The effect of fish behaviour and spatial structures on acoustic and trawl surveys

by

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Summary

Time series of scientific survey estimates of fisheries resources are used to measure changes in stock size and composition. Standardization of sampling equipment and design is regarded crucial for reliable trawl and acoustic survey estimates, but in spite of established routines the reliability of the survey estimates are reduced due to variations in fish behavior and changes in their spatial distribution.

The main objectives of this thesis are to investigate the effects of spatial and temporal variation in fish distribution and behavior on acoustic and bottom trawl estimates, and the study presents methods to identify and correct for these sources of errors. A large variety of data are examined ranging from acoustic recordings from the spawning grounds of blue whiting (*Micromesistius poutassou*) and Norwegian Spring Spawning herring (*Clupea harengus*) to bottom trawl survey data and commercial CPUE of Namibian hake (*Merluccius capensis* and *M. paradoxus*) and the results are presented in six scientific papers.

We show that blue whiting is distributed deeper and covers a narrower depth range at daytime than at night during its spawning west of the British Isles. As a consequence the tilt angle distribution changes and reduces the average acoustic target strength of the measured fish. This explains why we observed higher acoustic densities of blue whiting at daytime than at night. The effect of the diel variation on the survey estimates varies between years and therefore reduces the reliability of the survey time series (Paper I). Not surprisingly we observed that the diel oscillation in the sample values is closely related to rise and set for the sun. However, time-dependent variation in the catch rates and echo density also occur within daylight and the density measures increase from dawn to noon and then subsequently decrease to dusk (Papers I and IV). For the catch rates of Namibian hakes we found that the maximum is reached when the sun is about 20 degrees above the horizon, but the amplitude of the diel oscillation decreases with depth and increases with density of hake. Highest amplitude values are found in shallow waters which are dominated by the *M. capensis* species (Paper IV). The effect of weather and environmental conditions on the diel variation is not investigated in our studies due to lack of adequate data, but a in situ experiments we carried out in Namibia indicates a between-year difference in the escapement of hake under the fishing line due to annual differences in the oxygen levels near the seabed (Paper III). This type of escapement is likely to change with time of the day as hake lifts from the bottom at night and may also explain some of the differences in the diel oscillation we found in the different areas of the Namibian waters.

It is often stressed that the assessment surveys should be repeated at the same time each year, as many fish stocks move in more or less repeating geographical migration patterns. However, the substantial geographical dynamic we identified in the Namibian trawler fleet (Paper V) suggests substantial annual variation in the spatial distribution of the hakes and changes in survey estimates may therefore be a sampling artifact due to variable environmental conditions and location of fish. Fish populations are usually patchily distributed and show gradient structures and the individuals within a shoal or a limited area tend to have more similar characteristics than those of the entire population. An example of small scale patchiness is found in the herring trawl samples with a significant relationship between depth distribution and maturity state of herring where the spawners dominated the trawl catches taken close to the sea-bed (Paper II). In Paper VI, the precision of the abundance estimates by length group of Namibian hake is increased by including the information of spatial autocorrelation. Using geo-statistic, the geographical structure of the distribution can be model and thus enhance the quality of the survey estimates.

The overall result shows that the catch rates and acoustic density of fish are influenced by the fish's location and its response to the approaching trawl which vary with time of the day. The swimming performance and reaction pattern to catching device are also affected by the density of fish, species and length dependent behavior, bottom depth, level of dissolved oxygen and temperatures. All these parameters can be included in the generic term "survey condition", and any change in the survey condition tend to influence the relationship between measured and true fish density. The survey errors investigated in this thesis are not included in standard estimation procedures, and obviously it is a difficult task to correct for errors caused by variation in the survey condition. We have applied statistical modeling to identify systematic spatial and diel variability in large survey and commercial fishing data-sets, which can be used to correct for these errors. However, diel variation and geo-statistical models depend on the correct estimation of several parameters, which negatively affect the precision of the survey estimates. Therefore, a better approach is to integrate several sampling methodologies so the effect of variable survey conditions can be directly measured. Many places on the globe are also on the doorstep to a complex ecosystem management approach which demands scientific surveillance of several species and trophic levels. A simultaneous monitoring of inter-specific interaction is a fundament of this types of surveys and requires advanced survey strategies where many sources of data collected with trawls, CTD probes, echo-sounders, transducers and sonars are integrated and together form the basis for the concurrent measurement of the environment, survey condition and fish densities.

Furthermore, the allocation of survey effort are occasionally sub-optimize due to variation in the spatial structure of the target stock between surveys. An adaptive sampling strategy which utilizes for instance satellite tracking data of the commercial fishing fleet to map the stock distribution in advance of the surveys may improve the effort allocation and hence increase the reliability of the survey estimates.

List of papers

- Paper I. Johnsen, E., and Godø, O.R. 2007. Diel variations in acoustic recordings of blue whiting (*Micromesistius poutassou*). ICES Journal of Marine Science **64:** 1202–1209.
- Paper II. Johnsen, E. and Skaret, G. Mass formations in giant fish shoals founded in conflicting motivation. Submitted to Marine Ecology Progress.
- Paper III. Jørgensen, T., Engås, A., Johnsen, E., Iilende, T., Kainge, P. and Schneider, P. 2007. Escapement of Cape hakes under the fishing line of the Namibian demersal sampling trawl. South African Journal of Marine Science 29: 209-221.
- Paper IV. Johnsen, E., and Iilende, T. 2007. Diel variation in commercial CPUE and survey catch rates. Can fishery data improve Namibian hake survey estimates? Fisheries research **88:** 000-000.
- Paper V. Johnsen, E. 2004. A visualization of the spatial and temporal dynamics in the Namibian hake trawl fishery – a tool to understand the complexity of a fishery. In: Nishida, T., Kailola, P.J., and Hollingworth, C.E. (Eds.). GIS/Spatial Analyses in Fishery and Aquatic Sciences (Vol. 2). Fishery-Aquatic GIS Research Group, Saitama, Japan pp. 673-678.
- Paper VI. Johnsen, E. 2003. Improving the precision of length frequency distribution estimates from trawl surveys by including spatial covariance – using Namibian *Merluccius capensis* as an example. Fisheries Research 62: 7-20.

