Spatial density distributions of fish, a balance between environmental

and physiological limitation

by

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ABSTRACT

Data (trawl, acoustic, CTD) from four scientific survey series , i.e. along the Norwegian coast, in the North Sea, and in the Barents Sea summer and winter, are used to describe and discuss the spatial density distributions of blue whiting, cod, haddock, redfish, saithe, capelin, and herring, in banks and shelf sea of depth mainly < 500 m, in relation to environmental conditions (depth, change of pressure, temperature, salinity, daylight, and physiological limitations). For cod, also information from data storage tags (DST) is used.

For the demersal physoclists the relative vertical profiles are defined in terms of relative pressure reduction with reference to the pressure at the bottom. Thus vertical profiles with different bottom depth can be expressed in terms of free vertical range (FVR) and compared on a physiological basis. This restriction to rapid vertical movement is evident in the studied physoclist species. The acoustic s_A-values show that blue whiting, haddock, saithe, cod, and redfish are mainly distributed within the bottom half of the water column, but also that they adapt to pelagic living. Haddock and blue whiting are more often found to distribute higher into the water column than saithe, cod, and redfish. Pelagic living is seen especially in areas with high acoustic s_A-values and where the bottom is deeper than 200m.

Day and night vertical profiles in terms of FVR are corrected for unequal day and night losses in the bottom acoustic dead zone. In most years, evidence of diurnal vertical migration for all seven species are found when day and night are clearly distinguishable. In many cases of demersal fish there is higher relative acoustic density in the mid-range of the bottom half of the water column at daytime than nighttime. At nighttime there is a degree of separation, one group of fish descends to aggregate near the seabed and another ascends.

Keywords: Acoustic dead zone, buoyancy status, diurnal vertical migration, free vertical range, hydrostatic pressure, physoclists, physostomes, swimbladder.

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INTRODUCTION

In marine teleosts with swimbladder, it occupies 3.1 – 5.7% of the body volume (Alexander, 1966; Marshall, 1972). One of its functions is to be a buoyancy organ (Blaxter and Tytler, 1978). However, its physiological limitation in adaptation to pressure changes imposes restrictions on vertical migration (Harden Jones, 1949, 1951, 1952; Brawn, 1962; Kutchai and Steen, 1971; Blaxter and Tytler, 1972, 1978; Ross, 1979; Harden Jones and Scholes, 1981, 1985; Arnold and Greer Walker, 1992). There are metabolic costs of swimbladder adaptation and of compensatory swimming when the buoyancy is not neutral (Alexander, 1970, 1972; Blaxter and Tytler, 1978).

During pressure reduction fish with open swimbladder (physostomes, e.g. herring and capelin), may release gas through a pneumatic duct. Gas secretion is known to be slow and insignificant in physostomes. Brawn's experiment indicates that herring take in air at the surface. The amount of air determines the level of neutral buoyancy, which may be no more than 50 to 100 m. In experiments physostomes respond to rapid pressure increases by ascending. (Brawn, 1962; Blaxter and Tytler, 1978; Sundnes and Bratland, 1972).

Fish with closed swimbladder (physoclists, e.g. blue whiting, cod, haddock, redfish and saithe) produce gas by secretion in response to under-buoyancy and remove gas by resorption in response to over-buoyancy. At any time the gas content determines a plane of neutral buoyancy. Around that plane is a zone of free vertical range (FVR) within which the fish can swim freely and compensate for the deviation from neutral buoyancy by means of swimming movements (Harden Jones, 1949, 1951, 1952; Harden Jones and Scholes, 1981, 1985; Tytler and Blaxter, 1973, 1977; Blaxter and Tytler, 1972, 1978; Arnold and Greer Walker, 1992). Because of gas loss by passive diffusion due to permeability of the swimbladder wall, there may be a maximal depth where neutral buoyancy maintenance is possible (Kutchai and Steen, 1971; Ross, 1976, 1979; Blaxter and Tytler, 1978).

By ascending too far above the neutral buoyancy plane, the physoclists get too over-buoyant, risking uncontrollable ascent to the surface or a swimbladder rupture (Harden Jones, 1951, 1952; Tytler and Blaxter, 1973; Harden Jones and Scholes, 1985), while physostomes get rid of surplus gas through their duct (Brawn, 1962). On the other hand, at deep dives physoclists has an advantage over physostomes because their gas secretion reduces under-buoyancy so that excessive under-buoyancy below the limit of FVR does not impose a serious problem. Thus

physoclists and physostomes are naturally disposed for different patterns of vertical distribution and vertical migration.

The FVR allows rapid vertical movement among physoclists between the depth planes at M and m meters, the limit depth levels for under- and over-buoyancy given the gas content of the swimbladder. Therefore the ratio (m+10)/(M+10) can be considered a "theoretical" physiological limit to pressure changes which allow controlled swimming despite the deviation from neutral buoyancy. Experiments (Harden Jones and Scholes, 1985) determined that the ratio is ca. 50% in the case of cod (Materials and Methods). We expect that saithe, haddock, redfish and blue whiting have an FVR, perhaps with a different pressure ratio than cod.

How is this migration restriction in individual physoclists reflected in the large-scale vertical distribution? Assuming that the fish often go to the bottom channel, then large-scale vertical distributions should stretch up to as much as one FVR from the sea bottom. By using the same method on different physoclist species, one may get some idea about the extent of their FVR.

Temperature and salinity impose environmental barriers to fish distribution. In cod a physiological adaptation process starts when it enters waters colder than 2ºC, and enables it to live in colder temperatures. It also tolerates cold shocks from 4ºC to 0ºC in normal sea-water. High temperature (above 10ºC) with low salinity may be lethal for large cod. (Woodhead and Woodhead 1959, 1965; Harden Jones and Scholes, 1974). Björnsson $et\ al.$ (2001) found that large Icelandic cod ($\geq$ 2 kg) cannot tolerate prolonged exposure to 16ºC with salinity 32°/$_{oo}$. The optimal temperature for cod's growth found in laboratory experiments is higher than its natural ambient temperature. In the natural environment preferred temperature is just one of many concerns, like availability of food and avoidance of predation (Björnsson $et\ al.$, 2001; Kristiansen $et\ al.$, 2001).

Time series of depth and temperature from data storage tags (DST) attached to adult North-east Arctic cod (1996-97) have shown that the cod's movements are related to daylight, season, depth, temperature, tidal current, and free vertical range (FVR) (Stensholt, 2001). In August-November a diel vertical migration (DVM) was common. The few series that were long enough showed periods of DVM with short daytime visits to the upper layer in January – March. DVM generally occurred at depth below 200 m and the extent of the daily range was typically from 50 to 100m. In terms of FVR-units the daily ranges were larger in summer and autumn than in winter and occasionally exceed the FVR. Temperature generally varied between 2°C and 6°C in

winter while in summer and autumn it has large variation, sometimes in warm waters up to 10°C and sometimes in cold waters down to −1.7°C, with indication that cod migrate near fronts or penetrate through the thermocline.

In the present study the information from acoustic registrations (s_A-values), trawl sampling, and CTD, are combined to investigate the vertical distribution of cod, haddock, saithe, redfish, blue whiting, herring, and capelin, as well as their relationship with environment, e.g. depth, pressure, tidal current, temperature and salinity.

The fish vertical migration behaviour has effect on the accuracy of acoustic stock estimate of demersal physoclists due to the buoyancy status and the loss of acoustic fish information in the bottom dead zone. The accuracy can be improved, when the amount that is lost varies according to predictable environmental conditions, e.g. daylight and tidal current. How should one interpret vertical profiles, which are based on the observed acoustic s_A-values of the variable proportion of fish above the dead zone? In the case of cod the results are discussed in view of information from DST. It gives essential details on the daily vertical ranges and the time spent at each depth level.

MATERIALS AND METHODS

The Institute of Marine Research, Bergen performs several annual acoustic surveys for fish stock assessment. In this study observations of acoustic backscattering (s_A-values) from several acoustic surveys aimed at demersal fish have been used. Data from the selected surveys contains acoustic values that are allocated to the demersal species cod, haddock, saithe and redfish, and in addition values allocated to the pelagic species capelin, blue whiting, and herring. The latter are non-target species that are not completely covered by the selected surveys.

Data from the following annual surveys have been used: saithe, haddock, blue whiting, herring from a saithe survey along the Norwegian coast from 62ºN to 72ºN during October-November in the years 1992-2000 (Nedreaas, 1995; Korsbrekke and Mehl, 2000) and a demersal fish survey in the North Sea also during October-November in the years 1992-2000 (Anon., 1999), and cod, haddock, redfish, capelin, herring from two different annual demersal fish surveys in the Barents Sea, one during July-August in the years 1995-2000 (Aglen and Nakken 1996; Aglen 1999, 2001a; Aglen *et al*. 2001) and one during February-March in the years 1996-2001 (Mehl and Nakken 1996; Mehl 1997, 1998, 1999; Michalsen *et al*, 2000). All surveys mainly cover banks and shelf sea of depth < 500 m.

The saithe survey is a pure acoustic survey, which means that the decision regarding when and where to make trawl hauls (both demersal and pelagic) is largely based on the acoustic observations. This survey covers areas with highly variable topography, and the survey design therefore varies between regions. The other surveys are combined bottom trawl and acoustic surveys, where there is a fixed grid of predetermined bottom trawl positions used both for a swept area estimate and for the interpretation of the acoustic data. Some additional hauls (both demersal and pelagic) are made for identifying acoustic recordings, and these are only used for the acoustic estimate. These surveys mainly follow parallel transects with regular spacing. In all the surveys CTD-measurements (vertical profiles of salinity and temperature) are made at nearly all trawl positions. The exceptions to this are the Barents Sea summer surveys in 1996 and 1997, and the Barents Sea winter survey in 2000, where parts of the area were covered by hired fishing vessels not equipped for CTD measurements. Typical survey line transects and trawl stations for each of the surveys are shown in bathymetric maps in Figures 1-3.

To investigate the relationship between fish and environmental variables, their values must exist at the same location over the entire studied area. The values of temperature, salinity, sea bottom depth, acoustic s_A-values, and density of the studied species at unsampled locations are estimated on the basis of observed values from neighbouring locations by application of geostatistical methods (Cressie, 1991; Stensholt and Sunnanå, 1996) available in the software ISATIS (ISATIS, 1997), i.e. kriging with moving window.

Acoustic data and vertical density profile

Area back scattering (s_A-values), as defined in MacLennan et al. (2001), were sampled with echo-integrators (Knudsen, 1990; Foote *et al.,* 1991). During the surveys the acoustic data were scrutinized and the s_A-values were allocated to a number of categories (species or groups of species). For each survey series there is a list of standard categories, where usually the target species and several non-target species are defined as separate categories. Cod, haddock, redfish, herring and capelin are each defined as separate categories in the Barents Sea surveys, while values representing saithe are merged with several non-target species in the category "other demersal". In the coastal saithe survey and the North Sea survey saithe, haddock and blue whiting is defined as separate categories.

During daily scrutinizing onboard the survey vessel, the post-processing system (BEI, Knudsen, 1990) presents the echogram data (from surface to bottom) in blocks of 5 nautical

miles (nm) horizontal. Within such a block the user can define a number of sub-blocks (regular or irregular depth intervals or rectangular boxes). Within each sub-block the operator partitions the s_A-values (averaged over 5 nm) into the separate categories by using the trawl catch species composition of neighboring stations and subjective judgment based on experience. Thus for each acoustic sample within the same sub-block all species have the same vertical s_A density profile (in relative terms). When the scrutinized data are stored in the database, single values are averaged within blocks of 1 nm horizontal resolution and 10m vertical resolution, relating to the sea surface. In addition the values from bottom up to 10m above bottom are stored with 1 m vertical resolution. For the present study this database is used to obtain the vertical s_A density profiles for each 1 nm interval for each selected species. These profiles are used for investigating vertical distributions of fish in relation to bottom depth, as well as the day/night differences for a joint study of fish distribution, temperature and salinity.

To investigate the vertical distribution of a physostome species, we select the acoustic samples with reasonably large total aggregated s_A-values along the water column over 1 nm, as in Stensholt and Nakken (2001). To normalize the large spatial variation in absolute values, for each sample s the cumulative relative acoustic s_A-values, C(s,v)% of fish are calculated in 10 m depth intervals from surface down to 10·v meters, v=1, 2, …, D, with bottom depth in the interval (10·(D-1) , 10·D]. For each depth step (v=1,2, …) the calculations of C(s,v) need samples with bottom depth at least 10v meters, and thus the set of samples is reduced with increasing v. To correct for this effect, we subdivide the bottom depth in a fixed number of equal intervals and accumulate the relative s_A-values from the surface down to the chosen fractions of the bottom depth. For each level of relative depth, say 0%, 5%, 10%, …, 100% of the bottom depth, the distribution over all samples of the cumulative relative values are presented in terms of median and inter-quartile range (Figure 14).

For physoclists a description of the large-scale vertical distribution should be related to the physiological limitation due to pressure change of the vertical migration for individual physoclistous fish. Theoretically every physoclist has an FVR for rapid vertical movements. For cod it is determined experimentally to be the range between 25% reduction (at depth m) and 50% increase (at depth M) of the pressure (at depth d) where the fish is adapted to neutral buoyancy. (Harden Jones and Scholes, 1985). With neutral buoyancy at d meters, the pressure ratios are

$$(m + 10)/(d + 10) = 0.75 \text{ and } (M + 10)/(d + 10) = 1.5, \text{ so } M + 10 = 2·(m + 10).$$

Thus, for cod, a full FVR with the deeper limit at M (>10) meters stretches up the water column to m = M/2 - 5 meters, and in particular, the "bottom restricted FVR" stretches to 5 meters above the mid-water level. The FVR increases with depth, and the FVR of physoclist fish adapted to pelagic living may be calculated using m (M) equal to the minimum (maximum) depth where the fish are found.

The vertical distribution of physoclist species, i.e. cod, haddock, saithe, blue whiting, and redfish, in terms of RPRL is shown e.g. in Figures 4a. The water column is partitioned into RPRL steps of 0.05 from "bottom" to surface, shown here along the horizontal axis. At each discrete RPRL, the box-plot informs about the distribution of the observed cumulative relative s_A-values. In each acoustic sample the relative s_A-value is accumulated from bottom up to RPRL = x. The distribution of these cumulative relative values over the entire sample set is represented by a box at RPRL = x. The box shows the inter-quartile range with a line inside each box marking the median. The accumulation levels in percent are read on the vertical axis. The cumulative relative distribution up to RPRL = x has median = y_{50}, lower quartile = y_{25}, and upper quartile = y_{75} (Figure 4). For example, the lower quartile = y_{25} means that 25% of the samples have the values below y_{25} and 75% of the samples have the values above y_{25}.

