.

			2-hour intervals in GMT												
Month year	Total tags	P	0 to 1	2 to 3	4 to 5	6 to 7	8 to 9	10 to 11	12 to 13	14 to 15	16 to 17	18 to 19	20 to 21	22 to 23	Day -time hours
Apr 96	12	2	1	-	-	1	-	-	-	-	-	-	-	-	0-20
May 96	12	1	2	-	-	-	1	-	-	-	-	2	3	2	0-24
Jun 96	12	1	3	1	1	1	-	-	2	1	3	2	3	2	0-24
Jul 96	10	6	6	7	7	6	6	4	6	2	6	9	6	6	0-24
Aug 96	8	4	1	2	-	-	-	1	-	-	-	1	2	3	0-21
Sep 96	8	5	9	2	-	2	6	12	6	21	43	39	33	29	3-17
Oct 96	8	3	7	3	-	-	-	1	1	10	10	11	7	6	6-15
Nov 96	8	2	-	1	1	1	1	3	1	-	-	-	-	-	8-13
Dec 96	6	0	-	-	-	-	-	-	-	-	-	-	-	-	none
Jan 97	6	2	1	1	-	-	-	-	2	-	-	-	1	-	8-13
Feb 97	6	2	1	1	-	-	-	-	-	2	1	-	-	-	6-15
Mar 97	4	0	-	-	-	-	-	-	-	-	-	-	-	-	4-17



*Map 1. Winter surveys 1996 to 2002. Bathymetric maps (in m) with acoustic samples (•) that (a) have total acoustic s_A-value > 5 and satisfy criterion (1); have total sum of s_A-values from acoustic and trawl samples > 5 and (b) satisfy criterion (1) and have a_s >0.5; (c) satisfy criterion (2) and have a_s < 0.5. Circle (**o**) and triangle (**Δ**) indicate total loss in acoustic bottom dead zone at the trawl stations where the theoretical s_A-values from trawl catch is less than 1 and greater than 1, respectively. (d) Temperature distribution at 100m depth shows the Polar front area where Arctic water mass (<0 C°) meet Atlantic water mass (>3 C°) in February-March 1996.*



*Map 2. Summer surveys 1995 to 2001. Bathymetric maps (in m) with acoustic samples (•) that have total acoustic s_A-value > 5 and (a) satisfy criterion (1); (b) satisfy criterion (2); that have total sum of s_A-values from acoustic and trawl samples > 5 and (c) satisfy criterion (1) and have a_s >0.5; (d) satisfy criterion (2) and have a_s <0.5. Circle (**o**) and triangle (Δ) indicate total loss in acoustic bottom dead zone at the trawl stations where theoretical s_A-values from trawl catch < 1 and > 1, respectively. (e) Temperature distribution at 100m depth in August-September 1996; (f) vertical distribution of temperature and 0-group acoustic density along YOZ transect as indicated in (e).*

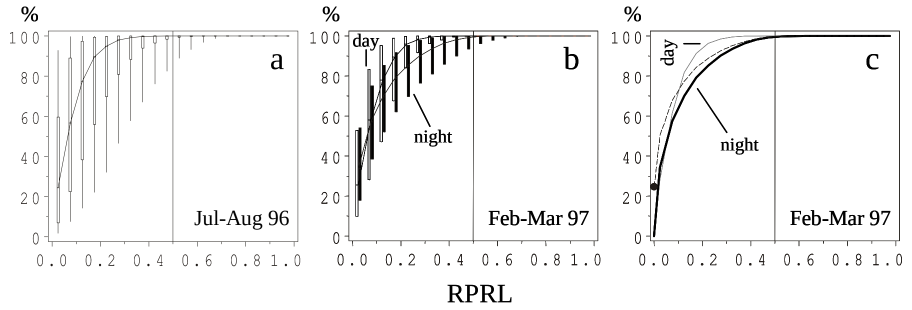


Figure 1. *Distribution of relative cumulative vertical profiles of acoustic density of cod from seabed to surface in terms of RPRL, (a) summer survey, 1996; (b) day and night profiles from winter survey 1997, (c) as (b) but with the night median curve (curve with •) adjusted upward for unequal day and night loss in the acoustic bottom dead zone. Lines join the medians. Thin boxes show the inter-quartile range, day - white boxes and night - black boxes. Whiskers show 10-90 percentile ranges. Reference line at 0.5 indicates FVR_{bot} of cod (RPRL range from 0 to 0.5).*