Introduction

Population trends in exploited fish stocks are normally monitored with catch statistics, commercial catch per unit effort (CPUE) data, standardized scientific surveys, or a combination of these (Gunderson 1993). Commercial CPUE and survey data can be used in the tuning process (Helser and Hayes 1995) in the classical surplus production and analytical models (Pitcher and Hart 1982), the Deriso and the depletion models (Xiao 2000). However, changes in catch efficiency and strategy in the fishing fleets (Shepherd 1988; Salthaug and Aanes 2003) and heterogeneity in fish distribution and variations in the area inhabited by the stock (Ulltang 1980) violates the assumption of a linear relationship between commercial CPUE and stock size. This has made fishery independent data increasingly important for stock assessment (Gunderson 1993; Godø 1994). It is a broad consensus that modern stock assessment is dependent on scientific surveys, and it is argued that survey estimates appear to produce better assessments of the current stock than the more complex catch-based assessment methods due to a lack of catch-at-age data, miss-reporting and unknown discard fractions (Pennington and Strømme 1998).

Bottom trawl and acoustic surveys are the most widespread scientific survey methods to assess marine fish (Gunderson 1993; Aglen 1994; Godø 1994; Simmonds and MacLennan 2005). To maximize the survey reliability it is crucial to calibrate the sampling equipment and standardize the survey design (Gunderson 1993; Weinberg and Somerton 2006), however, temporal and spatial variation in fish behaviour and distribution may bias the survey estimates. The significance of this variation has received considerable scientific attention (e.g. Wardle 1993; Fréon *et al.* 1993), but the achieved knowledge is seldom implemented in standard acoustic and bottom trawl surveys.

The main objectives of this thesis is to share light on the reasons for the lack of implementation of the observed variability in bias and investigate various effects of spatial and temporal variation in fish distribution and behavior on acoustic and bottom trawl estimates, and based on this suggest a general fundament where these effects can be implemented in the survey estimates. The challenges and potential solutions are illustrated and discussed using a great variety of data from acoustic and bottomtrawl assessment surveys, commercial CPUE data and experimental in situ data. Acoustic data from the spawning grounds of blue whiting (*Micromesistius poutassou*) and Norwegian Spring Spawning herring (Clupea harengus) are examined. Furthermore, the Namibian bottom trawl survey data, which from 1990 to 1997 was the only source of data used in Namibian hake (Merluccius spp.) assessment (Butterworth and Geromont 2001), are comprehensively studied. The effect of diel variation in echo density and catch rates on the survey estimates (e.g. Bowman and Bowman 1980; Engås and Soldal 1992; Casey and Myers 1998; Aglen et al. 1999; Benoit and Swain 2003; McQuinn et al. 2005) will in combination with the effect of variation in small and large scale spatial structures be the major focuses of this work. Further, the importance of reliable and rigorous survey monitoring will be discussed in the context of modern ecosystem surveillance and sustainable resource management.

Summary of papers

Paper I: Annual landings of blue whiting (*Micromesistius poutassou*) in the northeast Atlantic have exceeded 2 million metric tonnes in recent years, and overexploitation is an increasing concern in terms of the sustainability of the fishery. The most important fisheries-independent dataset used for tuning the analytical stock assessment comes from the Norwegian surveys of blue whiting west off the British Isles. The survey is carried out in March/April during peak spawning, and improving its quality will have a direct positive effect on stock assessment. Here, we analyse diel effects on the abundance and vertical distribution as recorded by acoustics in 1995 and 1996 and from 1998 to 2002, and evaluate the potential effects on the survey estimates. On average, the acoustic density of blue whiting was 20% higher by day than by night. However, the diel bias varied considerably among years, and surprisingly, the acoustic density in shallow water (<350 m) was in general highest at night, when the blue whiting were distributed higher in the water column and more dispersed. The span in the vertical depth range increased considerably with bottom depth in water shallower than 550 m. In deeper water, where blue whiting had little or no bottom association, the day-night differences in vertical distribution were smaller and not affected by bottom depth. The inconsistency of the diel effect from year to year negatively affects the time-series used during annual stock assessments.

Paper II: Organising principles behind adaptive collective formations in animals are not well understood. Particularly challenging to marine scientists is to grasp the mechanisms decisive of dynamics in shoal structure and formation in free-ranging pelagic fish shoals operating in a dynamic environment. Here we document that persistent vertical hourglass formations occur frequently during the critical spawning period in aggregations involving billions of herring *Clupea harengus*. Through biological sampling we show that the individual maturation state is significantly different between the upper and lower components of the formations, strongly indicating conflicting individual motivation founded in the trade-off between survival and reproduction as the underlying mechanism of the collective behaviour.

Paper III: Swept area surveys in Namibian waters provide input data to the stock assessment model. To evaluate the model's predictions, it is important to understand the catch efficiency of sampling trawls. The objective of this study was to establish whether Cape hakes (Merluccius capensis and M. paradoxus) escape under the fishing line and to identify any species or length dependence of escape rates. Experiments were carried out in Namibian waters during two cruises in October 2002 and October 2003. A collection bag was mounted under the trawl to catch fish escaping below the fishing line. Environmental data and photographs of fish in front of the trawl were also taken. Escapement of hake varied by length, species, depth and year. It was generally below 5% for *M. capensis* but escapement in 2002 averaged 10–20% for *M.* paradoxus, and in 2003 it was over 50% in the shallow area (300m), decreasing to 10% in the deep area (570m). Oxygen level seemed to explain the marked betweenyear difference in escapement. Escapement of M. capensis decreased marginally with increasing fish length, whereas escapement of *M. paradoxus* showed a marked increase with increasing fish length in shallow waters and no length dependence in deep waters. Species differences in behaviour and vision may partly explain the observations.

Paper IV: Diel variation in bottom trawl catch rates of hake (Merluccius capensis and *M. paradoxus*) was studied by applying a stochastic model to logbook records of the Namibian trawler fleet and data from the standard hake assessment surveys. The commercial CPUE standardized by the vessel-day average were about 3.6 times higher around noon compared to CPUE during the night, and the diel variations was higher in areas dominated by *M. capensis* than in those mainly inhabited by *M. paradoxus*. The day-night difference in commercial CPUE decreased with depth and increased with density of hake and varied with latitude, whilst no significant seasonal or annual patterns were observed. Further, the time of transition from night to day level was correlated with time of sunrise which changes with season. Trawling in shallow waters at night is avoided during the Namibian hake surveys, and the systematic survey design complicated the diel variation modelling of the survey data. However, by utilizing the parameters which describe the diel variation transition estimated from the commercial CPUE data and compensating for the survey design effect, the survey hake catch rates at noon were estimated to be 27% and 86% higher than at night for *M. capensis* and *M. paradoxus*, respectively. More important, we also demonstrate that the transition period from night-level catches to maximum day-level is long, which implies that the catch efficiency in the morning and the afternoon are in general lower than at noon, and consequently may bias the survey estimates.