The line joining the medians for all RPRL is used to represent the cumulative relative acoustic s_A-values from bottom up to each RPRL. The inter-quartile range represents the variation of the distribution. If an RPRL has large inter-quartile range, there is large variability among the samples of the cumulative relative acoustic s_A-values up to that level.

The FVR unit for each species is then estimated from the median, i.e an RPRL range where the median starts to grow from 0% until it approaches 100 %, and with the quartiles indicating the uncertainty. A sample with fish above the bottom restricted FVR indicates that some of the

fish have adjusted to pelagic living, i.e. each individual fish has a current FVR that does not include seabed.

The day/night time are calculated according to the sun's angle with the horizon (for winter survey the daytime started from 5º below horizon). Each acoustic sample was accordingly classified as a day- or night-sample, and thus the above distribution can be presented taking day/night into account as shown e.g. in Figure 4c.

If the bottom is within the individual FVR for each fish in a sample, cumulative distribution of the relative s_A-values upwards for one FVR-unit measured from the bottom should reach 100%. When a sample has fish beyond this bottom restricted FVR, this indicates that some of the fish have adjusted to pelagic living. The lower quartile may show that such samples exist. This interpretation of the figures assumes that the restriction to one FVR is effective for rapid movements. If an RPRL has large inter-quartile range, there is large variability of vertical profiles up to that level among the samples.

The acoustic dead-zone and the cumulative relative acoustic s_A

A variable amount of fish is in the acoustic bottom dead zone, which is the zone near seabed where echo from fish cannot be discriminated from the bottom echo (Aglen, 1994; Ona and Mitson, 1996). The loss in acoustic abundance may vary significantly with day and night or other environmental conditions, e.g tidal currents. Thus the basis for calculating relative frequencies changes correspondingly**.** Only when the daytime profile and nighttime profile are based on the same total acoustic abundance, will the comparison of day/night profiles give evidence of absolute vertical densities and movements. Thus the observed relative frequencies must be adjusted using the relative change in an average of observed acoustic s_A-values or observed total acoustic abundance between day and night.

Let A(h) be the observed cumulative relative acoustic s_A-value from seabed up to h% RPRL in one sample. With bottom depth b meter, $h = 1 - [(d+10) \cdot (b+10)^{-1}]$ at depth d meters. At the surface, d= 0, so h = b/(b+10), and $N = A(b \cdot (b+10)^{-1})$ is the observed total s_A-values.

The observed cumulative relative s_A-value is $F(h) = A(h) \cdot N^{-1}$. Let X be the loss due to the bottom acoustic dead-zone. If the equipment had been able to detect fish at the bottom, A(h) would have been replaced by X+A(h), the total acoustic s_A-value would have been X+N, and the

cumulative relative s_A-value at level h would have been $G(h) = (X+A(h))\cdot(X+N)^{-1}$. The relation between the observed F and the "correct" G is therefore expressed by

$$G(h) = X\cdot(X+N)^{-1} + [N\cdot(X+N)^{-1}]\cdot F(h) = X\cdot(X+N)^{-1} + \{1 - [X\cdot(X+N)^{-1}]\}\cdot F(h) \qquad (EQ1)$$

The intercept $G(0) = X\cdot(X+N)^{-1}$ is the relative loss due to the dead-zone, and $N\cdot(X+N)^{-1}$ is the reduction factor for the slope. Increased loss X means higher intercept and lower slope for G.

In particular, $F(0) = 0\%$, $G(0) = X\cdot(X+N)^{-1}$, $F(b\cdot(b+10)^{-1}) = G(b\cdot(b+10)^{-1}) = 100\%$, $G'(h) = F'(h)\cdot N\cdot(X+N)^{-1}$, $1-G(h) = (1-F(h))\cdot N\cdot(X+N)^{-1}$.

For each sample, s, one could draw a similar curve. The observed total s_A-value is $N(s)$, and the unknown relative loss is $X(s)\cdot(X(s)+N(s))^{-1}$, which could have been used to correct the curve. All sample curves would have been shifted upward according to (EQ1).

We use the median curve as a "virtual sample" to represent the data. Let virtual dead-zone losses be X_d and X_n, and observed total s_A-values be N_d and N_n for day and night, respectively. The total amount of fish at any location does not change between day and night, hence $X_d + N_d = X_n + N_n$. For N_d and N_n respectively, we use the median of the observed day and night total s_A-values. For the purpose of day and night comparison, we only need the difference $X_n - X_d = N_d - N_n$.

Typically the daytime and nighttime median curves are concave, reach 100%, cross each other at a certain RPRL, say h_c (Figure 4d, 6d and 7d), and in an interval around h_c the daytime curve is steeper than the nighttime curve. There is then a higher relative density of fish at day than at night in this interval.

If $X_n - X_d = 0$, both curves are shifted the same way, and h_c remains the same.

If $X_n - X_d = N_d - N_n > 0$, the corrected night curve is shifted upwards more than the day curve, and for the discussion of intersection it is enough to shift only the night curve upwards to intercept at $(N_d - N_n)\cdot(N_d)^{-1}$. This intercept indicates the day-night relative difference in the acoustic s_A-values that is lost due to fish in the bottom dead-zone.

With $X = N_d - N_n$, $N = N_n$, (EQ1) can be rewritten in terms of the observed values as

$$G(h) = (N_d - N_n)\cdot(N_d)^{-1} + \{1 - [(N_d - N_n)\cdot(N_d)^{-1}]\}\cdot F(h) = F(h) + [(N_d - N_n)\cdot(N_d)^{-1}]\cdot[1-F(h)].$$

Now, in the typical case, daytime accumulation reaches 100% at a level RPRL = h^* where the night value is < 100%. It is then geometrically clear that the corrected night curve still crosses the day curve, say at RPRL = h_k, where $h_c < h_k < h^*$. Hence the median curves show that in fact

there must be net evening migrations both upwards and downwards away from the level RPRL = h_k

If $X_n - X_d = N_d - N_n < 0$, there must be a similar upward shift of the daytime curve. For small shifts the intersections at 0 and h_c are replaced by two intersections between 0 and h_c, and for large shifts there is no intersection.

The above remarks concern the interpretation of the median curves alone. The figures also describe the spread of the acoustic s_A-values by indicating the quartiles. Sometimes there is an $h** > h*$ where the lower daytime quartile is 100% and the nighttime quartile is well below 100%, indicating that as much as 25% of the samples have a significant proportion of fish above the maximum daytime level.

Three constructed numerical examples of scenarios with 100 fish in the table below show the need for such correction. In the day scenario 20 fish are in the acoustic dead-zone and in the two night scenarios 50. The observed fish (s_A-values) are distributed in 10 depth zones from bottom up as shown in line 1 of each scenario. The relative frequencies and cumulative frequencies as detected acoustically appear from lines 3 and 4. The relative density is higher at day than at night in the midrange (zones 2, 3, 4) but below and above (zones 1, 5, 6) the opposite is true. It would be illogical to conclude from line 3 or 4 that any fish had moved upwards in night scenario 1, as is shown by line 1 or the "correct" cumulative distributions in line 2. Line 3 contains evidence for upward moves in night scenario 2, but gives no clue to how many fishes that must have moved.

When the dead-zone losses are unknown, the percentages in terms of the full stock (lines 1 and 2) cannot be obtained. The only available clue to a correction is the difference between the total observed values, 80 – 50 = 30. The correction therefore increases the night basis from 50 to 80 fish, equal to the day basis. The observed night percentages in line 3 are accordingly multiplied by 50/80 = 0.625, and line 4 is updated, with relative abundance 30/80 = 37.5% for starting value. The corrections are shown in lines 5 and 6 of the night scenarios. These new lines may be compared with lines 3 and 4 in the day scenario. The basis now is 80 fish in all scenarios.

The full loss in the bottom dead-zone, 20 at day, and 50 at night, can not be determined from the observations, but the difference, 30 = 50-20 = 80-50, is enough for a comparison of the day-time and night-time profiles on an equal basis.

		Dead zone	1	2	3	4	5	6	7	8	9	10
Day	Total (%)	20	10	30	20	10	5	5	0	0	0	0
	cumulative (%)	20	30	60	80	90	95	100				
	observed (%)		12.5	37.5	25	12.5	6.25	6.25				
	cumulative(%)		12.5	50	75	87.5	93.75	100				
Night 1	Total (%)	50	15	12	7	6	5	5	0	0	0	0
	cumulative (%)	50	65	77	84	90	95	100				
	observed (%)		30	24	14	12	10	10				
	cumulative (%)		30	54	68	80	90	100				
	corrected (%)	37.5	18.75	15	8.75	7.5	6.25	6.25				
	cumulative (%)	37.5	56.25	71.25	80	87.5	93.25	100				
Night 2	Total (%)	50	15	12	7	5	4	1	2	2	1	1
	cumulative (%)	50	65	77	84	89	93	94	96	98	99	100
	observed (%)		30	24	14	10	8	2	4	4	2	2
	cumulative (%)		30	54	68	78	86	88	92	96	98	100
	corrected (%)	37.5	18.75	15	8.75	6.25	5	1.25	2.5	2.5	1.25	1.25
	cumulative (%)	37.5	56.25	71.25	80	86.25	91.25	92.5	95	97.5	98.75	100

Before correction, day and night cumulative relative acoustic s_A-values of each sample are based on different total acoustic s_A-values in the water column. In order to draw conclusions about vertical migration, one must consider the correction for difference in bottom dead-zone loss, so that both curves are based on the same total acoustic s_A-value.

RESULTS

Organisation of figures

Figures concerning physoclists (cod, haddock, redfish, saithe, and blue whiting) are according to survey, and the last figure concern the physostomes (capelin and herring).

Figures 1 – 3: Maps of the survey areas.

Figures 4 – 7: Cod, haddock, redfish; winter surveys in the Barents Sea.

Figures 8 – 10: Cod, haddock, redfish; summer surveys in the Barents Sea.

Figures 11, 12: Saithe, haddock, blue whiting; surveys along the Norwegian coast.

Figure 13: Saithe and blue whiting; surveys in the North Sea

Figure 14: Capelin and herring; winter surveys in the Barents Sea.

Effect of pressure change on fish vertical distribution

The cumulative relative acoustic s_A-values is calculated annually for each physoclistous species of each survey (e.g. Figure 4b, 6b - 10b) as well as for all years combined (e.g. Figure 4a, 6a - 10a). In order to compare the vertical profiles, the large spatial variation in absolute s_A-values among samples is normalized by the use of relative numbers. Samples with high and

samples with low acoustic s_A-values are treated on equal terms as profiles of the relative values in each sample.

The figures are presented for each species separately, and within each species data are grouped according to survey, bottom depth, density, or other criteria. When the day/night distinction is clear the figures also show the day/night effect. There are data sets where a few samples of very high density have special profiles and account for a high proportion of the sampled fish, and this is not reflected in the overall median. It is therefore sometimes natural to select samples according to fish density.

The annual median curves of the cumulative relative s_A values show the variation in vertical distribution (e.g. Figure 4b). The reference line at 50% RPRL indicates one bottom restricted FVR for cod. For other species, the RPRL where the median gets close to 100% and the inter-quartile range approaches 0 may indicate their FVR unit. They seem to be of roughly the same size (Figures 4a, 6a - 11a, c, e). Near the bottom the inter-quartile range is relatively large. This means that within one FVR the fish are free to distribute along the water column in a way suitable to local conditions.

Pelagic living for some fish in the sample is indicated when the cumulative relative acoustic s_A-values shows there are fish higher than 50% RPRL i.e. the lower quartile reaches 100% beyond the reference line (50% RPRL) (Figures 4c, f, 6c, 7c, 8e, 9e, 11c, 13c, e). This criterion is discussed in some detail below (Discussion). The most notable species may be blue whiting, which mainly is pelagic when the sea bottom is deeper than 300m (Figure 13e,f). Besides blue whiting, other physoclist species occasionally show indication that in more than 25% of the samples some fish had adapted to pelagic living, especially in deep water (Figures 4f, 6c, 7c, 8e, 9e, 12b, d).

Figures 4-13 show that the vertical profiles are similar for all physoclist species. They are restricted by their individual FVR, but they can adapt to pelagic living, especially in areas of high acoustic s_A-values where the seabed is deeper than 200m. The distribution at each RPRL has larger variance in the summer survey than during the winter survey (Figures 4a, 6a - 10a). This variation may be explained partly by the variation over different years in the summer survey coverage, partly by fish migration and that the vertical distribution is location dependent. The distribution in summer 1999 shows more pelagic living for cod and haddock than in most years, but this may be due to the survey line transect coverage, which was mainly along the Polar

front and Svalbard Bank. The depth distribution of individual cod from data storage tags has larger variation in summer than in winter (Table 1) in agreement with above results.

Proportion of fish in the bottom channel

For the physoclist species, the ratio of the s_A-value from the bottom channel (≤10m above seabed) to the total s_A-value was calculated in each sample, and the distribution of the ratio investigated. Parameters for the distribution are reported in tables 3 – 6 (mean, standard deviation, standard deviation of the mean, median, lower and upper quartile). A general feature is that in deep water fish distribution tends to spread further up into the water column.

Table 2, based on time series from data storage tags, shows that individual cod mainly spend more time in the lower part of the daily depth range during winter than during summer. Most tag records from the bottom channel are likely to be included in this "lower part", and thereby also records from the acoustic dead-zone.

Some results species by species

Cod: The distribution of samples supports the assumption that the limit of FVR applies to all locations (Figure 4). Data from winter and summer surveys (Figures 4 and 8) show that vertical distribution in relation to RPRL is in agreement with a theoretical FVR unit as determined by Harden Jones and Scholes (1985). Winter survey data show DVM, with indication that two parts of the stock have opposite DVM patterns (Figure 4d). During daytime a high proportion of acoustic abundance is concentrated around the midrange of the bottom half of the water column. At nighttime part of the acoustic abundance descends to concentrate closer to seabed and another part ascends higher up in the water column than during daytime. The size of each proportion varies over years. In 1996 a large proportion descend during nighttime and there is no crossing between day and night median curves (Figure 5). In most years there is no big difference in the descent and ascent parts so that the day and night median curves cross each other.

For the winter survey the data are split in two, for bottom depth less than and more than 200m, and the results are presented in Figure 4 e,f**.** The samples with bottom depth less than 200 m has vertical profile within the bottom restricted FVR. The samples with bottom depth more than 200m combined with high acoustic s_A-values show that more cod adapt to pelagic living both winter and summer (Figure 4 and Table 3).

