

The effects of behaviour on the acoustic target strength
of capelin (*Mallotus villosus*) and implications for
acoustic abundance estimation

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Preface

This thesis is a part of the project “Improved accuracy of acoustic abundance estimates of the capelin stock”, a joint project between the Norwegian College of Fishery Science (NCFS) and the Institute of Marine Research (IMR). These two institutions and the Research Council of Norway funded the project (grant no. 133736/120). The work was carried out partly at the Tromsø Aquaculture Research Station and on cruises with the research vessels “Johan Hjort” (IMR), “Johan Ruud” (NCFS), and “Michael Sars” (IMR). I thank the crew and scientific personnel who took part in the surveys and made this thesis possible.

I wish to express my sincere thanks to my supervisor, Professor Kjell Kr. Olsen at NCFS, for all his help throughout my studies. His enthusiasm for new ideas and his interest for fisheries management have inspired me, and his help has been invaluable. During three surveys of the Barents Sea capelin, I came to know Harald Gjøsæter (IMR) as a skilful scientist, a caring and responsible cruise leader, and a good co-author. Egil Ona and Ingvald Svellingen at the IMR in Bergen provided software and valuable technical know-how as well as valuable comments to manuscripts. I am also very thankful for the kind and helpful co-operation of my co-authors, Nils Olav Handegard and Aril Slotte (IMR). Further, I extend my gratitude to Leif Peder Jørgensen and his staff at the fish farming plant at Tromsø Aquaculture Research Station for all their assistance. Special thanks are due the crew of RV Johan Ruud and local fisherman Hugo Frydenlund (Balsfjord) for catching the capelin necessary for my experiments, and to Jørgen S. Christiansen, Kim Præbel and Bjørn S. Sæther (NCFS) for keeping them in tanks and providing me with live material and X-ray pictures.

Several anonymous reviewers have provided valuable comments scientifically to the first three articles in this thesis. Hugh M. Allen and Linda S. Bennett are thanked for proofreading of manuscripts.

Elvar Hallfredsson and Bernt J. Bertelsen had to deal with me as a roommate, always making me feel welcome, and supporting my huge consumption of instant coffee.

Finally, I wish to thank my girlfriend Linda for her patience and support during these years, and my daughters Malin and Julie.

Tromsø, June 30th 2004

Roar Jørgensen

**To my mother and father, who urged me to study marine biology,
and to Linda, who always stood by me.**

Summary

The general objective of this thesis was to collect improved knowledge about the target strength (TS) of capelin (*Mallotus villosus*) through experimental studies, as well as to undertake adequate observations of behaviour of capelin during surveying situations, including the effect of different depth distributions and of vessel avoidance.

Pre- and post-spawning capelin from the Balsfjord and the Barents Sea stock were observed in a net pen and in a submersible rig with a calibrated 38-kHz scientific split-beam echo sounder. The net pen experiment showed that the acoustic TS of capelin depended on swimbladder length. In females, TS tended to be negatively influenced by condition. The experiments in the submersible rig demonstrated that the TS of capelin depends on the tilt-angle distribution and ambient pressure.

The avoidance reactions of Barents Sea capelin to Norwegian research vessels were studied by means of the Bergen Acoustic Buoy (BAB), which was equipped with a 38 kHz echo sounder. BAB experiments were carried out in the capelin's feeding area in the Barents Sea in the autumn, and on its spawning grounds in Varangerfjord in North Norway in early spring. There was no significant influence of the avoidance reactions of capelin to survey vessels on the volume scattering coefficient, either in the feeding area or on the spawning grounds. However, there were indications of changes in the centre of depth distribution (diving) before the pass, especially in dense concentrations on the spawning grounds.

The findings of this thesis indicate that differences in vertical distribution of capelin in different areas and seasons, or between years with differences in oceanographic conditions or predation, may bias absolute estimates of stock abundance of capelin if the depth distribution of the fish is not taken into consideration. It is therefore recommended that the effects of ambient pressure are included in the TS equation used in surveys in order to make the acoustic stock size estimate of capelin in the Barents Sea a better absolute estimate of the stock abundance.