Paper V: Commercial catch and effort data are widely used to track changes in the abundance of fish stocks, hence the stock assessment methods used are dependent on an understanding of the behaviour of the fishing fleet. This work has used Namibian hake (*Merluccius capensis* and *M. paradoxus*) log sheet data to visualise the dynamics that exist in the distribution of the Namibian freezer trawlers. An animation was created which aimed to show the geographical distribution of the fleet over time and the fluctuations and trends in the catch rates. Both these factors are used in stock assessments of Namibian hake. The visualisation is a simple production, which is easy to interpret, understand and generate.

Paper VI: Trawl survey estimates of the distribution of fish population characteristics are not likely to give an absolute true reflection of the population. Errors and biases can be introduced in sampling and calculation techniques of the population characteristics. Analysis done on trawl survey sampled length data of Namibian *Merluccius capensis* indicates a better precision of length frequency distributions if spatial covariances were included in the calculations. Spatial covariance was detected using experimental semi-variograms, from which variogram models were derived and used in kriging. Arithmetic and kriged means of the density (#/nm2) of *M. capensis*' length groups were calculated, and 97% of the length groups gave lower coefficient of variation using the geostatistical method. Hence, the geostatistical approach provided improvements of the population characteristic estimates for a low cost.

Discussion

Reliable survey time series depends on standardized procedures to minimize the variability in abundance indices between samples, survey vessels, and over time. Nevertheless, changes in the environment^{*}, and variation in fish behaviour and distribution influence the relationship between the survey estimates and the true population size and structure. In this thesis I will re-introduce the concept "survey condition" (Godø and Wespestad 1993) to describe the bias caused by these factors on the relationship between measured and true fish density. The survey condition may change considerably with time and space in dynamic ecosystems and affecting the density estimates of species and length groups. Further, the individuals' reaction patterns towards vessel and sampling equipment may also vary with size and with variable motivation for spawning, feeding et cetera. Therefore, an important question is; can variation in spatial structures and behavior be taken into consideration in the planning of surveys and calculation of fish density and population characteristics?

Common problems for acoustic and trawl surveys

The objectives of measuring the state of the fish stocks are the same in acoustic and bottom-trawl assessment surveys. However, methodological difficulties have been approached differently. A dominating focus in bottom trawl survey has been to keep the survey design and equipment unchanged over time. In contrast, new instrumentations such as scientific echosounders (Andersen 2001), echo-processing software (Wilson 2006; Korneliussen *et al.* 2006) and drop-keels to house the acoustic instrumentation on survey vessels (see e.g. Ona *et al.* 1990) have been implemented in many acoustic surveys. Other important improvements were the introduction of standard-sphere calibration (Foote and Maclennan 1984) and split-beam transducers (e.g. Ehrenberg 1983a,b; Foote *et al.* 1986), which enabled an accurate correction of the echo-signal to normalize the scattering returns from targets of interest (Dragonette *et al.* 1981). In bottom trawl surveys, as an illustration, distortions of the trawl geometry may have a negative impact on the catch rates (Kotwicki *et al.* 2006; Weinberg and Somerton 2006). In spite of this, the measurements of the trawl geometry are ignored in standard biomass estimation.

A catchability factor (q) is often included in swept-area surveys (see Gunderson 1993), which is the most common bottom trawl survey strategy and used in the Namibian hake surveys (Papers IV and VI), and reflects the ratio between measured and true density. The total number of fish (N) is estimated as:

$$N = A \cdot c/a \cdot q, \tag{1}$$

where *a* is the area swept (m^2) , *c* is the number of fish and A is the area surveyed (m^2) (Godø 1994).

^{*} Environment should be understood as the sum of all external factors, both biotic and abiotic or a combination of those, to which an organism is exposed. Biotic factors include the influence of members of the same and other species, and important abiotic factors are light, noise, weather, temperature and dissolved oxygen concentration.

Generally, no catchability factor is included in acoustic surveys as the estimates assumedly represent absolute abundance. In typical acoustic surveys, such as the Norwegian blue whiting and the herring surveys (Papers I and II), the backscattered acoustic energy is scrutinized as averages over 1-5 nautical miles and allocated to species or groups of species based on trawl samples and inspection of the echograms (Aglen 1994). For historical reasons (MacLennan *et al.* 2002), the scientific echosounders often provide data in terms of the nautical area scattering coefficient (the NASC, symbol s_A). This is the integrated echo energy over a defined depth interval and is converted to number of fish with a scaling factor based on the average target strength (*TS*) or the equivalent backscattering cross-section (σ_{bs}). The relationship between these parameters is TS = $10 \log_{10}(\sigma_{bs})$. Thus the number of fish (*N*) in the surveyed area (A, m²) is:

$$N = A \cdot \frac{s_A}{4\pi \cdot 1852^2 \cdot \sigma_{bs}} \qquad , \tag{2}$$

where *NASC* is the mean nautical area scattering coefficient (Maclennan *et al.* 2002). N is sensitive to changes in target strength and acoustic detectability and a correction factor may be added (q[']):

$$N' = N q', \tag{3}$$

where the N' is the bias-adjusted number of fish.

Survey condition, random and systematic errors

Inter-calibration studies with standardised sampling equipment show that catch rates and acoustic densities are fairly precise measures of a fish density at a given site at a given time (Kieser et al. 1987; Strømme and Iilende 2001; Hjellvik et al. 2002b; Ona et al. 2007). In other words, the measurements are relatively constant with stable survey conditions. Still, the sample values may not accurately reflect the density, species or length composition at the sampling location. The biases are caused by several factors (Freon et al. 1993; Aglen 1994; Godø 1994), but a general assumption is that the sum of the biases are constant in time and space (between locations and surveys) (Godø 1994). In reality, variation in the survey conditions can introduce both random and systematic errors, where the precision decreases with increased variations in the survey conditions. In contrast to the random errors which can be evaluated through statistical analysis and are reduced by more samples, the systematic errors result from biases introduced by the sampling methodology (Everitt 1998) and cause systematic over -or underestimation in the measured values (Figure 1). Also the assumption of a constant catchability factor is questionable (Papers I-IV); for instance, the level of escapement of hake under the fishing line varies with level of oxygen (Paper III), which changes considerably between years in Namibian waters (Paper III; Hamukuaya et al. 1998). Similar, the diel bias in the acoustic density of blue whiting is not constant between years (Paper I). Despite such variability, the catchability is wrongly assumed constant between years - but what is the alternative?

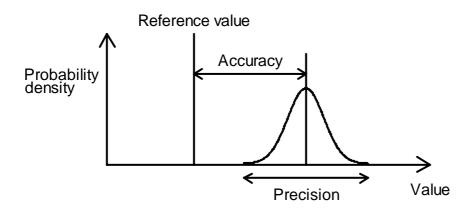


Figure 1. Illustration of systematic (accuracy) and random (precision) errors.