In all years the samples from summer surveys, which are restricted to the Svalbard bank with depth < 200m, the median of the accumulated vertical profiles of the relative acoustics s_A-values

reach 100% at an RPRL well below 0.5. But for samples along the Polar front with depth between 200 to 350 m the cumulative vertical profiles stretch up to and beyond the 0.5 RPRL, which show that some cod adapt to pelagic living. The profiles of some samples show two concentrations, one in the bottom half and another one in the upper half of the water column.

Haddock: Data from winter and summer surveys show a similar vertical profile as cod. Haddock mainly stay within one "cod" bottom restricted FVR, but more often adapt to pelagic living (Figure 6 and 9). Summer samples have larger inter-quartile range than winter samples, which shows greater variation in vertical profiles (Figures 6a and 9a).

The vertical distribution in terms of bottom restricted FVR seems to depend on bottom depth and the size of acoustic s_A-values (Figure 9c, d, e, f). Samples from both surveys with high acoustic s_A-values, in areas deeper than 200m, show clearly that part of the fish adapt to pelagic living. (Figure 9e,f) and Table 4, but spread more upward into the water column in summer than in winter samples (Figure 9c,d). The summer 1998 median curve in Figure 9f shows that a majority of the samples had more than half of the relative acoustic s_A-values from well above the bottom restricted FVR-range (50% RPRL). The two selection criteria together were satisfied by samples in one stretch of line transects along the northern coast of Norway. Most individual samples were similar to the median curve, with two separated high concentrations of acoustic s_A-values, one close to the bottom, and another in the upper half of the water column.

Haddock data from the surveys along the Norwegian coast have cumulative relative s_A-values stretching higher than for haddock in the winter survey in the Barents Sea (Figures 11c,d, 12c,d).

Redfish: In general redfish are found in regions with bottom deeper than 100m. The vertical profile shows that redfish mainly stay well within the 50% RPRL in both summer and winter (Figures 7 and 10). Even with bottom deeper than 300m only small parts of the samples go into the upper half of the water column.

Saithe: Along the Norwegian coast, saithe mainly stay in the bottom half of the water column for all bottom depths, but with deeper bottom they spread relatively higher into the water column (Figures 11a,b, 12a,b). For depth less than 200m the saithe stay close to seabed, and for depth greater than 300m the median of cumulative relative s_A-values in some years is well below 100% at 50%RPRL. The demersal nature of saithe appears more clearly when estimates of the loss in the acoustic dead-zone are added to the bottom channel values (Figure 12b).

In the North Sea survey, saithe are mainly found in the N and NW part of the survey area, west of the Norwegian Trench. Saithe in the North Sea mainly stay within the bottom channel (10 m above seabed) (Figure 13a,b) and Table 6.

Blue whiting: Along the Norwegian coast in areas with bottom deeper than 300 m, blue whiting usually have relatively high acoustic s_A-values, and the distribution stretches over more than one cod FVR in some years. In areas shallower than 200m, however, the cumulative relative s_A-values mainly reaches 100% well below the 50% RPRL (Figures 11e,f, 12e,f, and Table 5).

Blue whiting samples in the North Sea are few in 1998. The median curves of most years, except 1999, has relative acoustic s_A-values within 50% RPRL (Figure 13 d). Samples from deep areas (> 300 m) are mainly from the area north of Shetland. The annual median curves indicate pelagic living in mid water (Figure 13e, f). The reason for the S-shape of the median curve may be that a large part of the acoustic s_A-values comes from schools stretching over roughly one FVR in mid water. For 1999 (August-September) the cumulative relative s_A-values indicates a mixture of pelagic and demersal living. For 1998 there are only night samples, and they show that the effective accumulation starts higher in the water column and reaches 100% at a level higher than 50% RPRL.

Capelin: Data from winter surveys show that the capelin's vertical profile has large variation over the survey area (Figure 14a,b,c). In general, capelin ascends for the night. High acoustic s_A-values is found along the Polar front, in mid-water, mainly with bottom depth more than 200m. There is only a small amount of samples during summer, and all of the fish are then found close to the surface.

Herring: Samples from the North Sea show that herring are mainly found in the upper half of the water column. The samples along the Norwegian coast have a large variation of vertical profiles. The influx of herring in the Barents Sea is variable. In most years the data are insufficient for conclusions on DVM. In winter herring in the Barents Sea mainly distribute in the bottom half of the water column (Figure 14d, e, f), and samples from year 2000 have DVM with nighttime ascents.

Dead-zone loss at day and night

The typical case in the Barents Sea winter surveys 1996-2001 was that the observed total acoustic s_A-value of each sample at daytime was often higher than at night time, $N_d > N_n$, i.e. that night time loss in the acoustic dead-zone exceed daytime loss. To calculate the cumulative

relative vertical profile based on the same total s_A-values for the two median curves, usually the nighttime median curve is corrected by an upward shift. The values for N_d and N_n are the medians of the total acoustic s_A-values over the day and night samples, respectively. For these 6 winter surveys and the 3 species cod, haddock, and redfish, the dead zone corrections, i.e. the intercept.

$(N_d - N_n) \cdot (N_d)^{-1}$ if $N_d > N_n$ (night correction), or $(N_n - N_d) \cdot (N_n)^{-1}$ if $N_d < N_n$ (day correction), is given in a table 7. All samples with total s_A-value in the water column > 1 are counted. The material may be insufficient to allow the conclusion that 1996 with the large day corrections is an exceptional year (Figure 5). One possibility is that there is a separation of both the cod and the haddock stocks into groups with very different DVM-patterns, and that switches between $N_d < N_n$ and $N_d > N_n$ from one year to another is explained by relative changes in the composition of such groups. The cumulative relative acoustic s_A-values figures for day and night indicate that such separation exists, although the acoustic data give no information on the age or length composition of the stock.

Effect of day and night on vertical distribution

In most cases, when the samples from winter surveys (cod, haddock, and redfish 1996-2001) are classified as day/night, the distribution of the cumulative relative s_A-values near the sea bottom shows lower median values at daytime than at nighttime, while the order is reversed somewhere in the mid-range of the distribution range. Usually this is the lower half of the water column (Figure 4d, 5d, 6d). The reversal appears as a crossing of the median curves for day and night. When the crossing remains after the correction for unequal dead zone loss, it shows that during nighttime a higher proportion of fish distributes near the bottom while a higher proportion also distributes further up into the water column than during daytime. During daytime there is a higher proportion of fish around mid-range of the bottom half of the water column.

The corrections show that, for cod and haddock, there is a higher loss during night than day in 4 out of 6 years, and for redfish night loss is the higher in all years (Table 7). Different parts of the stock move in opposite directions. For night one part ascends toward or beyond mid water and another part descends to near seabed, and more is lost in the dead zone at nighttime than daytime. For daytime one part ascends from near seabed and another descends from above. The higher density around mid-range of the bottom half of the water column is also shown by the slope of the median curves being steeper at day than at night.

After correction, the median samples for day and for night represent the majority of day and night samples, respectively. The acoustic data show the net effect if there are migrations in opposite directions, but do not show to what extent migrations with opposite direction cancel out.

The eastern part of the Barents Sea, which is an important feeding area for young cod, was not covered 1997-1998. In 1996, 2000, and 2001 there are sufficient samples east of 35°30′ longitude for analysis, and separate investigation shows a relative day correction of 39% for 1996 and relative night corrections of 60% in 2000 and 48% in 2001. The results from the areas west of 35°30′ longitude are similar to the overall results in Table 7.

Clear DVM is also found for capelin in every year during winter. Capelin distributed through the entire water column but the median indicates that capelin distribute higher into the water column at night (Figure 14c). The large inter-quartile range may indicate that the capelin's vertical profile varies according to local conditions. Similar DVM behaviour is found for herring in the years that we have a significant amount of data (1999-2000). In 1998 and 2000 most herring samples distribute in the bottom half of the water column (Figure 14d, e, f).

Day/night samples along the Norwegian coast are situated far apart in terms of geographic locations, so one must be cautious in drawing conclusions.

Clear DVM of blue whiting occurs all years both in samples from the Norwegian coast and from the North Sea survey. In 1998 (night samples) the effective accumulation starts around RPRL 0.15, well above seabed (Figure 13d, f).

The DVM of saithe and haddock is not clear from the combined data 1992-2000 (Figure 11a, c). Yearly data show some evidence of DVM, but the direction of migration may be different from year to year. The samples are spread along the coast (Figure 1) and the day/night samples are from very different geographic locations.

Temperature and salinity

The results from the Barents Sea surveys are summarized in the Tables 8-9. The data were weighted by acoustic s_A-value in each depth interval.

Summer and winter the vertical profiles for cod, haddock, and redfish show that in most samples the higher concentration is below 100 m, where the vertical temperature gradient is low. The survey coverage of the eastern parts varies, and in 1997-98 the survey vessels did not enter the Russian zone. This may effect the range of temperature distribution and also the relationship

between temperature and fish distribution. Most of the cod, haddock and redfish distribute in the temperature range from 2 - 6ºC, but a significant proportion of cod is in subzero temperatures where no haddock and very little redfish are found. The subzero records for cod are due to its high concentration along the Polar Front. For all species the temperature variance is smaller in winter than in summer, which may reflect that they spread more out in summer. For cod, this is in agreement with the distribution of temperature and depth in storage tag data (Table 1).

The variations in salinity are, to our knowledge, too small to make a significant physiological difference. The particularly low salinity variation for redfish may reflect that it does not migrate as much between different water masses as the other species. The average temperature where the fish were found can vary from year to year, the clearest difference is seen between the median winter temperatures of the water masses for redfish between 1997 and 1999.

DISCUSSION
Vertical distribution and relative pressure reduction

Because of swimbladder physiology, the vertical mobility of a physoclist, by rapid moves, is limited by the relative change in the pressure. A pressure reduction of 10% has the same consequence in terms of change in buoyancy status at all depth levels, e.g. whether there is an ascent from 90m to 80m or one from 190m to 170m. Because the acoustic s_A-values are integrated over 1 nm (6 minutes) and are related to the fish buoyancy status, it is meaningful to express vertical profiles of acoustic s_A-values in terms of bottom restricted FVR of the demersal physoclist species. Moreover this allows the comparison of profiles from locations with different bottom depth.

FVR as a unit

The cod's vertical distribution is related to the physiological restrictions to the individual cod's vertical movements. This was recognized by Ellis (1956), who reported from acoustic observations at the Skolpen Bank in the Barents Sea, September 1955, that cod shoals were found to be well within the theoretical limits imposed by the swimbladder. The cod's FVR was experimentally determined by Harden Jones and Scholes (1981, 1985), and is used here as a unit for comparison although other physoclists may have somewhat different FVR.

With increasing bottom depth, there are an increasing number of FVR-units from the seabed up to the surface. For a demersal fish an increased number of FVR-units up to the surface means

that the upper layers become less accessible by rapid ascents. The restriction to an FVR is not absolute. The tolerance of cod, saithe and haddock to swimbladder expansion (before it bursts) has been found experimentally (Tytler and Blaxter, 1973) and the limit can only be reached by an ascent far above the FVR

The cumulative relative frequencies of s_A-values often reach 100% at an RPRL of 50%, which indicates that the simple FVR rule of a pressure ratio of 0.5 between the upper and the lower end, is in fact a reasonable description of the cod's natural behaviour. Although DST records show some cases of cod in summer, autumn and winter occasionally having a larger daily vertical range than the FVR (Stensholt 2001), they are too rare to change the general picture. In these cases the cod seems to have accepted the excessive under-buoyancy.

The acoustic evidence is that the other physoclists are similarly restricted by their FVR, which seems to be of roughly the same size as cod.

One may regard the FVR as a logarithmic yardstick, and convert a depth of x meters to log(1+x/10), the logarithm of the pressure expressed in atmospheres. With the cod's FVR as unit, the logarithms have base 2, but when the purpose is to study vertical migration on a depth scale that is natural because of Boyle's law, the choice of base is inessential. When the bottom depth is D meters, a depth of x meters is converted to RPRL (D-x)/(D+10). For demersals it is more natural to consider the height D-x above seabed than x. Demersals generally have large x and small D-x, and unless x is small, nothing is gained by a strict use of logarithms. For small D-x the RPRL is roughly proportional to the difference of the logarithms, since ln[1+D/10] − ln[1+x/10] = -ln[1-(D-x)/(D+10)] ≈ (D-x)/(D+10).

Medians and cumulative relative acoustic s_A-values

The FVR unit expresses the capacity of the physoclists to perform rapid vertical moves, but the fish may adapt to make use of this capacity to a variable degree. This degree is reflected in the vertical profile of cumulative relative acoustic s_A-values. Investigating such profiles may reveal factors that influence the vertical migration behaviour.

The median profile represents the majority of the samples. Small samples of fish may have vertical profiles that are very different due to special factors, e.g. depth, density, and current. Thus the median of the entire set of samples may not be a good representative of these special cases. In these cases the analysis of such samples should be carried out separately. Results

indicate that great bottom depth, high density and strong current have effect on the vertical distribution in all studied physoclists species.

Because of the survey design only one sample is available in each geographic location. Classification of the locations for uniform environmental conditions, which may effect the vertical profiles, may become necessary in some cases. But higher uniformity means a reduced number of samples, and so over-refinement will also reduce reliability. For example are the surveys along the Norwegian Coast stretched out so that many samples have few neighbors. Because of the rapid change of geographic location, a classification may reduce the reliability of the day/night results.

Evidence for pelagic living

Physoclists must adapt to pelagic living if they have to reach prey that live above the bottom restricted FVR. Such adaptation means that the fish have individual FVRs that do not include the seabed. The relative acoustic density from the bottom channel to the total s_A-values generally decreases with increasing depth (Table 3-5). The profiles of cumulative relative s_A-values (Figures 4, 6-13) show more detail. In particular, the lower quartile sometimes reaches 100% beyond one bottom restricted FVR, which is evidence that there are fish above the bottom restricted FVR in 25% of the samples.

Each acoustic sample is a "snapshot" of the fish distribution in the water column, each fish staying in its own (individual) FVR. The cumulative relative frequency of the observed s_A-values in each water column represents the profile of this distribution. If all individual FVR include the seabed, the distribution of cumulative relative frequency of s_A-values, with its lower quartile, will reach 100% within one bottom restricted FVR. When the distribution of cumulative relative frequency reaches 100% well beyond one bottom restricted FVR, this indicates that a portion of fish has adapted to pelagic living.