List of papers

- I. Jørgensen, R., and K.K. Olsen. 2002. Acoustic target strength of capelin measured by single-target tracking in a controlled cage experiment. ICES Journal of Marine Science, 59: 1081-1085.
- II. Jørgensen, R. 2003. The effects of swimbladder size, condition and gonads on the acoustic target strength of mature capelin. ICES Journal of Marine Science, 60: 1056-1062.
- III. Jørgensen, R., N.O. Handegard, H. Gjøsæter, and A. Slotte (manuscript). Possible vessel avoidance behaviour of capelin in a feeding area and on a spawning ground. Accepted in Fisheries Research. 32 pp.
- IV. Jørgensen, R., and K.K. Olsen (manuscript). Effects of different tilt angle distributions and ambient pressures on the acoustic target strength of capelin (*Mallotus villosus*). 36 pp.

1. Introduction

The capelin (*Mallotus villosus*, Müller) is a small, silvery, pelagic schooling species and a member of the family Osmeridae. It is considered a cold-water species that occurs throughout the Northern Hemisphere (Carscadden and Vilhjálmsón, 2002). Capelin are in the lower range of the marine food web and are generally preyed upon by larger fish, marine mammals and seabirds (Gjøsæter, 1998; Vilhjálmsón, 2002). The capelin has a physostomous gas bladder that opens into the oesophagus. The capelin's swimbladder has limited or no ability for gas secretion (Fahlén, 1968). It can therefore traverse depths rapidly at the expense of being negatively buoyant at greater depths. It is likely that the depth at which they are found is one that represents, for that given point in time and space, the most advantageous combination of temperature, food supply, competition and predation risk (Mowbray, 2002; Stensholt *et al.*, 2002) or mating opportunity (Sars, 1879; Sætre and Gjøsæter, 1975). An example of diurnal vertical migration of capelin is shown in Figure 1.

The Barents Sea capelin stock is potentially the largest capelin stock in the world, its biomass in some years reaching 6-8 million tonnes (Gjøsæter, 1998). It is the largest stock of pelagic fish in the Barents Sea and has been exploited since the 1950s (Olsen, 1968). Since the acoustic surveys started on a regular basis in 1973, the stock has undergone large fluctuations in abundance with major collapses in stock size in 1985-1989, 1993-1997 and in 2003 (Gjøsæter, 1998; Anon, 2003). So far, acoustic surveys and information from catch statistics have provided the only information available on stock status (Toreisen *et al.*, 1998). According to Ushakov and Prozorkevich (2002), exploitation of the capelin stock should be effected with an expectation of keeping the spawning stock biomass sufficiently large as well as maintaining an adequate food supply for other species.

The method of fish stock abundance estimation from acoustic data combined with biological samples of size distribution (Gjøsæter, 1999) inherently contains a series of assumptions. The reliabilities of acoustic abundance estimates depend on proper survey designs and statistics for estimating fish abundance (Aglen, 1989; Gundersson, 1993; Rivoirard *et al.*, 2000). The measurement platform, usually a survey vessel, should not affect the object to be measured (Gundersson, 1993), assuming no vessel avoidance reactions. The interpretation of the acoustic measurements and species identification may

be affected by avoidance and trawl selection (Larsen, 1985; Godø, 1998), but can be improved by acoustic methods using multiple frequencies (Korneliussen, 2002).

In the method of fish abundance estimation by echo integration, the mean acoustic target strength (TS) in decibels is related to the average fish density (ρ_a) and the nautical area scattering coefficient (s_A) as:

$$s_A = \rho_a \times 4\pi 10^{0.1 \text{ TS}} \quad (\text{MacLennan } et al., 2002) \quad (1)$$

where the relationships between fish length and mean TS are usually species specific. The relation of TS to fish length at 38 kHz currently applied in the assessment of the Barents Sea capelin is the one recommended by Dommasnes and Røttingen (1984):

$$\text{TS}_{\text{survey}} = 19.1 \log_{10}(\text{length, cm}) - 74 \quad (2)$$

which was derived from measurements of maximum TS (Dalen *et al.*, 1976) and mean TS estimated by echo trace counting and echo integration (Midttun and Nakken, 1971, 1977; Dalen and Nakken, 1983). Several authors have acknowledged the importance of TS in relating echo integrator signal intensity to fish density (Dalen and Nakken, 1983; Dommasnes and Røttingen, 1984; Rose, 1998; O'Driscoll and Rose, 2001), and the assumed impact of behaviour on TS (Foote, 1980c; Olsen, 1990). In spite of this, relatively few experiments (Olsen and Angell, 1983; Olsen *et al.*, 1983a; Olsen and Ahquist, 1989) have dealt with the effects of fish behaviour on capelin TS.