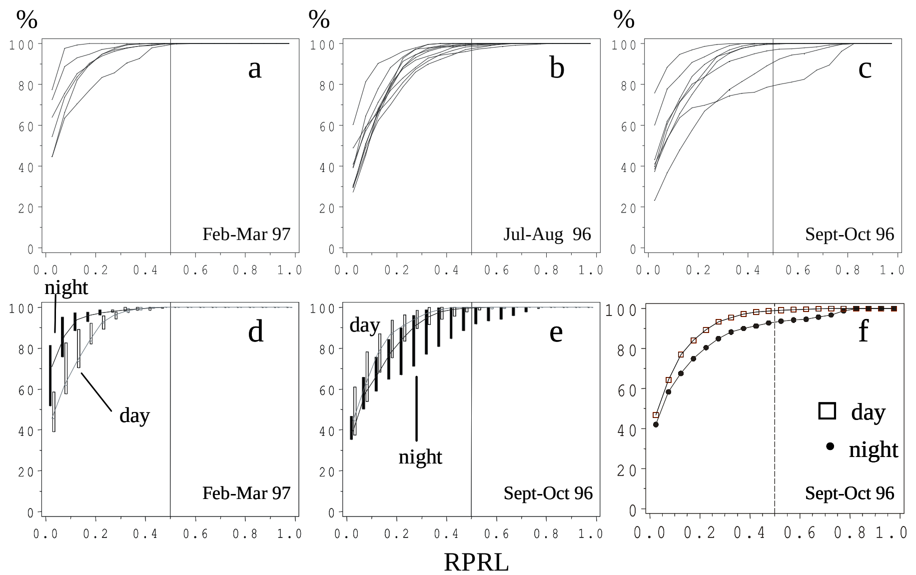


Figure 2. *From depth time series of each tagged adult cod. Distribution of relative cumulative frequencies of depth records in terms of RPRL; (a) – (c) each line is the vertical profile for one cod; (d) – (f) day and night distribution for all tagged cod; in (f) after conversion to theoretical s_A-values. Lines join the medians. Thin boxes show the inter-quartile ranges of the distributions of the cod vertical profiles at the indicated RPRL level, day - white boxes and night - black boxes.*

3.3 The extent of vertical migration and diurnal pattern

Relative cumulative vertical profiles from acoustic data and from DST both show that cod mainly distribute within the FVR_{bot}, (Figures 1 and 2)**,** which reflects that a physiological limitation to change of pressure is imposed on its vertical movement. Profiles from both sources show diurnal patterns for cod. Adult, tagged cod have day ascent in winter (Figure 2d) and night ascent in autumn (Figure 2e, 2f). In some years the winter profiles of acoustic samples show a crossing between day and adjusted night median curves (Figure 1c). The winter vertical profiles of tagged cod (Figure 2a, 2d) support the explanation that this crossing is due to small fish ascending at night and large fish ascending during the day (Aglen *et al*., 1999; Einarsson, 2001; Stensholt *et al*., 2002). In winter surveys small cod dominate in the pelagic trawl catch, but there is a relatively high component of large cod in the day catch (Figure 3a, 3b). In all surveys large cod are rarely caught in the pelagic trawl hauls above FVR_{bot} (Figure 3c) compared to the observed fraction in tagged cod. For example, in September, 7.2% of the recorded depths of tagged cod are at depths above FVR_{bot}."