The expression "pelagic living" is here used in a somewhat restricted sense: a physoclist has adapted to pelagic living when its individual FVR does not include the seabed. If it still goes to the seabed it will be more under-buoyant than at the lower limit defined in FVR. Fish that are detected within the bottom restricted FVR may well have an individual FVR that only partially overlaps with the bottom restricted FVR, and does not include the seabed. As it is impossible to recognize from the acoustic signals that fish within the bottom restricted FVR have adapted to pelagic living, it is necessary to use a very strict criterion before concluding that part of the stock

has adapted to pelagic living. In order to draw such conclusion, it is necessary to detect fish more than one bottom restricted FVR above the seabed. When the lower quartile of the vertical profile is clearly below 100% for accumulation up to one bottom restricted FVR, it means that fish have been detected this high in more than 25% of the samples.

A criterion thus linked to the lower quartile, or to any low fractile, must be considered as quite conservative. When pelagic living can be detected this way (based on the assumption that the FVR-restriction to rapid vertical movement is effective) for a small proportion of the stock, it is likely that a more substantial proportion in fact has adapted to pelagic living. The argument is that if the interval [m, M] is the bottom restricted FVR, and there are several fishes with individual FVR equal to [m', M'] such that m' < m < M' < M, many of them may happen to be detected in the depth interval [m, M']. They have adapted to pelagic life, but this cannot be verified. Only those that are detected in [m', m] satisfy the criterion.

Although physoclists are restricted by their FVR in their vertical migration, they occasionally adapt to pelagic living. Generally, with higher fish density and deeper water, a larger fraction of the fish is found to adapt to pelagic living. With increased density there is increased competition for food, and this may cause more individuals to search for prey relatively higher in the water column. With increased bottom depth, the larger advantage has a pelagically living fish in the higher layers. There are clear differences between the species. Among the physoclists studied here, blue whiting is most often seen to be pelagic, while redfish almost always stay within the bottom half of the water column in the banks and shelf sea areas. Pelagic distribution layers of blue whiting, deep sea (or oceanic) red fish, and occasionally cod are found in areas of great depth (Harden Jones and Scholes, 1985; Monstad et al., 1995; Magnússon et al., 1996)

Tidal currents

Most saithe found in the North Sea stay mainly within 10m from the bottom (Figure 13a,b) and Table 6. They are found mainly N and NE of the survey area, along the west side of the Norwegian Trench. Saithe along the Norwegian coast, north of 62°N, are clearly distributed higher in the water column (Figure 11a,b, 12a,b). The different behaviour in the two survey areas is most likely due to a difference in the environmental conditions. The strong tidal currents in the North Sea are a possible cause. A similar observation was made in the cod's acoustic s_A-values around Svalbard bank. Analysis of DST data shows several examples of cod with reduced

vertical activity in connection with tidal currents (Stensholt, 2001), and the saithe may stay close to the bottom for the same reason.

Size composition, vertical movement, and dead-zone loss

In most winter surveys the cumulative vertical profiles of cod, haddock, and redfish show that during nighttime a higher proportion of fish distributes near the bottom while a higher proportion also distributes further up into the water column than during daytime. During daytime there is a higher proportion of fish around mid-range of the bottom half of the water column.

Several studies indicate that large fish ascend for daytime and descend to the bottom for nighttime, while the opposite holds for small fish (Aglen *et al*., 1999; Korsbrekke and Nakken, 1999; and Einarsson, 2001; Stensholt and Nakken, 2001). The DST data also confirm a daytime ascent of 50-100 m for large cod during winter (Stensholt, 2001).

In 1996 there is a larger proportion of acoustic s_A-values lost during daytime than nighttime. After an upward correction shift of the daytime curve, a majority of the samples show higher acoustic s_A-values at night than day from the upper part of the distribution range. In year 1996 the survey transect has the most extensive coverage of the eastern part of the Barents Sea, the main nursery ground for young cod together with very high proportion of 1 and 2 years old in the age composition (Aglen, 2001b). In 1997 - 1999 there are no surveys east of 40° longitude. The age composition of the stock each year is significant, and it may be influenced by the 0-group strength in previous years. In 1992 - 1997 the cod 0-group index was relatively high, and intermediate for haddock (Anon., 1998).

A bias due to bottom slope

There exists, however, also an effect that may lead to an over-estimation of the range of vertical distribution. Let d and D meters be the minimal and maximal bottom depth within a 1 n. mile sampling unit, and assume the fish is distributed up to depth x meters. Here calculations are based on D, and x corresponds to the RPRL-value

$$(D-x)/(D+10) = 1- (x+10)/(D+10) > 1- (x+10)/(d+10) = (d-x)/(d+10).$$

A fish may have d but not D meters depth inside its FVR, and regularly visit the bottom at d meters or even less. Then the calculated RPRL is too large, and the fish may be falsely classified as pelagic. To reduce this bias one may disregard samples with D-d > k for some k. Experimentation with k=10, 20, 50 shows that increased k gives some change in the inter-quartile ranges, but the general picture remains the same. The bathymetry of the survey areas

also indicates that relatively few samples will have a high bottom slope. (Figures 2 and 3), but disregarding samples with high bottom slope means elimination of data which may particularly affect species with high density at the shelf break, e.g. blue whiting and saithe. For Norwegian coast and North Sea surveys we restricted the slope by D-d < 50 m, in the Barents Sea by D-d < 20 m.

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FIGURE DESCRIPTIONS

Figure 1: 1996 acoustic surveys in the North Sea south of 62° N, and along the Norwegian coast north of 62° N. Trawl stations are marked with Δ. Depth isolines in meters.

Figure 2: 1996 winter survey in the Barents Sea. Trawl stations are marked with Δ. Depth isolines in meters.

Figure 3: 1996 summer survey in the Barents Sea. Trawl stations are marked with Δ. Depth isolines in meters.

Figure 4: Cod Distribution of cumulative vertical profiles of relative acoustic s_A-values in relation to relative pressure reduction level, RPRL, accumulated from bottom to surface. Reference line indicates 50% RPRL. Cod data are from winter surveys in the Barents Sea, 1996-2001.

    a) Median and inter-quartile range of the distribution, from combined data 1996-2001;

    b) Yearly median curves for the distribution;

    c) As in a) but with day- and night samples presented separately;

    d) Day and night median curves as in c). Broken line shows the corrected median curve after compensation for the dead-zone loss. Dot indicates that night loss exceeds day loss, and the night curve is corrected by an upward shift;

    e) and f) are as c) but split according to bottom at 50-200m and 200-600m. The lower quartile indicates that more cod get pelagic with increased bottom depth.

Figure 5: Cod Distribution of cumulative vertical profiles of relative acoustic s_A-values in relation to relative pressure reduction level, RPRL, accumulated from bottom to surface. Reference line indicates 50% RPRL. Data are from the winter survey in the Barents Sea, 1996.

Day and night median curves for cod. Broken line shows the corrected median curve after compensation for the dead-zone loss. Circle indicates that day loss exceeds night loss, and the day curve is corrected by an upward shift.

Figure 6: Haddock Distribution of cumulative profiles of relative acoustic s_A-values in relation to relative pressure reduction level, RPRL, accumulated from bottom to surface. Reference line indicates 50% RPRL. Haddock data are from winter surveys in the Barents Sea, 1996-2001. (a)-(d) are as in Figure 4.

Figure 7: Redfish Distribution of cumulative vertical profile of relative acoustic s_A-values in relation to relative pressure reduction level, RPRL, accumulated from bottom to surface. Reference line indicates 50% RPRL. Redfish data are from winter surveys in the Barents Sea, 1996-2001. (a)-(d) are as in Figure 4.

Figure 8: Cod Distribution of cumulative vertical profiles of relative acoustic s_A-values in relation to relative pressure reduction level, RPRL, accumulated from bottom to surface. Reference line indicates 50% RPRL. Cod data are from summer surveys in the Barents Sea, 1995-2000.

  a) Median and inter-quartile range of the distribution, from combined data 1995-2000;
  b) Yearly median curves for the distribution;
  c) and d) are as a) and b) with bottom at 50-200m;
  e) and f) are as a) and b) with bottom at 200-600m and high density.

Figure 9: Haddock Distribution of cumulative vertical profiles of relative acoustic s_A-values in relation to relative pressure reduction level, RPRL, accumulated from bottom to surface. Reference line indicates 50% RPRL. Haddock data are from summer surveys in the Barents Sea, 1995-2000.

  a) Median and inter-quartile range of the distribution, from combined data 1995-2000
  b) Yearly median curves for the distribution;
  c) and d) are as a) and b) with bottom at 50-200m;
  e) and f) are as a) and b) with bottom at 200-600m and high density.

Figure 10: Redfish Distribution of cumulative vertical profiles of relative acoustic s_A-values in relation to relative pressure reduction level, RPRL, accumulated from bottom to surface. Reference line indicates 50% RPRL. Redfish data are from summer surveys in the Barents Sea, 1995-2000.

  a) Median and inter-quartile range of the distribution, from combined data 1995-2000
  b) Yearly median curves for the distribution;
  c) and d) are as a) and b) with bottom at 50-200m;
  e) and f) are as a) and b) with bottom at 200-1000m and high density.

Figure 11: Saithe, haddock, and blue whiting Distribution of cumulative vertical profiles of relative acoustic s_A-values in relation to relative pressure reduction level, RPRL, accumulated

from bottom to surface. Reference line indicates 50% RPRL. Data are from surveys along the Norwegian coast 1992-2000.

a) Saithe. Median and inter-quartile range of the distribution, day and night, from combined data 1992-2000;

b) Saithe. Median curves for day and night corresponding to a). Broken line shows the corrected median curve after compensation for the dead-zone loss. Dot indicates that night loss exceeds day loss, and the night curve is corrected by an upward shift;

c) and d) Haddock: analogues to a) and b);

e) and f) Blue whiting: analogues to a) and b).

Figure 12: Saithe, haddock, and blue whiting Annual median curves for the samples with the specified combinations of bottom depth and acoustic s_A-values. Reference line indicates 50% RPRL. Data are from surveys along the Norwegian coast 1992-2000.

a) Saithe stay within the bottom half of the water column, bottom depth 30-200m;

b) Saithe spread more out and some become pelagic, bottom depth 300-600m;

c) and d) Haddock: analogue to a) and b);

e) and f): Blue whiting: analogue to a) and b).

Figure 13: Saithe and blue whiting Distribution of cumulative vertical profiles of relative acoustic s_A-values in relation to relative pressure reduction level, accumulated from bottom to surface. Reference line indicates 50% RPRL. Data are from surveys in the North Sea 1992-2000.

a) Saithe: Median and interquartile range;

b) Saithe: Annual median curves. The saithe stays in the deeper water layers;

c) Blue whiting, bottom at 30-600m. Median and interquartile range;

d) Blue whiting, bottom at 30-600m. Annual median curves. Some become pelagic. Blue whiting, bottom at 300-600m. Median and interquartile range;

e) Blue whiting, bottom at 300-600m. Annual median curves. In most years blue whiting are mainly pelagic.

Figure 14: Capelin and herring: Distribution of cumulative vertical profiles of relative acoustic s_A-values in relation to relative depth (0.0 at surface, 1.0 at bottom), accumulated from surface to bottom. Reference line indicates mid-water level. Data are from winter surveys in the Barents Sea, 1996-2001.

a) Capelin: Median and inter-quartile range of the distribution of, combined data 1995-2000;

b) Capelin: Day and night median curves;

c) Capelin: Yearly median curves for the distribution;

d), e) and f) Herring: analogues to a), b) and c).

Table 1: Cod. Temperature and depth distribution, in winter (January-March) and summer (July-August). From 1996 -1997 time series of 6 data storage tags attached to North East Arctic cod released in the Barents Sea.

	Tag no.		mean	std	min	max	P5	Q1	median	Q3	P95
Temperature	117	summer	3.1	2.0	-1	6.4	-0.6	1.3	3.9	4.7	5.4
		winter	3.9	0.8	1.5	5.2	2.5	3.4	4.2	4.5	4.8
	131	summer	2.2	1.5	-1.3	5.0	-0.1	0.9	2.1	3.6	4.1
		winter	2.4	1.4	-0.1	5.0	0.2	1.0	2.9	3.5	4.3
	191	summer	3.9	1.2	1.3	9.2	2.1	3.4	3.9	4.3	6.3
		winter	4.0	0.3	3.4	4.7	3.6	3.8	4.0	4.2	4.6
	204	summer	2.6	1.5	-0.7	4.9	-0.4	1.3	3	3.8	4.4
		winter	4.0	0.4	3.0	4.9	3.4	3.8	4.0	4.4	4.6
	206	summer	3.1	1.2	-0.3	6.3	1.0	2.1	3.3	3.9	5.3
		winter	2.4	0.9	0.1	3.6	0.6	1.7	2.6	3.1	3.3
	246	summer	2.4	1.5	-1.0	5.3	0.2	0.9	2.7	3.7	4.4
		winter	4.2	0.3	3.5	5.3	3.5	3.9	4.1	4.4	4.6
Depth	117	summer	237	78	0	475	113	174	243	294	353
		winter	286	75	0	475	176	271	296	322	379
	131	summer	208	69	60	406	92	151	218	257	309
		winter	261	43	81	371	198	237	255	293	335
	191	summer	209	96	1	410	52	136	224	281	351
		winter	318	40	174	404	235	303	321	344	377
	204	summer	236	84	2.4	389	103	150	272	305	344
		winter	309	31	193	376	256	288	308	334	352
	206	summer	130	92	0	353	20	55	99	207	300
		winter	201	94	49	353	72	86	207	293	327
	246	summer	235	81	3	370	92	166	264	300	329
		winter	311	11	241	331	297	303	312	320	328

Table 2: Cod. Percentage of time spent within 10m channel over the daily maximal depth, (D-channel), and of time spent more than 10 m over the daily maximum depth, (P-channel), in winter (January-March) and summer (July-August). From 1996 -1997 time series of 6 data storage tags attached to North East Arctic cod released in the Barents Sea.