In situ experiments - the traditional approach

Results from *in situ* observations can be used to compensate for bias in the survey estimates. A typical study on diel variation in vertical distribution and acoustic density would investigate a small area in 24-hour periods. By assuming no horizontal migration, trawl samples and echogram registrations can be examined to study the effect of diel bias (see e.g. Engås and Soldal 1992; Fréon et al., 1996; Michalsen et al. 1996; Aglen et al. 1999; Neilson et al. 2003). A serious disadvantage with the design is that the observations may only be valid for the examined location(s), and the results may be seriously biased due to e.g. horizontal migration (Paper I). Still, the high temporal resolution of the recordings may provide important detailed behavioural knowledge. For instance, photos show that hakes swim in front of the trawl and actively avoid the gear (Paper III). These findings, in combination with a study of the herding effect on hakes (unpublished data, Engås et al.), indicate that the hakes are less passive in the catching process than previously believed (Huse et al. 2001). Clearly, when the escapement is size and species dependent (Paper III), any change in the species ratio or length composition could have important consequences for the Namibian hake assessment as neither species nor size dependent catchability are included in the assessment model for Age > 2 (Paper III). It is possible to generalize and estimate corrections factors based on *in situ* observations, and Huse *et al.* (2001) estimated a catchability factor for the Namibian hakes based on an experimental in situ study in 1999. Similarly, Dickson (1993 a,b) established correction models for smaller cod as they were under-represented in the catches. However, in dynamical and complex ecosystems the survey condition varies and the spatial and temporal variability is ignored when using constant multiplication factors.

Aggregated data studies

In contrast to the traditional *in situ* study approach, the effect of variable environmental conditions, temporal and spatial patterns can be statistical modelled and corrected for by using historical standard assessment survey data (Hjellvik *et al.* 2004; Papers I and IV).

Diel variation

The diel variation in fish behaviour is associated with the rhythm of the circadian cycles (Helfman 1993; Neilson et al. 2003). Activities such as feeding, breeding, aggregating and resting are all often closely related to the time of day (Helfman 1993). Changes in the internal individual motivation with time, in combination with diel variable factors such as changes in light intensity influence the availability and catchability of fish during surveys. Diel variation in acoustic backscattering is related to these cyclic changes in fish behaviour (Paper I). Similarly, the variation in bottom trawl catches (Paper IV) is a combined effect of natural diel variation and the reaction of the fish to the stimuli from the moving trawl (Wardle 1993). Diel vertical migration is known to directly affect the availability in both acoustic and bottom trawl surveys, as the proportion of fish that are in the acoustic dead zone, or above the head line of the trawl, will change with time of the day. As for many other pelagic species that form shoals (Freon et al. 1996; Neilson et al. 2003), the blue whiting (Paper I) stayed deeper and more aggregated in the daytime. In general, this type of dynamics will influence the acoustic target strength (TS) of a swimbladdered fish for two main reasons. First, the size of the swimbladder will decrease with depth, causing a reduced TS (e.g. Horne 2003). Secondly, vertical fish movement is often associated with a change in tilt angle and thereby different TS compared to stationary fish (Hazen and Horne 2003). The diel variation in echo abundance of blue whiting followed the expected pattern, as the NASC at day was on average about 20% higher than at night (Paper I). Still, this day-night difference is considerable smaller than that of other pelagic species like herring (Huse and Korneliussen 2000).

Not only abundance, but also estimated population characteristics such as the lengthfrequency distribution are influenced by diel variation (Paper IV). Smaller and younger individuals tend to undertake more extensive diel vertical movements (Korsbrekke and Nakken 1999; Iilende *et al.* 2001), which affect the length distribution in the trawl samples (Korsbrekke and Nakken 1999). Smaller individuals are also more sensitive to changes in light intensity as the scotopic system generally improves with fish size (Fernald 1990; Mas Riera 1991). This could influence the size-dependent diel variation in escapement and herding, and the spatial patterns in the diel variations of the catch rates of Namibian hake are partly an effect of a depthdependent size distribution (Paper IV).

To avoid diel bias the strategy of the South African hake (pers. comm. Tore.Stromme@fao.org) and the International Bottom Trawl Surveys (ICES 1999) is to restrict the sampling to daylight hours. However, time-dependent variation in the catch rates and echo abundances also occur in daylight (Adlerstein and Ehrich 2003) as illustrated by the increase in the CPUE of Namibian hake from dawn to noon and the subsequent decrease until dusk (Figure 2; Paper IV). Further, a survey strategy with both day and night sampling is more cost and time effective. In the Namibian hake surveys the two strategies are combined by assuming that the catch rates in deeper waters (>450 m) are not influenced by diel variation (Paper IV). Therefore, the deep-water areas are covered mostly at night and the shallow waters during daylight, but our results show that the catch rates of hake in deeper waters are not totally independent of time of day (Paper IV).

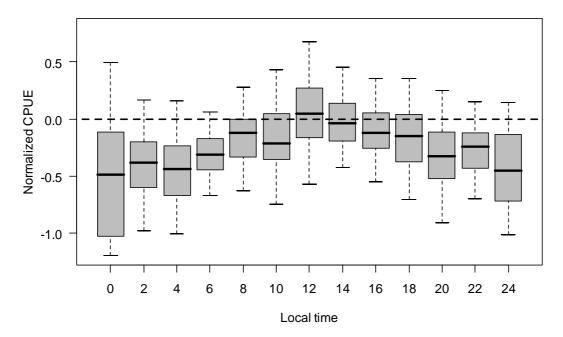


Figure 2. Diel variation in CPUE log(kgh⁻¹) grouped in intervals for the Namibian trawler having the highest number of tows in 1999. Normalized CPUE is estimated as illustrated in Equation 4 of Paper IV. The black line in a boxplot is the median, the grey box indicates the first and third quartiles, and the whiskers show the 1.5*inter-quartile-range.

Depth and time sampling dependencies may also occur in systematic acoustic transect surveys, and may explain some of the annual variability in diel bias in the blue whiting surveys as the diel variation in echo abundance change with bottom depth (Paper I). The depth-dependency in diel variation seems related to a migration of blue whiting along the seabed, up the slope in the evening and down at night (Paper I), and this behaviour should be considered in survey planning to reduce the impact of such spatial and temporal patterns.