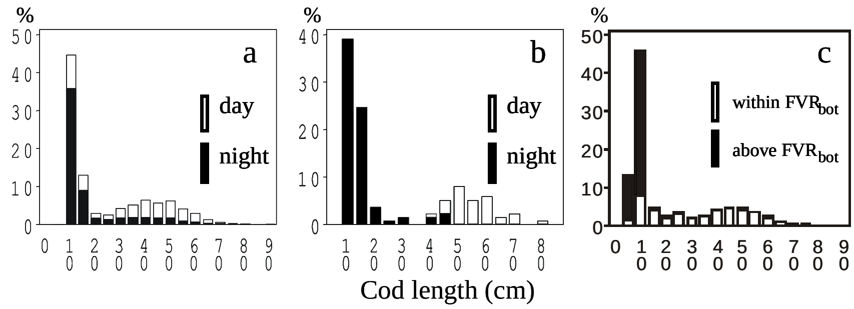


Figure 3. Winter surveys 1995-2002, day and night length distribution of cod caught in pelagic trawls from (a) all pelagic hauls; (b) pelagic hauls with maximal trawl depth above FVR_{bot}. Pelagic surveys in September (c) length distribution of cod caught in the trawls with maximal trawl depth above FVR_{bot} - black and within FVR_{bot} – white.

3.4 Modification of cod vertical migration patterns according to prey behaviour

Acoustic samples from summer and winter demersal surveys show that in areas where cod and capelin distributions overlap, a significant proportion of cod adapts to pelagic living (Figure 4). The average temperature there is around 0°C to 3°C and average salinity is around 34.9 to 35.0 ppt. In summer the cod distribute mainly below the thermocline (Figure 4a). In winter a higher fraction of the cod's s_A-value is found above FVR_{bot} at night than during the day **(**Figure 4b**)** and at daytime they are mainly within the FVR_{bot} (Figure 4c). But in winter tagged cod mainly distribute within the FVR_{bot}, ascend mostly during the day and stay close to the bottom more often at night (Figure 2d). The profiles of acoustic and tagged cod have lower variation in winter than in summer and autumn (Figure 1, 2, Table 2). This may be due to cod feeding mostly on a few species e.g. capelin (Orlova *et al.,* 2000).

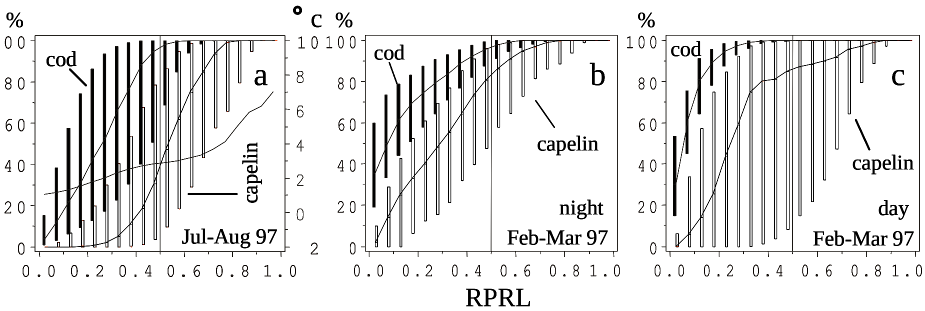


Figure 4. Distribution, across acoustic samples of cod and capelin where their distributions overlap, of relative cumulative vertical profiles of cod acoustic density (black boxes) and capelin acoustic density (white boxes), expressed in terms of RPRL with reference to the bottom pressure. (a) Summer survey 1997 with average temperature profiles. Winter survey 1997, (b) night samples, (c) day samples. Lines join the medians and thin boxes show the inter-quartile range of the distribution. Reference line at 0.5 indicates one FVR_{bot} of cod.

Table 2. For each tagged cod, relative frequency in percent of depth observations higher than 10 m above the maximal depth of the day, in April-May 1996, June-July 1996, August 1996, September-November 1996, December 1996-January1997, and February-March 1997. All, day, and night are for all, day, and night records in the season.