Tag number	summer		winter	
	D	P	D	P
117	48	52	55	45
131	34	66	66	34
191	47	53	67	33
204	51	49	51	49
206	53	47	62	38
246	39	61	82	18

Table 3: Cod: Distribution of the relative acoustic s_A–value from bottom channel (10m above seabed) in percent of total s_A–value. Summer and winter survey in the Barents Sea 1995-2000. Classification by bottom depth interval. std and stdmean are standard deviation and standard deviation of the mean; q1 and q3 are lower and upper quartiles.

```
   year     mean      std    stdmean        q1   median        q3

                  summer depth 50-200 m SA=1

   1995     78.5     29.3        0.9      60.2     97.3     100.0
   1996     68.7     32.5        0.6      41.8     81.2      99.2
   1997     73.2     34.2        1.9      44.0     95.4     100.0
   1998     77.0     33.8        1.1      54.0     99.9     100.0
   1999     61.1     39.2        1.1      18.5     74.7     100.0
   2000     87.4     26.3        1.0      99.5    100.0     100.0

                  summer depth 200-600 m SA=1

   1995     39.0     35.3        0.8       6.9     27.8      71.2
   1996     33.6     33.5        0.7       6.1     20.0      56.1
   1997     23.9     30.2        0.6       1.3      9.6      36.6
   1998     29.1     30.7        0.5       4.9     15.7      46.1
   1999     26.7     31.7        0.6       3.4     11.7      38.6
   2000     57.8     41.4        1.0      12.5     65.4     100.0

                  winter depth 50-200 m SA=1

   1996     61.3     27.7        1.1      40.0     65.7      85.6
   1997     62.2     28.0        1.1      40.5     65.8      87.3
   1998     52.3     31.1        1.6      23.9     54.7      80.8
   1999     59.1     34.0        1.5      30.0     57.7     100.0
   2000     67.0     28.9        1.3      44.5     70.7      97.3
   2001     63.6     33.6        1.7      32.8     68.6     100.0

                  winter depth 200-600 m SA=1

   1996     36.5     23.9        0.4      17.6     31.3      50.6
   1997     39.4     24.8        0.4      18.9     35.8      56.6
   1998     32.2     23.8        0.4      13.5     25.6      46.1
   1999     32.1     27.5        0.5      11.0     24.9      48.3
   2000     28.2     27.5        0.5       7.5     18.0      39.9
   2001     47.3     33.4        0.5      17.5     39.2      75.8
```

Tables 4: Haddock: Distribution of the relative acoustic s_A–value from bottom channel (10m above seabed) in percent of total s_A–value. Winter survey in the Barents Sea 1996-2001. Classification by bottom depth interval and day/night. std and stdmean are standard deviation and standard deviation of the mean; q1 and q3 are lower and upper quartiles.

year	mean	std	stdmean	q1	median	q3
			depth 50-200 m s_A > 1			
1996	65.6	25.9	1.2	46.5	69.6	88.3
1997	53.5	31.4	1.5	25.7	53.5	82.1
1998	67.7	26.1	1.5	54.7	68.5	90.0
1999	56.2	35.1	2.3	24.8	55.0	100.0
2000	60.7	23.9	1.1	42.7	62.6	80.0
2001	57.6	32.6	1.8	29.1	58.4	89.2
			depth 200-600 m s_A > 1			
1996	31.0	25.1	0.5	10.8	25.3	46.4
1997	29.9	25.0	0.5	10.3	22.3	44.2
1998	29.0	22.9	0.5	12.1	23.5	39.9
1999	27.0	27.6	0.6	3.5	19.3	42.4
2000	19.9	21.2	0.5	4.3	12.0	28.2
2001	46.6	32.2	0.6	19.2	39.5	72.2
			depth 50-600 m s_A > 1 day/night			
			day			
1996	29.2	26.4	0.8	9.0	21.9	41.0
1997	29.3	28.3	0.9	7.1	18.3	44.7
1998	29.2	29.1	1.1	8.8	17.3	40.1
1999	23.3	29.1	1.0	0.0	12.4	34.0
2000	26.9	29.3	1.0	4.0	14.3	43.9
2001	37.0	31.7	0.9	12.9	26.1	51.9
			night			
1996	41.3	28.3	0.7	16.9	37.5	63.6
1997	35.9	26.7	0.6	15.4	28.6	51.6
1998	37.5	25.3	0.7	18.4	31.4	50.5
1999	35.9	29.6	0.9	11.2	29.9	55.2
2000	27.5	25.6	0.6	6.6	18.1	44.2
2001	54.7	31.0	0.7	28.8	51.5	82.1

Tables 5: Blue whiting: Distribution of the relative acoustic s_A–value from bottom channel (10m above seabed) in percent of total s_A–value. Saithe survey along Norwegian coast N of 62°N 1992-1997. Classification by bottom depth and acoustic s_A–value interval. std and stdmean are standard deviation and standard deviation of the mean; q1 and q3 are lower and upper quartiles.

year	mean	std	stdmean	q1	median	q3
depth 30-200 m SA > 1						
1992	77.0	31.3	3.6	53.6	100.0	100.0
1993	63.4	32.7	5.4	39.8	68.3	96.6
1994	62.1	38.5	10.7	39.9	68.7	95.8
1995	83.8	28.1	1.7	75.6	100.0	100.0
1996	31.7	37.9	2.0	0.0	15.7	51.3
1997	91.7	21.4	1.2	100.0	100.0	100.0
depth 300-600 m SA > 1						
1992	16.0	24.6	1.0	0.0	2.5	25.2
1993	18.9	19.9	1.7	7.2	13.2	21.1
1994	35.9	20.0	1.8	19.8	35.1	49.7
1995	22.0	20.5	1.5	9.1	14.9	26.2
1996	15.1	14.7	0.7	4.6	11.2	21.3
1997	10.5	9.8	1.2	2.6	9.5	14.6
depth 300-600 m SA > 10						
1992	11.8	21.8	1.3	0.0	2.4	11.4
1993	23.5	22.9	3.2	7.8	16.4	28.6
1994	30.5	17.9	2.3	17.5	27.4	42.3
1995	17.4	16.4	1.5	8.3	12.8	21.1
1996	12.5	11.6	0.7	3.1	9.2	19.2
1997	6.4	7.6	1.3	0.0	2.7	12.0
depth 30-600 m SA > 1 Day/Night						
day						
1992	37.2	40.3	3.0	0.0	23.4	91.1
1993	48.5	40.9	6.2	11.6	28.8	100.0
1994	46.8	26.4	3.4	21.5	48.4	65.8
1995	78.8	27.6	2.0	71.1	91.1	100.0
1996	36.5	32.7	2.0	10.0	24.8	53.8
1997	77.2	36.7	2.4	51.4	100.0	100.0
night						
1992	34.7	35.2	1.3	0.0	28.6	57.0
1993	35.7	27.9	1.8	12.4	29.3	55.1
1994	54.4	32.2	2.0	24.9	49.5	88.7
1995	59.7	38.7	1.7	16.7	66.2	100.0
1996	23.1	29.2	1.0	0.0	12.3	31.7
1997	62.7	39.2	2.1	26.9	73.5	100.0

Tables 6: Saithe: Distribution of the relative acoustic s_A–value from bottom channel (10m above seabed) in percent of total s_A–value. North Sea survey S of 62°N 1992-2000. std and stdmean are standard deviation and standard deviation of the mean; q1 and q3 are lower and upper quartiles.

```
                       depth 30-600 m SA > 1
     year      mean    std   stdmean      q1    median       q3

     1992      69.5   33.6      1.0      41.3      81.2     100.0
     1993      94.5   18.6      0.6     100.0     100.0     100.0
     1994      86.1   30.6      1.9     100.0     100.0     100.0
     1995      88.5   26.6      0.9     100.0     100.0     100.0
     1996      73.3   30.0      1.0      46.9      86.3     100.0
     1997      96.1   16.2      0.4     100.0     100.0     100.0
     1998      82.2   28.1      0.8      63.9     100.0     100.0
     1999      91.0   22.4      1.0     100.0     100.0     100.0
     2000      92.1   18.6      0.5      97.2     100.0     100.0
```

Table 7: The relative difference between median of acoustic day and night s_A–value in percent of the larger of these two. Day column shows this correction percentage when day loss > night loss, and similarly for night column.

year	cod day	cod night	haddock day	haddock night	Redfish Day	Redfish night
1996	24.3		21.8			20.8
1997	0.7		4.8			31.6
1998		2.3		28.8		54.7
1999	4.7			31.67		7.0
2000		11.4		21.1		29.3
2001		63.4		38.1		39.9

Table 8: Salinity and temperature weighted by acoustic s_A–value for cod, haddock, and redfish. Summer surveys in the Barents Sea, 1996-2000 All years together and annual average. SD is standard deviation; P1, P5, … are the percentiles.

Summer Salinity 1996-2000, Barents Sea

species	mean	SD	P99	P95	P75	median	P25	P5	P1
cod	34.82	0.20	35.06	35.02	34.94	34.87	34.76	34.39	34.22
haddock	34.70	0.15	35.05	35.01	34.89	34.83	34.55	34.22	34.13
redfish	35.02	0.03	35.12	35.11	35.05	35.02	35.00	34.92	34.71
capelin	34.93	0.17	35.07	35.05	35.01	34.97	34.90	34.71	34.35
herring	34.64	0.36	35.07	35.04	34.92	34.66	34.38	34.11	33.90

Summer temperature 1996-2000, Barents Sea

species	mean	SD	P99	P95	P75	median	P25	P5	P1
cod	2.76	1.45	7.13	5.20	3.30	3.06	1.99	0.21	-0.57
haddock	4.33	1.03	8.34	7.58	5.77	3.40	3.18	1.93	0.98
redfish	3.41	0.68	6.49	6.23	4.39	3.11	2.22	1.54	0.86
capelin	2.80	2.57	8.09	6.74	4.32	2.10	1.26	0.11	-0.78
herring	7.98	2.01	10.39	9.73	9.07	8.56	7.38	3.80	2.71

Cod summer temperature, Barents Sea

year	mean	SD	P99	P95	P75	median	P25	P5	P1
1996	2.86	1.51	5.4	3.6	3.3	3.16	2.7	1.0	-0.4
1997	2.62	1.76	7.8	6.5	3.9	2.40	1.0	-0.3	-0.5
1998	2.10	1.32	6.2	4.8	3.0	2.27	1.1	-0.5	-1.1
1999	3.36	1.52	8.2	7.0	4.0	3.32	2.5	1.0	-0.4
2000	2.45	0,87	6.4	5.6	3.6	2.59	1.1	0.2	-0.8

Haddock summer temperature, Barents Sea

year	mean	SD	P99	P95	P75	median	P25	P5	P1
1996	3.30	0.97	6.6	6.2	3.3	3.2	3.2	1.8	1.0
1997	5.69	0.78	8.1	7.6	6.6	5.8	5.0	3.0	2.1
1998	5.93	0.61	8.8	8.1	7.0	6.1	5.1	2.8	1.8
1999	5.26	0.92	8.7	8.3	7.2	4.9	3.6	2.3	0.9
2000	5.19	0.60	8.3	7.2	6.1	5.4	4.5	2.3	0.8

Redfish summer temperature, Barents Sea

year	mean	SD	P99	P95	P75	median	P25	P5	P1
1996	3.81	0.88	6.5	6.4	5.5	3.9	1.9	1.2	1.0
1997	2.99	0.36	6.2	5.2	3.7	2.8	2.4	1.0	0.1
1998	3.58	0.53	6.2	6.1	5.2	3.1	2.5	1.2	0.6
1999	3.54	0.70	6.6	6.5	4.1	3.1	2.6	1.6	0.8
2000	3.10	0.69	6.2	5.4	4.0	3.0	1.9	1.6	1.6

Table 9: Salinity and temperature weighted by acoustic s_A–value for cod, haddock, and redfish. Winter surveys in the Barents Sea, 1996-2000 All years together and annual average. SD is standard deviation; P1, P5, … are the percentiles.

Winter salinity 1996-2000, Barents Sea

species	mean	SD	P99	P95	P75	median	P25	P5	P1
cod	34.92	0.10	35.10	35.06	35.00	34.96	34.89	34.64	34.41
haddock	34.90	0.11	35.10	35.06	35.00	34.96	34.83	34.56	34.24
redfish	34.97	0.06	35.11	35.08	35.03	35.00	34.96	34.76	34.34
capelin	34.92	0.12	35.05	35.04	35.01	34.94	34.87	34.56	34.50
herring	34.76	0.11	35.15	35.07	34.93	34.73	34.63	34.38	34.21

Winter temperature 1996-2000, Barents Sea

species	mean	SD	P99	P95	P75	median	P25	P5	P1
cod	3.10	1.28	6.8	5.8	4.3	3.17	1.9	0.1	-0.5
haddock	4.12	0.63	6.8	5.9	4.6	4.09	3.6	2.5	1.8
redfish	3.66	0.62	6.8	6.1	4.7	3.70	2.4	1.8	1.3
capelin	1.25	1.51	5.6	4.0	2.3	1.46	0.02	-1.2	-1.3
herring	3.23	0.75	6.8	5.7	4.1	3.32	2.2	1.2	-0.4

cod winter temperature, Barents Sea

year	mean	SD	P99	P95	P75	median	P25	P5	P1
1996	2.33	1.11	6.0	5.3	3.3	2.3	1.3	-0.3	-0.5
1997	2.97	1.00	5.4	4.5	4.0	3.4	2.0	0.4	-0.4
1998	2.97	1.37	6.3	5.3	4.3	3.1	1.8	0.2	-0.4
1999	3.13	1.18	6.9	6.1	4.5	3.2	1.8	0.3	-1.1
2000	4.10	1.33	7.0	6.6	5.2	4.2	3.0	1.5	-0.03

Haddock winter temperature, Barents Sea

year	mean	SD	P99	P95	P75	median	P25	P5	P1
1996	3.81	0.64	6.2	5.9	4.4	3.6	2.9	2.3	1.6
1997	4.00	0.49	5.7	4.6	4.4	4.0	3.7	3.0	2.1
1998	4.21	0.43	6.4	5.8	4.7	4.2	3.7	2.6	1.7
1999	4.17	0.60	6.9	6.4	5.0	4.2	3.3	2.2	1.5
2000	4.54	0.78	7.0	6.6	5.2	4.5	3.7	2.8	1.9