Spatial structures

Standard assessment surveys are regarded as a synoptic coverage of the spatial distribution of the stock size and structure, and are repeated at the same time each year. The precision of the survey estimates is influenced by the effort allocation and stratification (Bhattacharyya and Johnson 1977), which is often decided by using information of the spatial distribution from previous surveys (Conan and Wade 1989). However, variation in the spatial distribution of the stock between surveys may suboptimize the effort allocation (Paper VI), and thereby reduce the precision. In contrast to survey data, commercial CPUE data have generally a good seasonal coverage (Papers IV and V), and the geographical distribution of the fishing effort reflects fish density distribution (Gillis *et al.* 1993). Hence, updated satellite tracking data of the fleet can provide information on the geographical fish distribution, as recent collected fishery independent data is seldom available prior to a survey. Paper V shows the large temporal and spatial dynamic in the Namibian hake fisheries, and if the seasonality in the Benguela ecosystem and hake density distribution changes the stratification may become sub-optimal.

Migrating fish stocks such as blue whiting and herring move in more or less repeated geographical migration patterns each year, which is the major argument for maintaining the standard surveys on a fixed calendar schedule. Nevertheless, the migration cycle may change and create a mismatch in area surveyed and the stock distribution overlap. Changes in survey estimates may therefore be a sampling artifact due to variable migration and movement of the fish (Samb and Pauly 2000). Hence, spatial information from the fishing fleet seems under-utilized in much survey planning. The determination of area surveyed and effort allocation can be improved by using updated information on the fleet distribution. Satellite tracking data of the Norwegian Industrial trawlers fleet catching sandeel (Ammodytes marinus) were utilized to map areas with fishing activity. These maps were hence used to allocate the survey effort in the Norwegian 2006 and 2007 sandeel surveys (Figure 3). Many fisheries target the adults in the stock, whereas information on the younger individuals is generally also of major interest in scientific surveys. This difference of interests complicates the usefulness of commercial data for some surveys. Nevertheless, the main objective of for instance the Norwegian blue whiting, the Namibian hake and the Norwegian herring surveys is to monitor the adult and fishable proportion of the stocks.

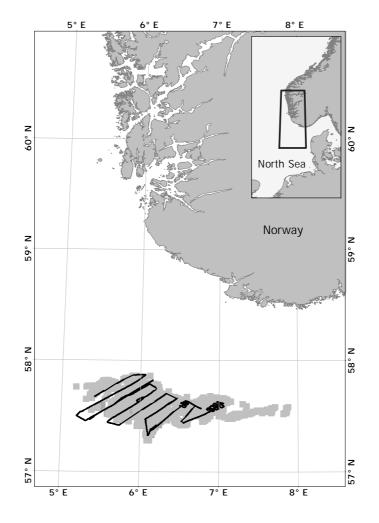


Figure 3. Cruise track (black line) of the Norwegian sandeel survey 2006. The spatial distribution of commercial trawling in 2001-2005 on this specific fishing ground is indicated in grey underneath the cruise line.

Not surprisingly, depth and spatial dependencies in species ratios, density, maturity stage and size in various geographical scales were observed in the studied data (Papers I-VI). It is a well known that fish are distributed according to migration patterns, size, depth preferences, environmental conditions and ecological niches (Pitcher and Hart 1982). As a result, the spatial distributions of fish populations are usually patchy or show gradient structures (Legendre 1993). By including the autocorrelation and geographical structure information of Merluccius capensis, it was found that the abundance estimates of larger individuals are more precise than those of smaller individuals (Paper VI). This is a result of the spatial structure of the population and the Namibian hake survey design. First, like most benthic and demersal fish species, Namibian hakes have a size-dependent depth distribution; the average length of the fish increases with depth (Gordoa and Duarte 1991; Burmeister 2001; Paper VI). In addition, smaller *M. capensis* tend to have a patchier distribution (Gordoa and Duarte 1992; Paper VI), and the number of young individuals may be underestimated because, depending on the environmental conditions, they may aggregate in high densities inshore of the surveyed area (Paper VI). Secondly, the survey has a systematic transect design with trawl stations semi-randomly allocated along the transects, with roughly one station within each 100-meter depth interval (Sætersdal et al. 1999). Hence, the density of stations is not necessarily equal between the various depth strata and fish-length classes. In order to decide on the best survey design the major survey objectives should be clearly defined. As shown above, if the main objective of the Namibian survey is to provide precise information on the youngest individuals, more sampling effort is needed in the shallower waters off Namibia.

On smaller spatial scales, heterogeneous distribution is also common and the individuals within a shoal tend to be segregated according to phenotypical traits like length, body colour, parasite load (Krause et al. 2000; Couzin and Krause 2003) and state of maturity (Paper II). As a result, fish caught together tend to have more similar characteristics than those of the entire population (Pennington et al. 2002; Paper II). Due to this clustering effect the effective sample size is often markedly smaller than the number of fish actually sampled during a survey (Pennington et al. 2002). In Paper II we analyses clustered trawl data, and found a significant relationship between depth distribution and maturity state of herring where the spawners dominated the trawl catches taken close to the sea-bed (Paper II). The depth dependent structure should be considered during sampling and data analysing, as population characteristic estimates can easily become biased if the clustering is ignored (Paper VI). In acoustic surveys, the allocation of backscattering energy to species and length groups is a challenging task, which still largely depends on the trawl samples (Horne 2000). If the trawl samples incorrectly reflect the overall population characteristics, the allocation of the total echo energy between fish-length and species groups is inaccurate. For instance, the acoustic-energy allocation in the winter surveys in the Barents Sea (Jakobsen et al. 1997) depends largely on bottom trawl samples. As the smaller individuals tend to be higher in the water column and unavailable to the bottom trawl the variable fish-size distribution in the water column leads to underestimation of small cod and overestimation of larger cod (Aglen et al. 1999).

Measuring the survey condition - the future survey design?

Diel variation and geostatistical models depend on the correct estimation of several parameters, which negatively affect the precision of the survey estimates (Hjellvik *et al.* 2002a). Another major disadvantage when analysing trends in aggregated data is the lack of detailed behavioural data to explain the proximate causes for the observed patterns. Future survey methods should combine different methodologies to continuously monitor the survey condition and implement these observations in the standard density measures. For instance, the extent of vessel avoidance by fish is likely to vary between years and may have an effect on the biomass estimates of many pelagic species (e.g. Vabø *et al.* 2002; Ona *et al.* 2007). Until now, variable vessel avoidance has been ignored in the standard survey procedures. However, by examining artificial echograms constructed from sonar data, it is possible to quantify the effect of vessel avoidance on abundance estimates (Ona *et al.* 2006) and thereby adjust the survey estimates.