Tag no.	Length (cm)	Apr - May	Jun - Jul	Aug	Sep-Nov			Dec - Jan	Feb-Mar		
					all	day	night		all	day	night
106	59	39	64	60	35	32	37	-	-	-	-
110	82	64	53	16	59	61	58	-	-	-	-
117	74	49	74	44	29	41	23	24	71	87	63
131	72	51	67	61	63	67	60	35	48	65	31
191	56	45	74	37	67	55	74	50	43	54	32
204	65	51	66	41	43	32	49	30	69	76	65
206	73	41	71	38	25	13	32	27	56	72	44
246	64	26	60	54	58	59	58	26	44	66	33

In summer capelin migrate across the polar front to feed in the Arctic waters until autumn (Gjøsæter, 1998). From 670 hauls from the pelagic surveys in September-October 1996-2001, 331 hauls contained cod which confirmed that cod migrate into the autumn feeding areas of capelin and polar cod. In autumn tagged cod stay close to the bottom equally often at day and night with large variation among individual vertical profiles (Figure 2c, 2e, 2f). A higher proportion of tagged adult cod distributes above the FVR_{bot} in July-October (Figure 2b, 2c, 5b, 5c, 5e, 5f, Table 1) than in the rest of the year, e.g. in winter (Figure 2a, 2d, 5a, 5d). In July-October, some tagged cod migrate to areas mainly shallower than 250m. For shorter or longer duration, cod stay in different environments, e.g. the polar front (-1°C to 3°C) or a coastal front (4°C to 6°C) (Figure 5b, 5c, 5e, 5f, Stensholt and Stensholt, 1999; Stensholt, 2001). Occasionally tagged cod adapt to pelagic living and ascend to the warmer water above or around the thermocline (Figure 5b, 5c, 5e, 5f). These ascents occur mainly just before sunset or at night (Table 1). Common prey for adult cod have night ascent and some distribute above or around the thermocline e.g. 0-aged fish (Map 2f) (Stensholt and Nakken, 2001), capelin, polar cod, herring, and other small fish (Figure 6, 7).

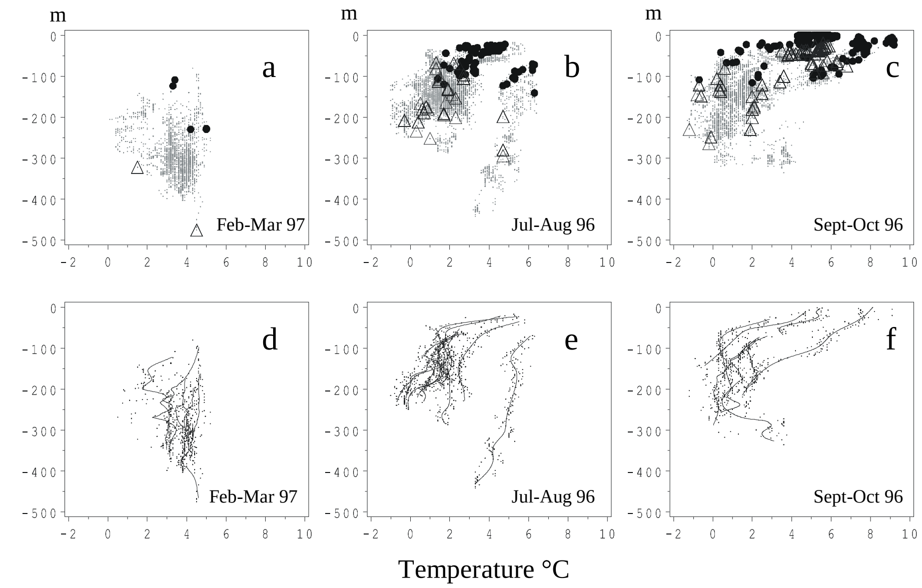


Figure 5. (a) – (c) Large dot (●) shows depth (m.) and temperature (°C) records from above the FVR_{bot}; triangle (Δ) shows maximal depth of each day with ascents beyond FVR_{bot}; small dot (•) shows depth and temperature distribution from data storage tag records. (d) - (f) Depth-temperature profiles of each cod.