Redfish winter temperature, Barents Sea

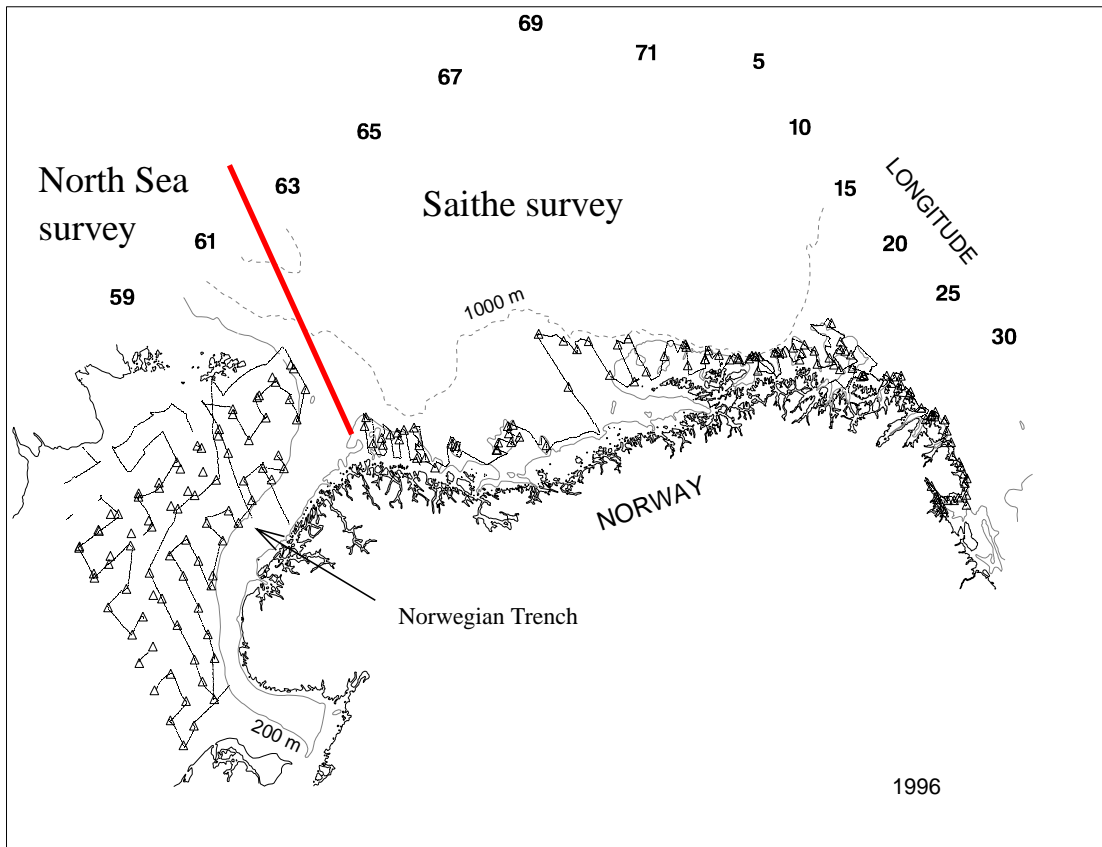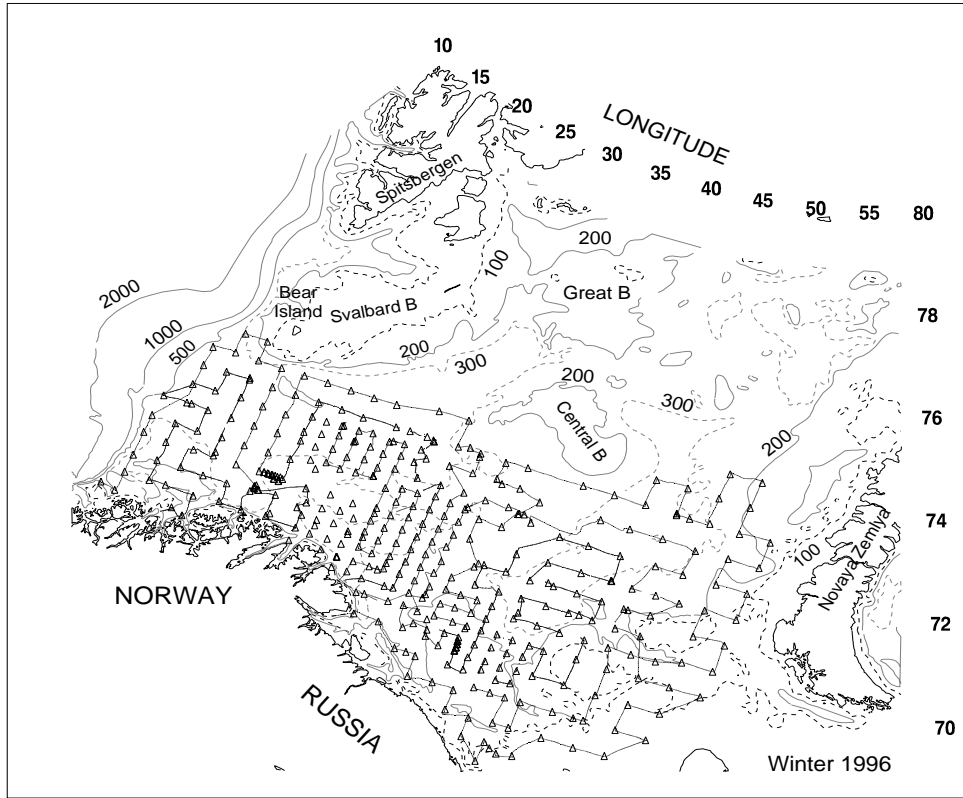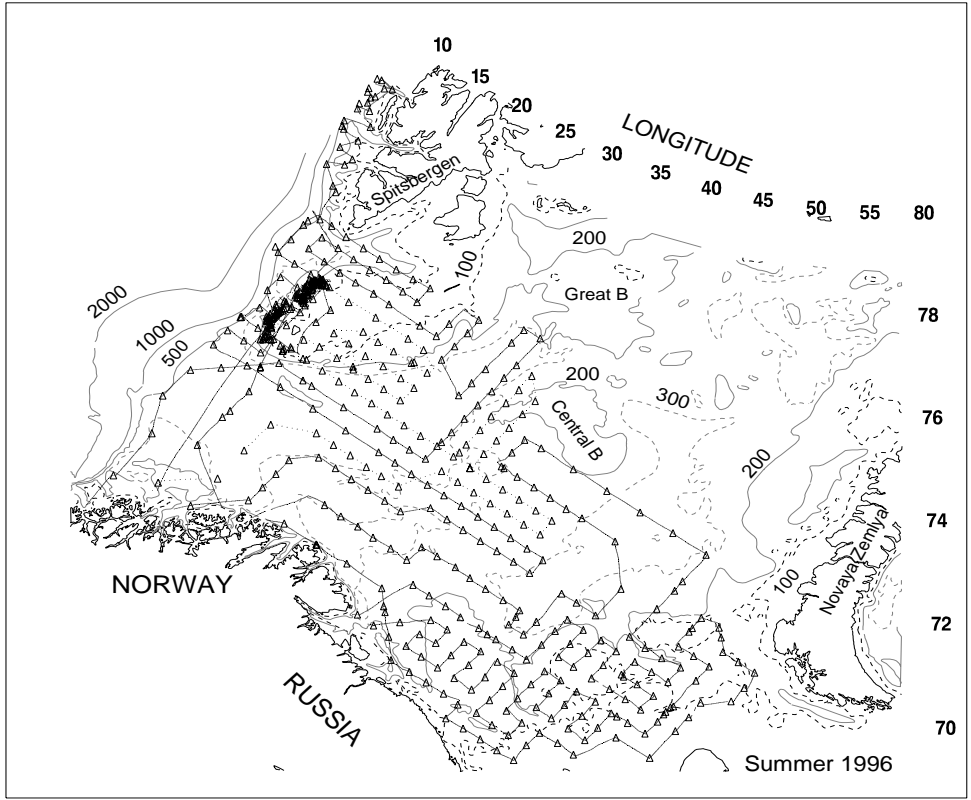| year	mean	SD	P99	P95	P75	median	P25	P5	P1
1996	3.23	0.60	6.2	5.6	4.2	2.72	2.1	1.7	1.0
1997	3.28	0.59	5.5	5.0	4.0	3.58	2.3	1.6	1.3
1998	3.85	0.73	6.5	6.3	4.7	4.04	2.7	1.8	1.4
1999	4.19	0.37	6.9	6.4	5.1	4.32	3.3	1.6	1.3
2000	4.87	0.47	7.0	6.8	5.9	5.08	3.8	2.4	2.3

Figure 1

Figure 2

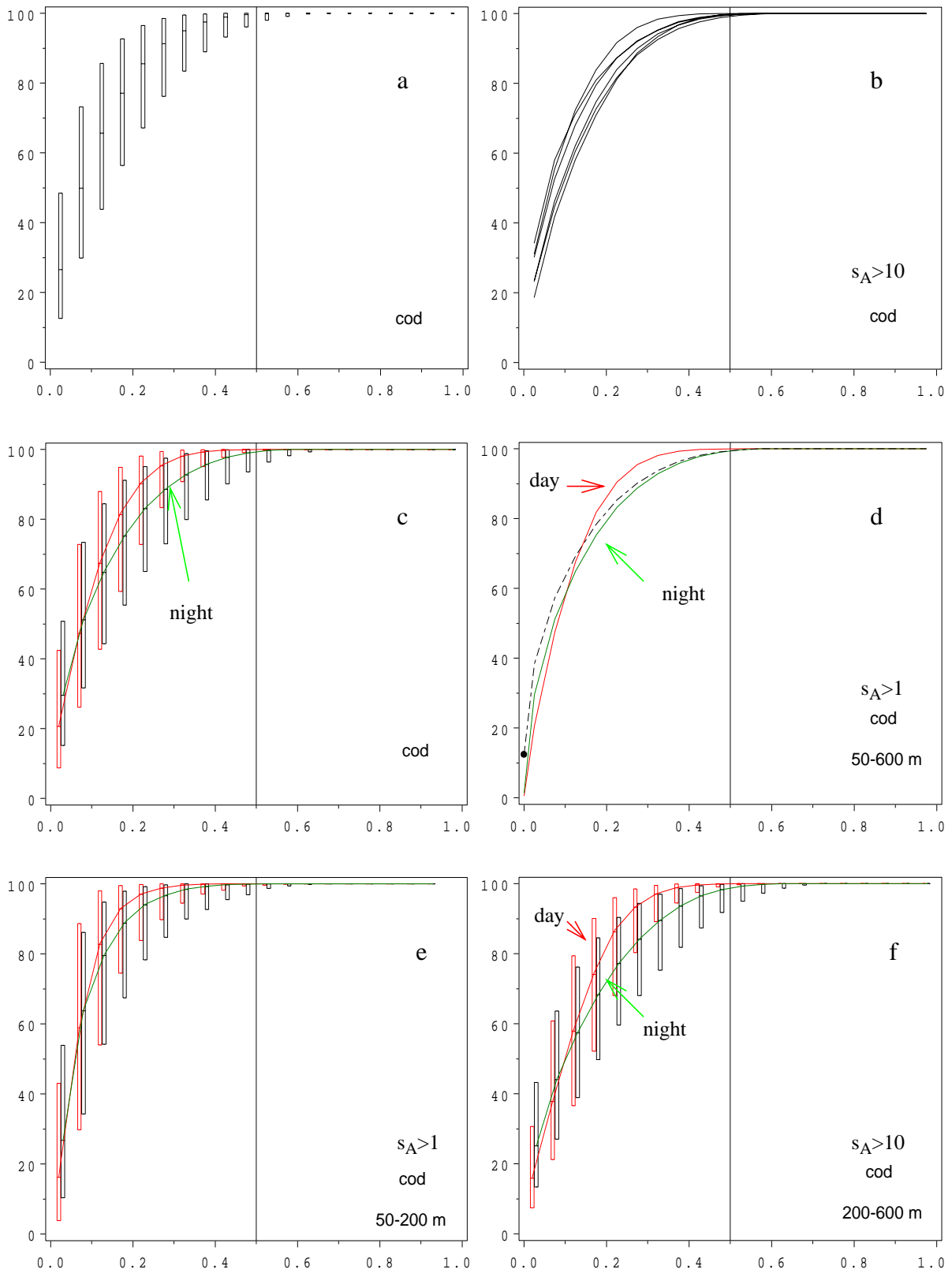Figure 3

Winter survey

Figure 4
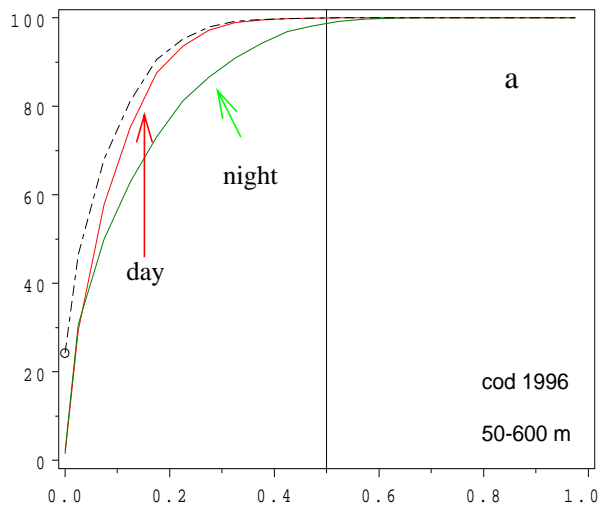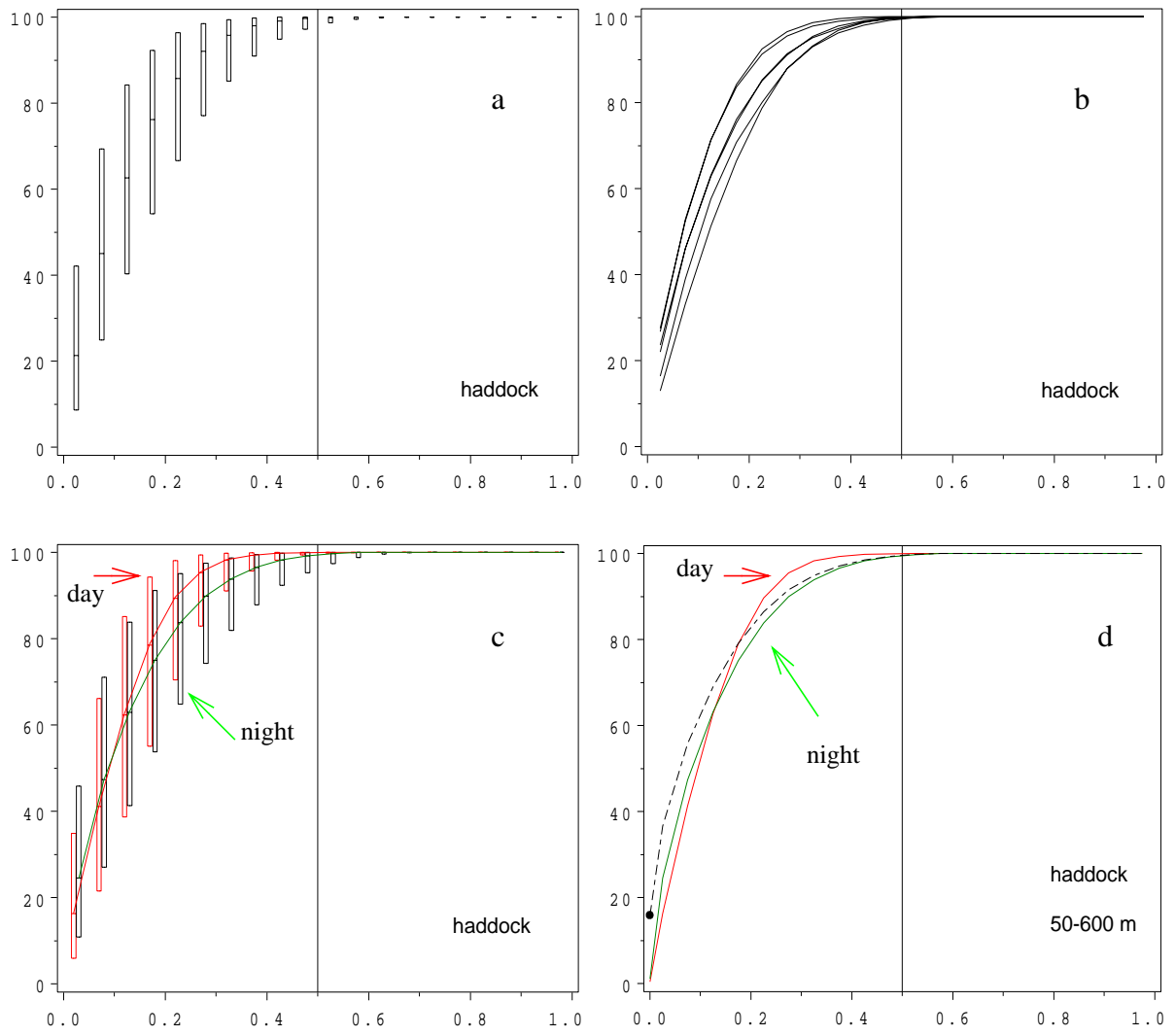
Winter survey