The acoustic dead zone (Ona and Mitson 1996; Lawson and Rose 1999) is a main difficulty for detection of demersal fish in acoustic surveys, similar, the "trawl dead zone" (McQuinn *et al.* 2005; Gauthier and Rose 2005) in bottom trawl surveys is major source of bias if fish are distributed off the bottom. The ratio of fish distributed in the two dead-zones may vary with age-composition, density (Godø and Wespestad 1993), and with time and space (Lawson and Rose 1999; Iilende *et al.* 2001; McQuinn *et al.* 2005). In addition to variability, it seems extremely difficult to combine acoustic and trawl samples into one reliable abundance estimate due to the unknown vertical and horizontal swimming behaviour of the fish (Handegard 2004). Still, by equipping the bottom trawl with an upward-looking transducer, it may be feasible to quantify the vertical distribution and movement of fish (Michalsen *et al.* 1999; Handegard 2004).

Concluding remarks and perspectives

Results from fishery independent surveys are important components in modern assessment of fisheries resources and have in many cases replaced unreliable commercial CPUE time series (Gunderson 1993). Standardization of the sampling equipment and survey design is considered crucial for reliable estimates from stockassessment surveys (Gunderson 1993). Nevertheless, large spatial, seasonal and diel variations in commercial CPUE and survey data are common (Paper I, IV-VI). Such patterns are mainly a result of variable environmental (Paper III) and internal physiological (Paper II) factors which affect the behaviour of individual fish. As shown in these works, statistical modelling may correct for the identified systematic diel patterns in echo abundance and catch rates. However, every modelled correction factor or adjusted function is constrained with an uncertainty, which is added to the initial estimate error. Therefore, retrospective analyses may not substantially improve the original estimates of stock size and structures. On the other hand, the knowledge gained on the effect of fish behaviour on survey estimates through statistical modelling and in situ studies may enable more suitable survey designs and more efficient survey effort allocation. Still, new knowledge and improved methodologies, especially for swept-area surveys, are rarely incorporated in the standard survey procedures, which for many time series have continued remarkably unchanged. A major argument for this conservatism is the perceived need to keep the surveys standardized and therefore unchanged over time. The challenge is hence complicated,

as there are strong and compelling arguments to keep the present surveys unchanged, which is in conflict with the need to reduce the impact of systematic errors. However, including information from the distribution of the fishing fleet or initiate other types of adaptive survey design (see e.g. Ona and Vølstad 1991; McQuinn *et al.* 2005) can make the allocation of effort more appropriate and thereby increase the precision of the survey estimates without invalidate the time series. Similar, spatial autocorrelation and distribution of cluster should be considered to optimize data sampling and avoid biased estimates of population structure and size.

In traditional single-stock assessment and management, where the use of commercial data is fundamental, the long-term trends in the survey estimates are usually used to tune the assessment models. Time seems due to install acoustics in trawl systems to monitor the vertical distribution of target species. Obviously, this is a tremendous scientific challenge, however, the effect of variable survey conditions are not possible to measure without combined sampling tools and we will forever have estimates that may be seriously affected by for instance dial bias. We are also on the door step to a more complex ecosystem management approach which demands scientific surveillance of several species and trophic levels (Hall and Mainprize 2004). This simultaneous monitoring of inter-specific interaction requires advanced survey strategies where many sources of data collected with trawls, CTD probes, echosounders, transducers and sonars are integrated and together form the basis for the concurrent measurement of the environment and fish densities.

References

- Adlerstein, S., and Ehrich, S. 2003. Patterns in diel variation of cod catches in North Sea bottom trawl surveys. Fisheries Research **63**: 169-178.
- Aglen, A. 1994. Sources of error in acoustic estimation of fish abundance. *In* Marine fish behaviour in capture and abundance estimation. *Edited by* A. Fernö and S. Olsen. Fishing News Books, Oxford pp. 107-133.
- Aglen, A., Engås, A., Huse, I., Michalsen, K., and Stensholt, B.K. 1999. How Vertical Fish Distribution May Affect Survey Results. ICES Journal of Marine Science 56: 345-360.
- Andersen, L.N. 2001. The new Simrad EK60 scientific echosounder system. Journal of the Acoustical Society of America **109**: 2336.
- Benoit, H.P., and Swain, D.P. 2003. Accounting for length- and depth-dependent diel variation in catchability of fish and invertebrates in an annual bottom-trawl survey. ICES Journal of Marine Science **60**: 1298-1317.
- Bhattacharyya, G.K., and Johnson, R.A. 1977. Statistical concepts and methods. Wiley, New York, 639 pp.
- Bowman, R.E. and Bowman, E.W. 1980. Diurnal-variation in the feeding intensity and catchability of Silver Hake (*Merluccius bilinearis*). Canadian Journal of Fisheries and Aquatic Sciences **37:** 1565-1572.
- Burmeister, L.M. 2001. Depth-stratified density estimates and distribution of the Cape hake *Merluccius Capensis* and *M. paradoxus* off Namibia deduced from survey

data, 1990-1999. *In* A decade of Namibian fisheries science. *Edited by* A.I.L. Payne, S.C. Pillar and R.J.M. Crawford. South African Journal of Marine Science **23**: 347-356.

- Butterworth, D. S., and Geromont, H. F., 2001. Evaluation of a class of possible simple interim management procedures for the Namibian hake fishery. *In A* decade of Namibian fisheries science. *Edited by* A.I.L. Payne, S.C. Pillar and R.J.M. Crawford. South African Journal of Marine Science 23: 357-374.
- Casey, J.M., and Myers, R.A. 1998. Diel variation in trawl catchability: is it as clear as day and night? Canadian Journal of Fisheries and Aquatic Sciences **55**: 2329-2340.
- Conan, G.Y., and E. Wade. 1989. Geostatistical mapping and global estimation of harvestable resources in a fishery of northern shrimp (*Pandalus borealis*). ICES C.M. 1989/D:1.
- Couzin, I.D., and Krause, J. 2003. Self-organization and collective behavior in vertebrates. Advances in the Study of Behavior **32**: 1-75.
- Dickson, W. 1993a. Estimation of the capture efficiency of trawl gear .I. Development of a theoretical-model. Fisheries Research **16**: 239-253.
- Dickson, W. 1993b. Estimation of the capture efficiency of trawl gear .II. Testing a theoretical-model. Fisheries Research **16**: 255-272.
- Dragonette, L.R., Numrich, S.K., and Frank, L.J. 1981. Calibration technique for acoustic scattering measurements. Journal of the Acoustical Society of America **69:** 1186-1189.
- Ehrenberg, J.E. 1983a. A review of in situ target strength estimation techniques. Contribution no. 104, Symposium on Fisheries Acoustics, Bergen, Norway, June 12-24, 1982, pp. 85-90.
- Ehrenberg, J.E. 1983b. New methods for indirectly measuring the mean acoustic backscattering cross section of fish. Contribution no. 105, Symposium on Fisheries Acoustics, Bergen, Norway, June 12-24, 1982, pp. 91-98.
- Engås, A., and Soldal, A.V. 1992. Diurnal-variations in bottom trawl catch rates of cod and haddock and their influence on abundance indexes. ICES Journal of Marine Science **49:** 89-95.
- Everitt, B.S. 1998. The Cambridge dictionary of statistics. Cambridge University Press, Cambridge, 360 pp.
- Fernald, R.D., 1990. The optical system of fish. *In* The visual system of fish. *Edited by* R.H. Douglas and M.B. Djamgoz. Croon Helm Ltd. pp. 45-62.
- Foote, K.G., and Maclennan, D.N. 1984. Comparison of copper and tungsten carbide calibration spheres. Journal of the Acoustical Society of America **75**: 612-616.
- Foote, K.G., Aglen, A., and Nakken, O. 1986. Measurement of fish target strength with a split-beam echo sounder. Journal of the Acoustical Society of America **80**: 612-621.
- Fréon P., Soria M., Mullon C., and Gerlotto F. 1993. Diurnal variation in fish-density estimate during acoustic surveys in relation to spatial distribution and avoidance reaction. Aquatic Living Resources **6:** 221–234.