It may thus be expected that variability in echo intensities from fish is caused by physical factors associated with the transmission of sound through water and through the fish targets, and by biological factors associated with the ontogeny, physiology and behaviour of the fish (Horne, 2003; Horne and Clay, 1998).

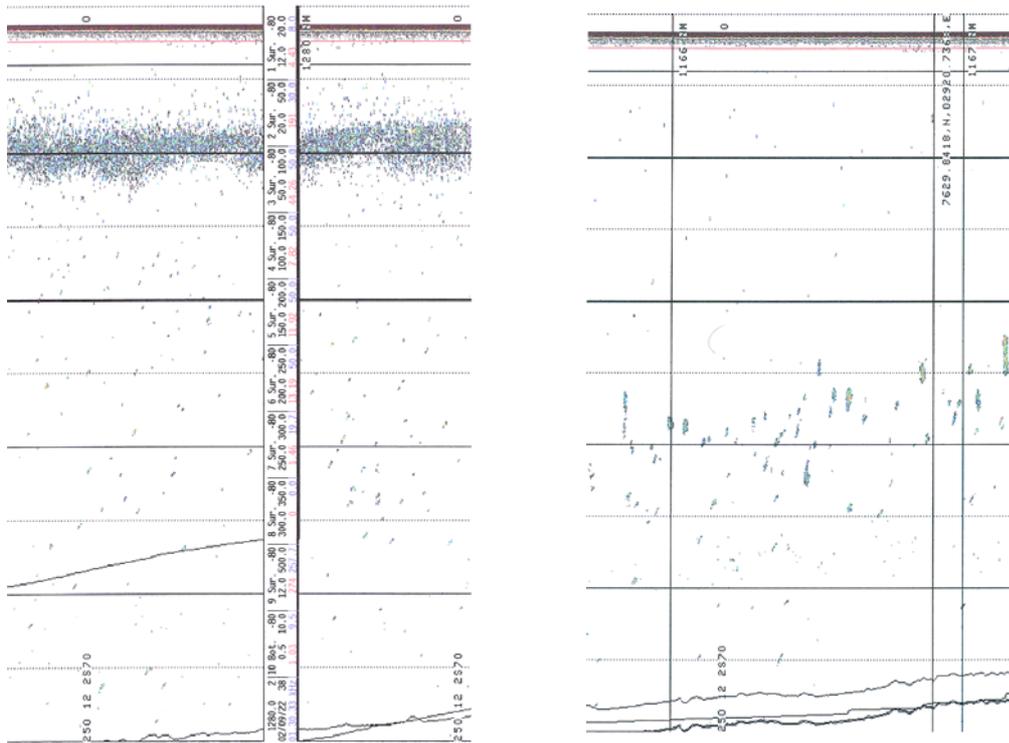


Figure 1: Vertical migration of capelin recorded on board RV “Johan Hjort” during an acoustic survey in the Barents Sea, 20-21 September 2002 in an area at about 76°30’N and 29°20’E. The left panel shows capelin at 30-60 m depths during nighttime, and the right panel shows capelin at 125-175-m depths during daytime. The bottom depth is 240-255 m.

Experiments at acoustic frequencies spanning from 25 to 200 kHz show that the TS of tethered fish changes with aspect angle (Midttun and Hoff, 1962; Nakken and Olsen, 1977; Foote and Ona, 1985; Miyanohana *et al.*, 1990). The consequence of the observed directivity in the reflection of fish is that the TS of wild fish will vary with fish behaviour, i.e., with aspect angle distribution (Olsen, 1979; Foote, 1980b, 1980c).