Figure 5

Winter survey
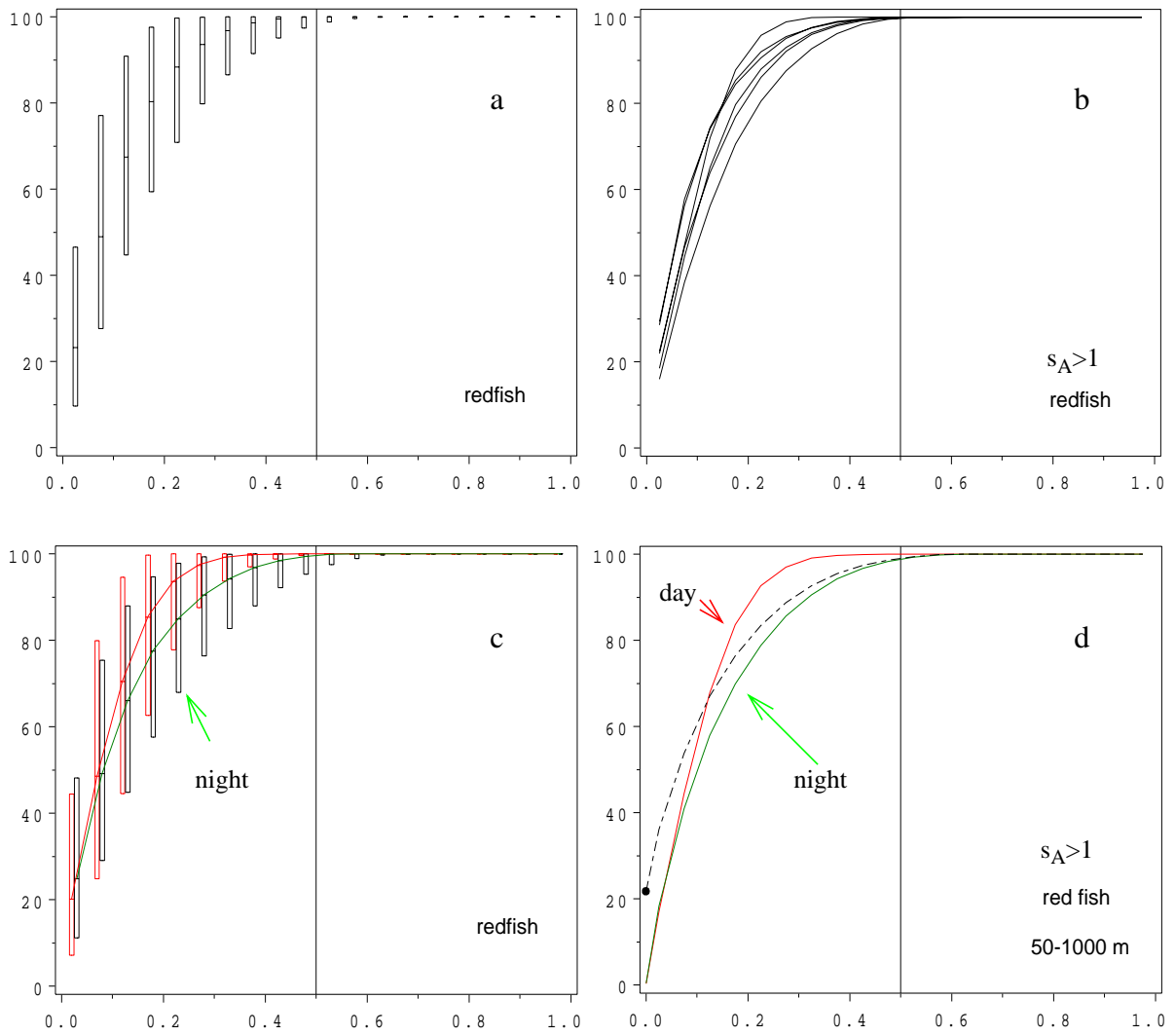

Figure 6

Winter survey and Irminger Sea survey
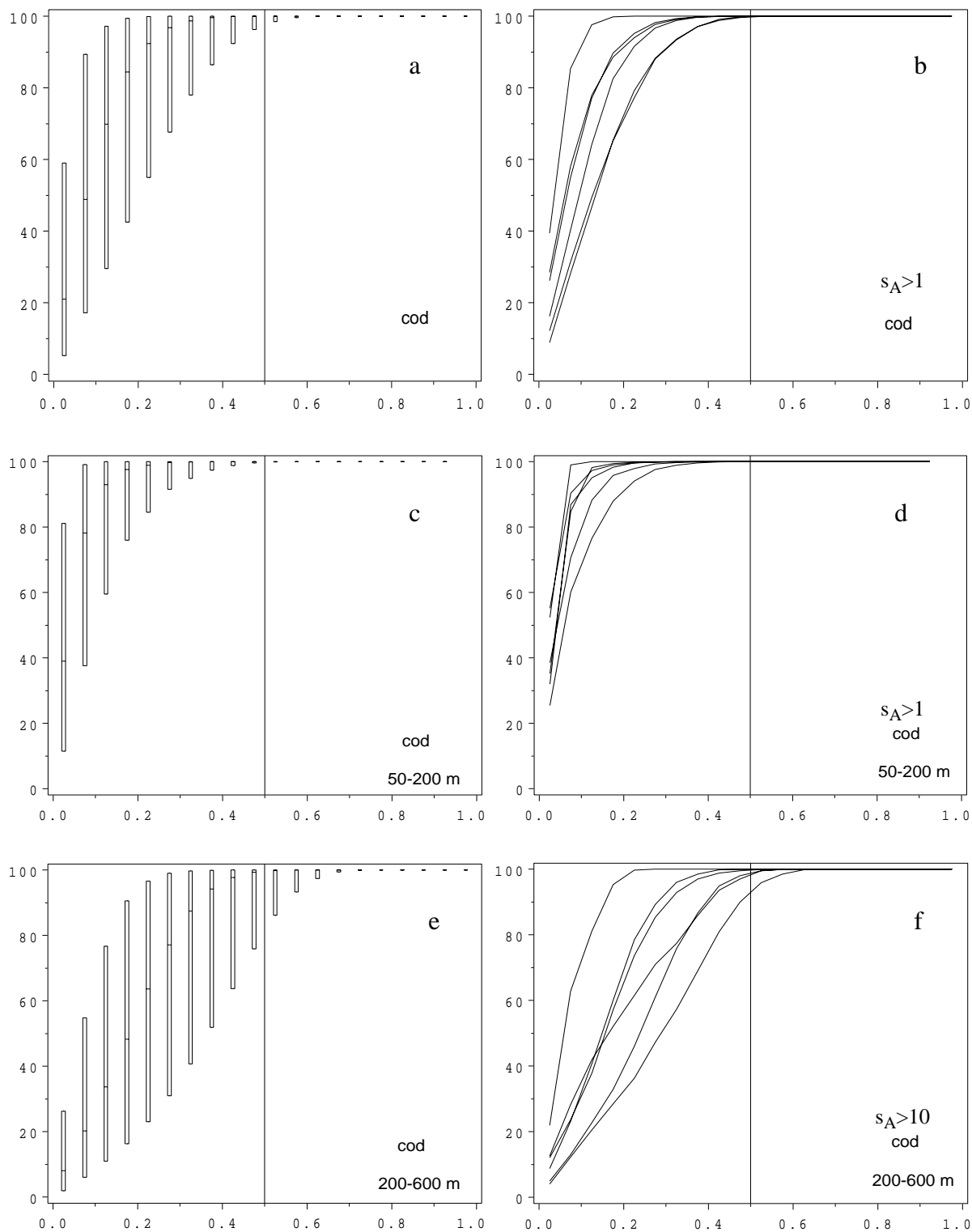
Figure 7