- Fréon, P., Gerlotto, F., and Soria, M. 1996. Diel variability of school structure with special reference to transition periods. ICES Journal of Marine Science **53**: 459-464.
- Gauthier, S., and Rose, G.A. 2005. Diel vertical migration and shoaling heterogeneity in Atlantic redfish: effects on acoustic and bottom-trawl surveys. ICES Journal of Marine Science **62:** 75-85.
- Gillis, D.M., Peterman, R.M., and Tyler, A.V. 1993. Movement dynamics in a fishery - application of the ideal free distribution to spatial allocation of effort. Canadian Journal of Fisheries and Aquatic Sciences **50**: 323-333.
- Godø, O.R., 1994. Factors affecting the reliability of groundfish abundance estimates from bottom trawl surveys. *In* Marine fish behaviour in capture and abundance estimation. *Edited by* A. Fernö and S. Olsen. Fishing News Books, Oxford pp. 166-199.
- Godø, O.R. and Wespestad, V.G. 1993. Monitoring changes in abundance of gadoids with varying availability to trawl and acoustic surveys. ICES Journal of Marine Science **50**: 39-51.
- Gordoa, A. and Duarte, C.M. 1991. Size-dependent spatial-distribution of hake (*Merluccius capensis* and *Merluccius paradoxus*) in Namibian waters. Canadian Journal of Fisheries and Aquatic Sciences **48**: 2095-2099.
- Gordoa, A. and Duarte, C.M. 1992. Size-dependent density of the demersal fish off Namibia patterns within and among species. Canadian Journal of Fisheries and Aquatic Sciences **49:** 1990-1993.
- Gunderson, D.R. Surveys of fisheries resources. 1993. JOHN WILEY & SONS. New York. 248 pp.
- Hall, S.J., and Mainprize, B. 2004. Towards ecosystem-based fisheries management. Fish and Fisheries **5:** 1–20.
- Hamukuaya, H., O'Toole, M.J., and Woodhead, P.M.J. 1998. Observations of severe hypoxia and offshore displacements of Cape Hake over the Namibian shelf in 1994. South African Journal of Marine Science **19:** 57-59.
- Handegard, N.O. 2004. Cod reaction to an approaching bottom trawling vessel investigated using acoustic split-beam tracking. Department of Mathematics, University of Bergen, Norway.
- Hazen, E.L. and Horne, J.K. 2003. A method for evaluating the effects of biological factors on fish target strength. ICES Journal of Marine Science **60**: 555-562.
- Helfman, G.S. 1993. Fish behaviour by day, night and twilight. *In* Behaviour of Teleost Fishes, pp. 479-512. *Edited by* T. J. Pitcher. Chapman and Hall, London.
- Helser, T.E., and Hayes, D.B. 1995. Providing quantitative management advice from stock abundance indexes based on research surveys. Fishery Bulletin **93**: 290-298.
- Hjellvik, V., Godø, O.R., and Tjøstheim, D. 2002a. Diurnal variation in bottom trawl survey catches: does it pay to adjust? Canadian Journal of Fisheries and Aquatic Sciences **59:** 33-48.
- Hjellvik, V., Godø, O.R., and Tjøstheim, D. 2002b. The measurement error in marine survey catches: the bottom trawl case. Fishery Bulletin **100**: 720-726.

- Hjellvik, V., Godø, O.R., and Tjøstheim, D. 2004. Decomposing and explaining the variability of bottom trawl survey data from the Barents Sea. Sarsia **89:** 196-210.
- Horne, J.K. 2000. Acoustic Approaches to Remote Species Identification: a Review. Fisheries Oceanography **9**: 356-371.
- Horne, J.K. 2003. The influence of ontogeny, physiology, and behaviour on the target strength of walleye pollock (*Theragra Chalcogramma*). ICES Journal of Marine Science **60**: 1063-1074.
- Huse, I. and Korneliussen, R. 2000. Diel variation in acoustic density measurements of overwintering herring (*Clupea harengus L.*). ICES Journal of Marine Science **57:** 903-910.
- Huse, I., Iilende, T., and Strømme, T. 2001. Towards a catchability constant for trawl surveys of Namibian hake. *In* A decade of Namibian fisheries science. *Edited by* A.I.L. Payne, S.C. Pillar and R.J.M. Crawford. South African Journal of Marine 23: 375-383.
- ICES, 1999. Manual of the International bottom trawl survey. Revision VI ICES C.M. 1999/D:2
- Iilende, T., Strømme, T., and Johnsen, E. 2001. Dynamics of the pelagic component of Namibian hake stocks. *In* A decade of Namibian fisheries science. *Edited by* A.I.L. Payne, S.C. Pillar and R.J.M. Crawford. South African Journal of Marine South African Journal of Marine Science 23: 337-346.
- Jakobsen, T., Korsbrekke, K., Mehl, S., and Nakken, O. 1997. Norwegian combined acoustic and bottom trawl surveys for demersal fish in the Barents Sea during winter. ICES CM 1997/Y:17
- Kieser, R., Mulligan, T.J., Williamson, N.J., and Nelson, M.O. 1987. Intercalibration of 2 echo integration systems based on acoustic backscattering measurements. Canadian Journal of Fisheries and Aquatic Sciences **44**: 562-572.
- Korneliussen, R.J., Ona, E., Eliassen, I.K., Heggelund, Y., Patel, R., Godø, O.R., Giertsen, C., Patel, D., Nornes, E.H., Bekkvik, T, Knudsen, H.P., and Lien, G. 2006. The Large Scale Survey System – LSSS, a new post-processing system for multi-frequency echo sounder data. Report of the working group on fisheries acoustics science and technology (WGFAST), 27-30 March 2006, Tasmania. ICES CM 2006/FTC:01, 50 pp.
- Korsbrekke, K., and Nakken, O. 1999. Length and species-dependent diurnal variation of catch rates in the Norwegian Barents Sea bottom-trawl surveys. ICES Journal of Marine Science **56**: 284-291.
- Kotwicki, S., Weinberg, K.L., and Somerton, D.A. 2006. The effect of autotrawl systems on the performance of a survey trawl. Fishery Bulletin **104:** 35-45.
- Krause, J., Butlin, R.K., Peuhkuri, N., and Pritchard, V.L. 2000. The social organization of fish shoals: a test of the predictive power of laboratory experiments for the field. Biological Reviews **75**: 477-501.
- Lawson, G.L., and Rose, G.A. 1999. The Importance of Detectability to Acoustic Surveys of Semi-Demersal Fish. ICES Journal of Marine Science **56**: 370-380.
- Legendre, P. 1993. Spatial autocorrelation trouble or new paradigm. Ecology **74**: 1659-1673.