Fish behaviour is known to change both seasonally and diurnally (Huse and Ona, 1996; Fréon and Misund, 1999), and to be affected by noise from the vessel (Olsen, 1969, 1971a, 1976, 1981, 1990) or by additional noise from fishing gear (Engås *et al.*, 1995; Handegard *et al.*, 2003). Vessel avoidance has been observed to affect acoustic abundance estimates among various species, especially at rather shallow depths at night (Olsen *et al.*, 1983a; Fréon and Misund, 1999; Vabø, 1999; Vabø *et al.*, 2002). On the basis of sonar observations, it has been the general opinion that capelin do not avoid research vessels (Misund *et al.*, 1993). A lack of avoidance during pelagic trawling (Gjøsæter pers. com.) and purse seine operations (skipper Gunnvald Wagelid, pers. com.), and other essentially

anecdotal observations of the behaviour of capelin in the presence of ships (Sars, 1879), support the view of capelin as a fish that apparently takes little notice of vessels and fishing gear.

Earlier direct experiments on capelin, however, have given indications of diving behaviour of capelin in the presence of a survey vessel, and possible implications for acoustic abundance estimates have been discussed in the 1980s (Olsen and Angell, 1983; Olsen *et al.*, 1983a, 1983b).

At echo sounder frequencies, the swimbladder is the major cause of scattering from fishes with a gas bladder (Haslett, 1962; Foote, 1980a). Empirical studies show that ambient pressures, variations in fat content and gonad development may influence the swimbladder dimensions (Ona, 1990; Machias and Tsimenides, 1995) and also the echo returned from fish (Olsen and Ahlquist, 1996; Ona *et al.*, 2001; Ona, 2003). In the past, it has been discussed whether the main role of the swimbladder of physostomous fish is to confer neutral buoyancy to the fish by maintaining its volume at some optimum value (Alexander, 1966; Sundnes and Bratland, 1972; Knudsen and Gjelland, 2003), or whether the swimbladder is required to be gas filled because it plays important roles in hearing and sound production (Blaxter and Batty, 1990; Wahlberg and Westerberg, 2003). To obtain a deeper understanding of the nature of the acoustic scattering process from fish, Midttun (1984) suggested that attention should be called to studies on the bladder itself, its form and deformations by varying pressure changes, and to comparisons of the acoustic wavelength with dimensions of the swimbladder. Changes in mean TS with increasing depth cannot only be attributed directly to a change in swimbladder volume (Ona, 1990; Mukai and Iida, 1996; Gorska and Ona, 2003a), but also to the possible change in the tilt-angle distribution due to under-buoyant “head up” swimming behaviour (Olsen and Ahlquist, 1996).

This thesis focuses on the effects of behaviour on the TS of capelin. The initial general objective was to collect improved knowledge about the TS of capelin through experimental studies, as well as to undertake adequate observations of behaviour of capelin during surveying situations, including the effect of different depth distributions and of vessel avoidance. The final objective was to develop improved parameters to algorithms applied in data processing routines, in order to improve the precision in stock abundance estimates obtained by echo integration.

2. Methodological aspects

The effects of different depths (5 to 50 m) on the TS of capelin were investigated *ex situ* in cage experiments by Olsen and Ahlquist (1989), but their study did not include detailed knowledge of the effects of different tilt-angle distributions on TS. Investigations performed to determine the effects of tilt angle on the TS of capelin have been performed by *ex situ* measurements (Dalen *et al.* 1976, Olsen and Angell, 1983) and by modelling backscattering from swimbladder models (Gauthier and Horne, 2002). The above-mentioned TS – tilt-angle approaches have, however, been limited to pressures close the surface (0 to 5 m depth). The experiments in this thesis were designed to focus on the combined effects of different ambient pressures and tilt-angle distributions on capelin TS, as well as the possible effects of differences in the physiological condition on the TS.