Summer survey
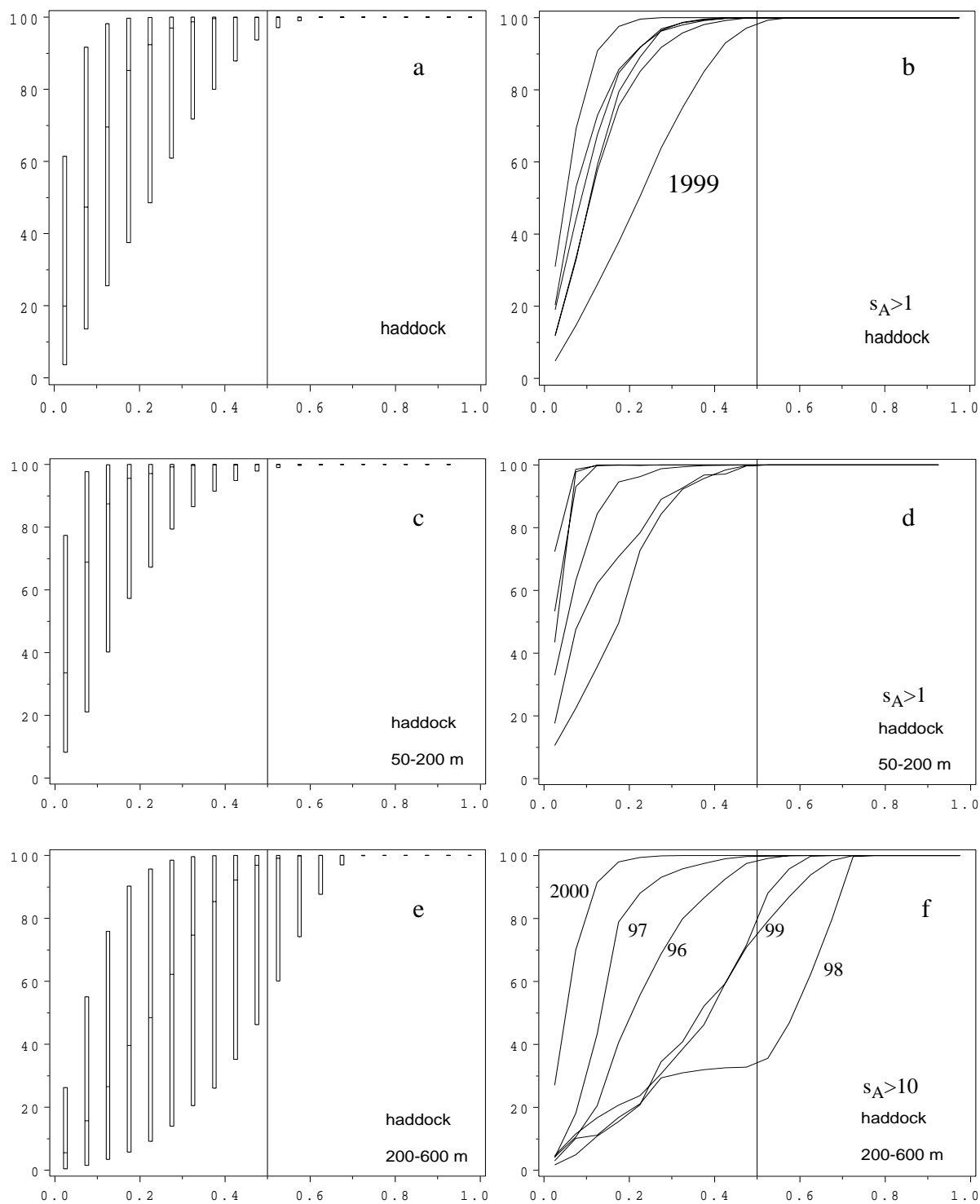

Figure 8

Summer survey
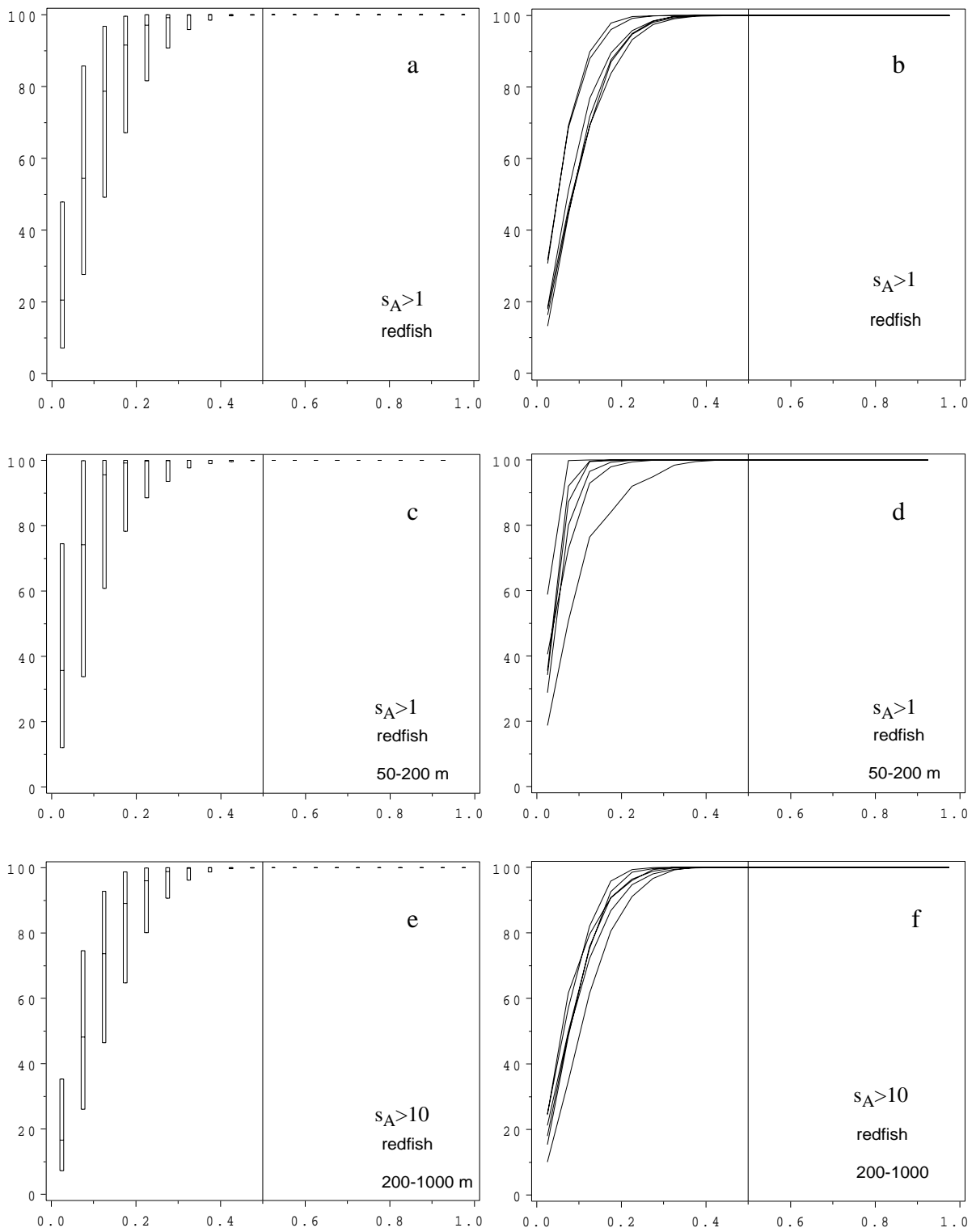

Figure 9

Summer survey

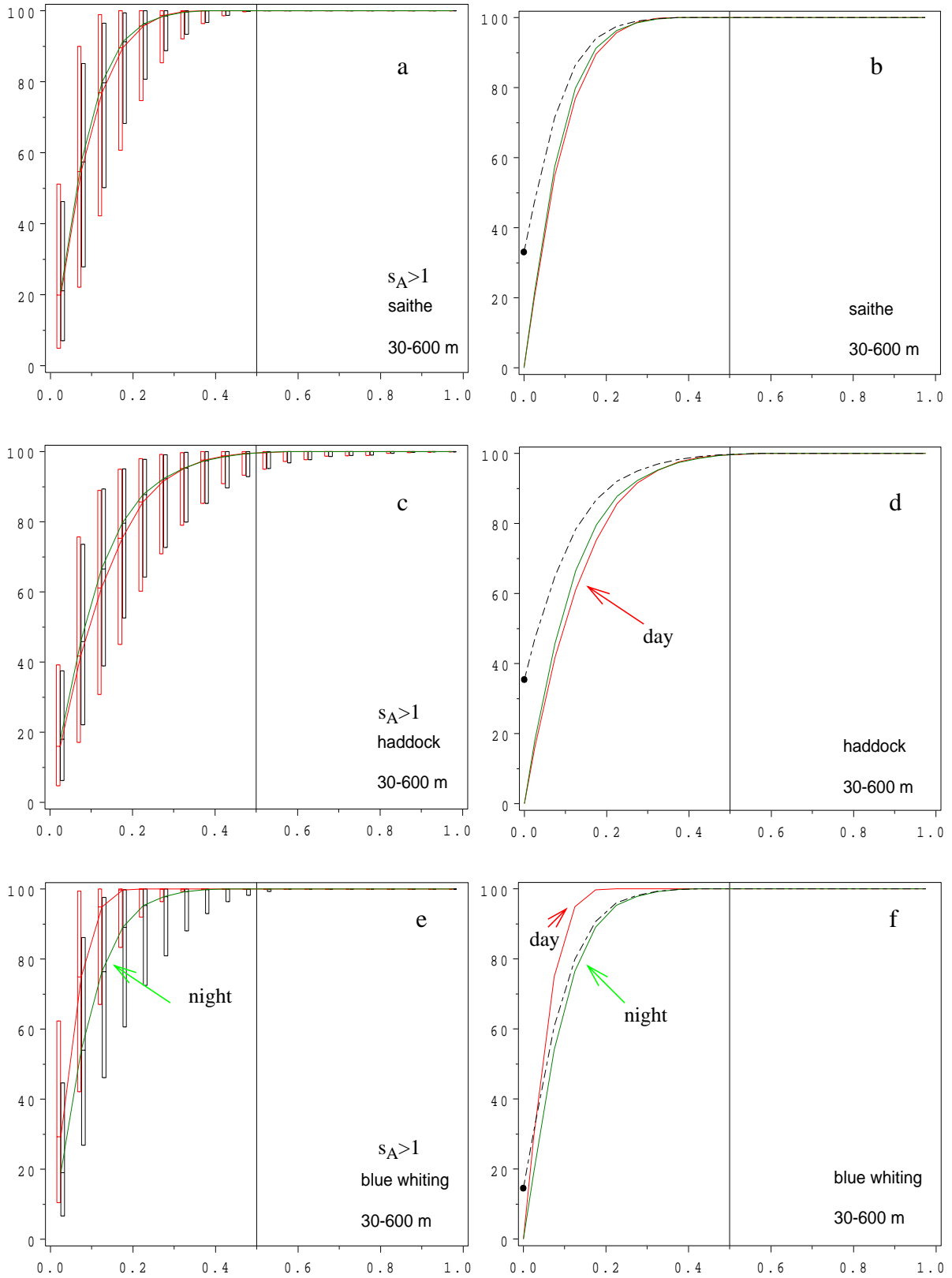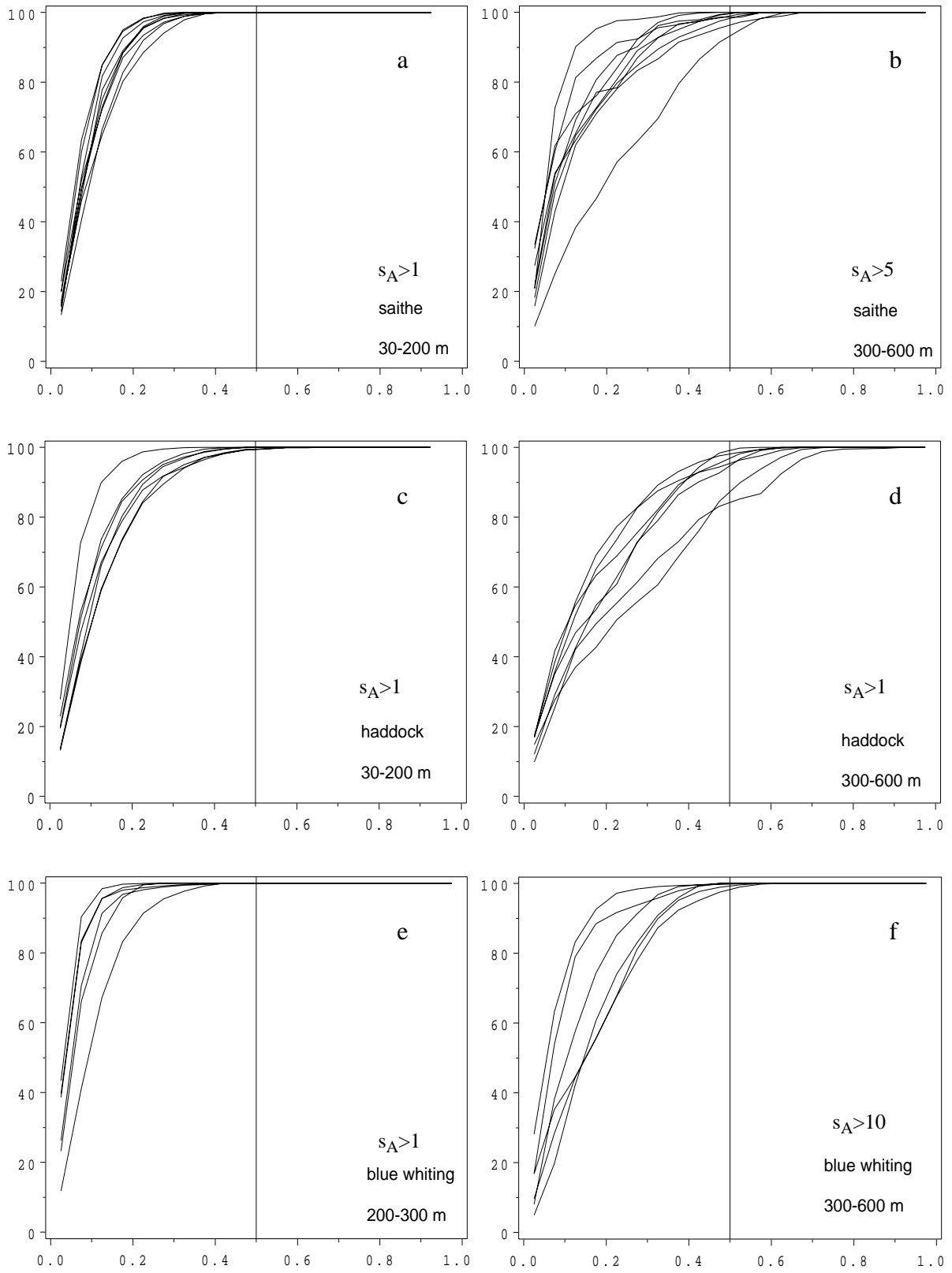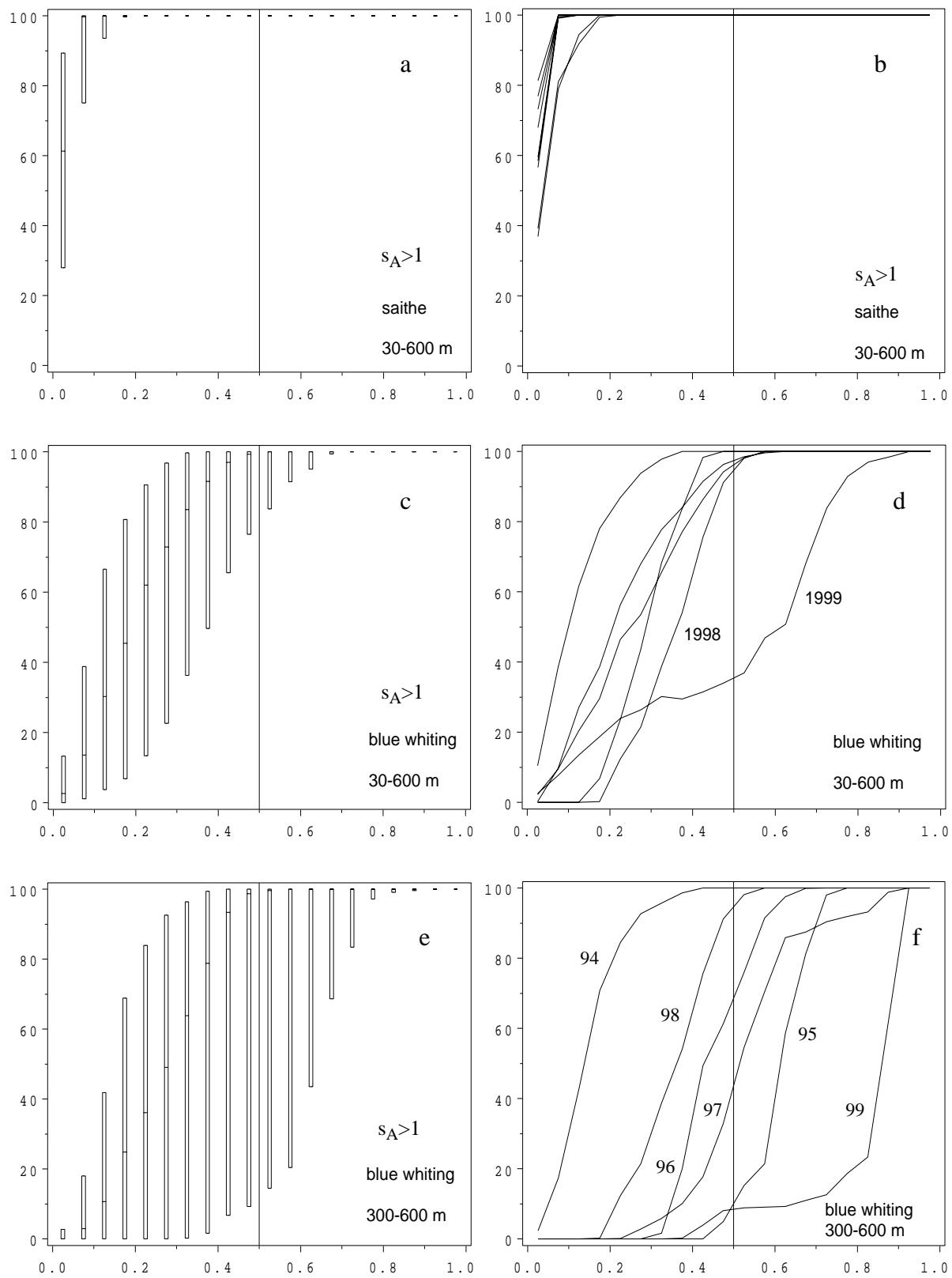Figure 10

Norwegian coast survey

Figure 11

Norwegian coast survey

Figure 12

North Sea Survey

Figure 13

Winter survey

Figure 14