Polar cod and capelin have diurnal vertical migration with night ascent (Figure 7a, 7b). A majority of samples show that the main concentration of capelin is higher up in the water-column than is the concentration of polar cod. Capelin have high concentration mainly around mid water or within the lower half of the water column at day, and they ascend to be mainly above the bottom half of the water column at night (Figure 7b). Polar cod mainly distribute within the FVR_{bot} (Figure 7a), confirming that their closed swimbladder imposes a restriction to rapid vertical movement but not so with capelin, an open swimbladder (physostomous) fish (Figure 7c).

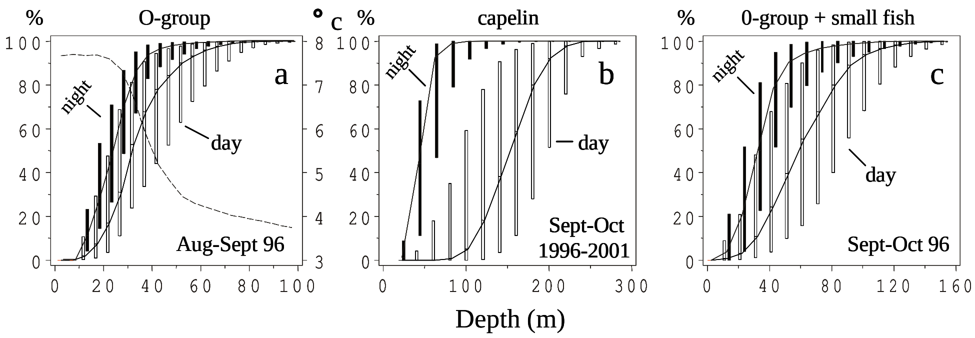


Figure 6. Distribution of the day and night relative cumulative vertical profiles of acoustic s_A-values of (a) 0-group fish, with median curve of the vertical temperature profile; (b) capelin; (c) 0-group and small fish. Lines join the medians. Thin boxes show the inter-quartile ranges of the distributions, day - white boxes, and night - black boxes.

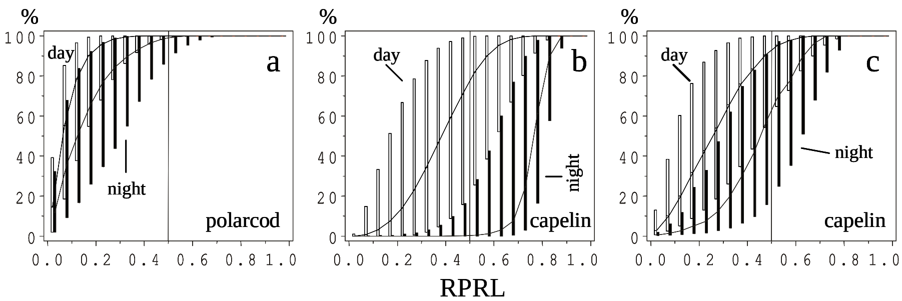


Figure 7. Distribution, over September 1996-2001 survey samples, of relative cumulative vertical profiles of acoustic density in terms of RPRL with reference to the seabed (a) day and night distribution of polar cod; (b) day and night distribution of capelin; (c) day and night distribution of capelin expressed in terms of RPRL with reference to the deepest end of the distribution range show that capelin, an open swimbladder, has a wider vertical distribution range than cod. Lines join the medians. Thin boxes show the inter-quartile range, day - white boxes, and night - black boxes.

4. Discussion

The vertical density distribution varies with time and the geographical region as shown when the acoustic relative cumulative vertical profiles are classified according to time of the day or season or according to the chosen criteria (1) and (2). An analysis of the environmental conditions of these regions suggests what factors cause the cod to modify its normal vertical distribution.