Experimental measurements of the TS of individual capelin were carried out with a 38-kHz split-beam echo sounder system on free-swimming fish kept in an enclosure (Papers I and II) and in a submersible measuring rig (Paper IV). Studies were undertaken for somewhat small mature capelin from the local Balsfjord stock (Paper I) and larger mature capelin from the Barents Sea stock (Paper II and IV). The relation between TS and tilt angle was studied in a specially designed submersible rig (Paper IV) or by relating the TS of free-swimming fish and tracking its echo trace (Papers I and II). In addition to measurements of depth, length, weight and gonad weight (Papers I, II and IV), swimbladder lengths (Papers II and IV) were also recorded.

Each rig experiment was of rather short duration (35 to 75 minutes) compared to the net pen experiment (4 to 30 hours), and in the rig the fish was continuously observed at close range by underwater television.

The TS of dispersed capelin have been assessed from echo integration combined with echo trace counting (Midttun and Nakken, 1977; Dommasnes and Røttingen, 1984) and from direct *in situ* TS measurements (Rose, 1998; O’Driscoll and Rose, 2001). The possible effects of ambient pressures have, however, not been properly addressed yet, even though Olsen and Angell (1983) did an experiment with echo integration combined with echo trace counting in different depth channels.

New field experiments involving possible vessel avoidance and *in situ* TS were planned and performed in the Barents Sea as a part of this thesis. The field experiments were carried out under true echo surveying conditions by studying backscattering characteristics of capelin and its behaviour. Vessel avoidance was studied in the feeding area during the autumn of 2001 and on the spawning grounds during the spring of 2002 by a stationary echo sounder platform, observing possible avoidance reactions (Paper III). TS observations and fish behaviour were attempted obtained by use of the hull-mounted transducer during the acoustic surveys for capelin in the Barents Sea in 2000, 2001 and 2002. However, the *in situ* TS measurements were difficult to interpret due to too high fish densities or inclusion of different species of 0-group fish at shallow depths and are not treated in detail in this thesis. Some measurements done with a submersible transducer in 2001 are described in Jørgensen *et al.* (2002), but a more intensive experimental approach for measuring *in situ* TS during the autumn 2002 were disrupted by a technical malfunction in the submersible transducer.

3. Results and discussions

3.1 Target strength

3.1.1 Tilt-angle dependence

The results from the net pen (Papers I and II) and rig experiments (Paper IV) show that the TS of capelin changes significantly with tilt angle. At about 5-m depth, the TS showed greatest variation with respect to tilt angle among large capelin (Paper II and IV). In small capelin (Paper I), the TS tended to change only slightly (<5 dB) with tilt angle. Compared with saithe *Pollachius virens*, the TS of capelin was less influenced by tilt angle (see Figure 2), which indicates that a change in the tilt-angle distribution of capelin will have less impact on the backscattered echo energy than a similar change in the tilt-angle distribution of saithe (see Paper IV).

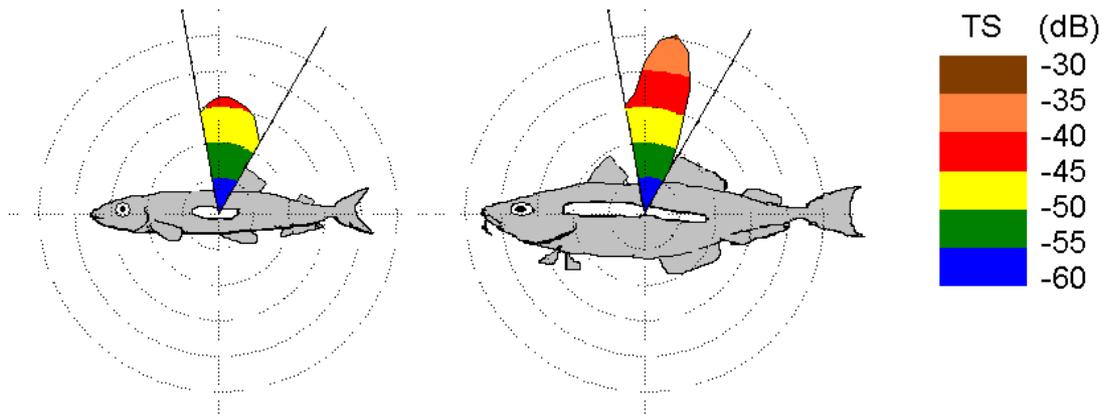


Figure 2: Mean target strength (TS) as a function of tilt angle at 5-m depth for capelin ($n = 10$) with mean length of 18.5 cm and saithe ($n = 3$) with mean length of 23 cm. Tilt angles range from 10° (head up) to -30° (head down). The data are from Paper IV. Gas bladder sizes are indicated as white areas.