- Michalsen, K., Godø, O.R., and Fernö, A. 1996. Diel variation the catchability of gadoids and its influence on the reliability of abundance indices. ICES Journal of Marine Science **53**: 389–395.
- Michalsen, K., Somerton, D., Aglen, A. and Øvredal, J.T. 1999. Quantifying the amount of fish unavailable to bottom trawl by use of an upward looking transducer. ICES CM 1999/J.
- Maclennan, D.N., Fernandes, P.G., and Dalen, J. 2002. A consistent approach to definitions and symbols in fisheries acoustics. ICES Journal of Marine Science **59**: 365-369.
- Mas Riera, J. 1991. Changes during growth in the retinal structure of 3 hake species, *Merluccius spp* (Teleostei, Gadiformes), in relation to their depth distribution and feeding. Journal of Experimental Marine Biology and Ecology **152**: 91-104.
- McQuinn, I.H., Simard, Y., Stroud, T.W.F., Beaulieu, J.L., and Walsh, S.J. 2005. An adaptive, integrated "acoustic-trawl" survey design for Atlantic cod (Gadus morhua) with estimation of the acoustic and trawl dead zones. ICES Journal of Marine Science **62**: 93-106
- Neilson, J.D., Clark, D., Melvin, G.D., Perley, P., and Stevens, C. 2003. The diel vertical distribution and characteristics of pre-spawning aggregations of pollock (*Pollachius virens*) as inferred from hydroacoustic observations: the implications for survey design. ICES Journal of Marine Science 60: 860-871.
- Ona, E., and Traynor, J. 1990. Hull mounted, protruding transducer for improving echo integration in bad weather. ICES CM 1990/B:31.
- Ona, E., Pennington, M., and Vølstad, J.H. 1991. Using acoustic surveys to improve the precision of bottom trawl indices of abundance. ICES CM 1991/D:13, 1-10.
- Ona, E., and Mitson, R.B. 1996. Acoustics sampling and signal processing near the seabed: the dead zone revisited, ICES Journal of Marine Science **53**: 677–690.
- Ona, E., Dalen, J., Knudsen, H.P., Patel, R., Andersen, L.N., and Berg, S. 2006. First data from sea trials with the new MS70 multibeam sonar. Journal of the Acoustical Society of America **120** (5), pt. 2, 3017 pp.
- Ona, E., Godø, O.R., Handegard, N.O., Hjellvik, V., Patel, R., and Pedersen, G. 2007. Silent research vessels are not quiet. The Journal of the Acoustical Society of America, **121**: 145–150
- Pennington, M. and Strømme, T. 1998. Surveys as a research tool for managing dynamic stocks. Fisheries Research **37**: 97-106.
- Pennington, M., Burmeister, L.M., and Hjellvik, V. 2002. Assessing the precision of frequency distributions estimated from trawl-survey samples. Fishery Bulletin 100: 74-80.
- Pitcher, T.J. and Hart, P.J.B. 1982. Fisheries ecology. Croom Helm Ltd, London, 414 pp.
- Salthaug, A., and Aanes, S. 2003. Catchability and the spatial distribution of fishing vessels. Canadian Journal of Fisheries and Aquatic Sciences **60**: 259-268.
- Samb, B., and Pauly, D. 2000. On `variability' as a sampling artefact: the case of Sardinella in north-western Africa. Fish and Fisheries 1: 206-210.

- Shepherd, J.G. 1988. Fish stock assessments and their data requirements. *In* Fish Population Dynamics. *Edited by* J.A. Gulland, Wiley, New York pp. 35–62.
- Simmonds, E.J., and MacLennan, D. 2005. Fisheries Acoustics. Theory and Practice, 2nd edn. Blackwell Science, Oxford, 437 pp.
- Strømme, T., and Iilende, T. 2001. Precision in systematic trawl surveys as assessed from replicate sampling by parallel trawling off Namibia. South African Journal of Marine Science **23**: 385-396.
- Sætersdal, G., Bianchi, G., Strømme, T., and Venema, S.C. 1999. The Dr. Fridtjof Nansen Programme 1975–1993. Investigations of fishery resources in developing regions. History of the programme and review of results. FAO Fish. Technol. Pap. 391. 452 pp.
- Ulltang, Ø. 1980. Factors affecting the reaction of pelagic fish stocks to exploitation and requiring a new approach to assessment and management. Rapports et Procés-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, **177**: 489-504.
- Vabø, R., Olsen, K., and Huse, I. 2002. The effect of vessel avoidance of wintering Norwegian spring spawning herring. Fisheries Research **58**: 59-77.
- Wardle, C.S. 1993. Fish behaviour and fishing gear. *In* behaviour of teleost fish. *Edited by* T.J. Pitcher. Chapman and Hall, London, pp 609-643.
- Weinberg, K.L., and Somerton, D.A. 2006. Variation in trawl geometry due to unequal warp length. Fishery Bulletin **104:** 21-34.
- Wilson, M. 2006. Recent developments and future plans for automated acoustic data processing in SonarData Echoview. Report of the working group on fisheries acoustics science and technology (WGFAST), 27-30 March 2006, Tasmania. ICES CM 2006/FTC:01, 50 pp.
- Xiao, Y.S. 2000. A general theory of fish stock assessment models. Ecological Modelling **128:** 165-180.