The polar front, coastal fronts and the thermocline are natural boundaries of the distribution of several fish species in the Barents Sea (Loeng *et al.,* 1992; Gjøsæter *et al.,*1992; Aglen, 1999; Stensholt and Nakken, 2001). Cod and important prey species of cod have high concentrations along these thermal fronts. Some cod prey species distribute pelagically and some are above the thermocline. Diel vertical migration is observed in some prey species of cod and occasionally in cod (Gjøsæter *et al.,* 1992; Stensholt and Nakken, 2001; Stensholt *et al.,* 2002). DST records confirm that during April and August-October cod, that adapt to pelagic living, migrate mostly in thermal front regions and occasionally have diel vertical migration (Stensholt, 2001). Samples from winter and summer surveys that satisfy criterion (1), and have acoustic density higher than trawl density, are found mainly along the warm side of the polar front. In winter immature cod concentrate and feed on capelin along the polar front (Aglen, 1999), which is a wintering area of capelin, and it is relatively high in the cod diet composition (Orlova *et al.,* 2000).

Samples from summer surveys that satisfy criterion (2) and have trawl density higher than the acoustic density occur persistently around the Svalbard Bank. The loss in the acoustic bottom dead zone is very high and sometimes total. The bank has a large biological production and has the most complicated hydrography in the Barents Sea (Loeng *et al.,*1992). Over and around the bank, there is a complicated structure of different water masses, such as melted water from ice, Arctic water, Atlantic water, and Svalbard Bank water, together with oceanic and tidal currents (Midttun, 1989; Gjevik *et al.,* 1990), eddies, thermocline, summer front, and polar front. It is difficult to single out the natural factors that affect the cod's vertical distribution. In areas with strong current, cod and saithe reduce the extent of their vertical distribution and stay mainly within 10 m above the seabed (Stensholt, 2001; Stensholt *et al.,* 2002). In general, current speed is reduced near the seabed. Disagreement between tag and acoustic relative cumulative vertical profiles in areas shallower than 200 m during summer and autumn may indicate an impact of vessel avoidance on acoustic samples (Stensholt *et al.,* 2002). Even so, the reduction of the vertical extensions is not as extreme as in samples found in areas with strong current.

In summer surveys, most samples indicate loss in the acoustic bottom dead zone even though a significant fraction of fish distributes above FVR_{bot}, in agreement with tag observations (Table 2). Thus one must expect larger uncertainty in a stock estimate based on summer surveys than in one based on winter surveys. To reduce uncertainty, the survey area should be subdivided into several strata, each stratum containing stations satisfying specified criteria, such as our criteria 1 or 2. The assessment method should be modified accordingly within each stratum.

The larger variation among vertical profiles in summer and autumn than in winter (Table 2) shows that different individuals adapt to very different foraging strategies for a large variety of prey species (Orlova *et al.,* 2000). Our results confirm that cod is an opportunistic feeder, and the seasonal patterns in the cod's spatial distribution and migration are influenced by its prey species' abundance, spatial distribution, accessibility, and behaviour (Neilson and Perry, 1990).

5. Conclusion

The relative cumulative vertical density distributions of cod and its preys, obtained at different bottom depths from survey and tag data, are normalized and become comparable when they are expressed in terms of the free vertical range. Thus, the modification of the fish vertical distribution, due to the spatial and temporal variation in environmental conditions other than change of pressure becomes apparent and can be quantified. This provides information for assessing bias and variance in the estimation of fish abundance. Acoustic samples with a relatively high fraction of cod distributed above FVR_{bot} (5 m or more above midwater) are found along the warm side of the polar front and in deep water. The cod's adaptation to pelagic living as well as its diurnal vertical migration is related to foraging and the distribution of its prey species. Acoustic samples with relatively high loss in the acoustic bottom dead zone are found at and around the Svalbard Bank with the most complicated hydrographical conditions in the Barents Sea. The relative loss in the dead zone is estimated by $D = 1 - p_t \cdot (p_a)^{-1}$, where p_t and p_a are the fractions of cod found in the pelagic zone from tag and acoustic data, respectively.

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