The ratio of the swimbladder length to the total length of the fish (SBL/L) varies between species. Capelin observed in Papers II and IV had SBL/L between 0.08 and 0.19. According to data from Paper IV and other sources (Jørgensen, 1998; Foote and Ona, 1985), SBL/L of saithe ($n=28$) have been observed to vary between 0.29 and 0.44, and pollack *Pollachius Pollachius* ($n=13$) between 0.25 and 0.37. Gorska and Ona (2003b) set SBL/L of mature herring *Clupea harengus* to 0.26, while data from Haslett (1962) give SBL/L between 0.23 and 0.25 for several different species (e.g. sprat *Sprattus sprattus*, herring, haddock *Melanogrammus aeglefinus* and cod *Gadus morhua*). Thus, capelin tend to have lower SBL/L than the other mentioned fish species, and combined with the small size of capelin, this does have implications for capelin regarding maximum TS and the TS directivity with respect to different tilt angles at 38 kHz.

In the experiments, the ratio between total length and the acoustic wavelength at 38 kHz (L/λ) varied between 2.9 and 5.0 for capelin (Papers I, II and IV) and between 3.4 and 6.0 for saithe (Paper IV). Horne and Clay (1998) recommend frequencies be chosen to restrict values of L/λ from 2 to 10. As L/λ increases, the influence of tilt angle on TS generally increases.

The influence of tilt angle on TS is indirectly related to total length because only a limited part of the fish body, the swimbladder, is the major source of the backscattered sound. The L/λ of saithe in Figure 2 is 5.9, only 28% higher than in capelin ($L/\lambda = 4.6$). However, the

ratio between swimbladder length and the acoustic wavelength at 38 kHz (SBL/λ) of the saithe is 2.2, about 175% greater than in the capelin ($SBL/\lambda = 0.8$). Thus, the lesser maximum TS and the weaker tilt-angle dependence of the TS of capelin as compared to saithe (Paper IV) are explained by differences in SBL/λ .

3.1.2 Pressure effects

Capelin often undertake considerable vertical migrations, which apparently may lead to both compression of the swimbladder and to hydrostatic under-buoyancy. Both these effects have an impact on the acoustic backscattering of capelin and may lead to differences in estimated abundance when the capelin are positioned at different depths.

The negative depth dependence of the TS of capelin observed in Paper IV is significantly stronger than that observed in herring and under-buoyant saithe. This may be due to differences in swimbladder design. The relatively long and slender gas bladder of the physoclistous saithe is attached to the vertebra column and the long and slender gas bladder of the physostomous herring is stretched out between the anterior bullas and the posterior anal duct (Blaxter and Tytler, 1978). When the pressure increases rapidly, the volumes of the gas bladders decrease in accordance with Boyle's Law, but the designs of the herring and saithe swimbladders may lead to compression in width rather than in length (Ona, 1990; Gorska and Ona, 2003b). However, the shorter gas bladder of the physostomous capelin does not possess an anal duct and is loosely attached to the surrounding organs. It is, however, firmly attached anteriorly to the oesophagus (Fahlén, 1968). It may therefore be more easily compressed in length than the gas bladder of herring and saithe, leading to a stronger depth dependence of maximum TS of capelin (see Figure 3).

If we adapt the $23.3 \log_{10}(L)$ length dependence for TS as proposed by O'Driscoll and Rose (2001) for capelin (5 to 14 cm), and a tilt-angle distribution of free-swimming capelin as observed by Carscadden and Miller (1980), the contraction rate that accounts for the decrease in mean TS with pressure will be $\gamma = -0.49$. According to Paper IV, the pressure-dependent change in the mean backscattering cross section (σ_{bs}) at depth z is described by:

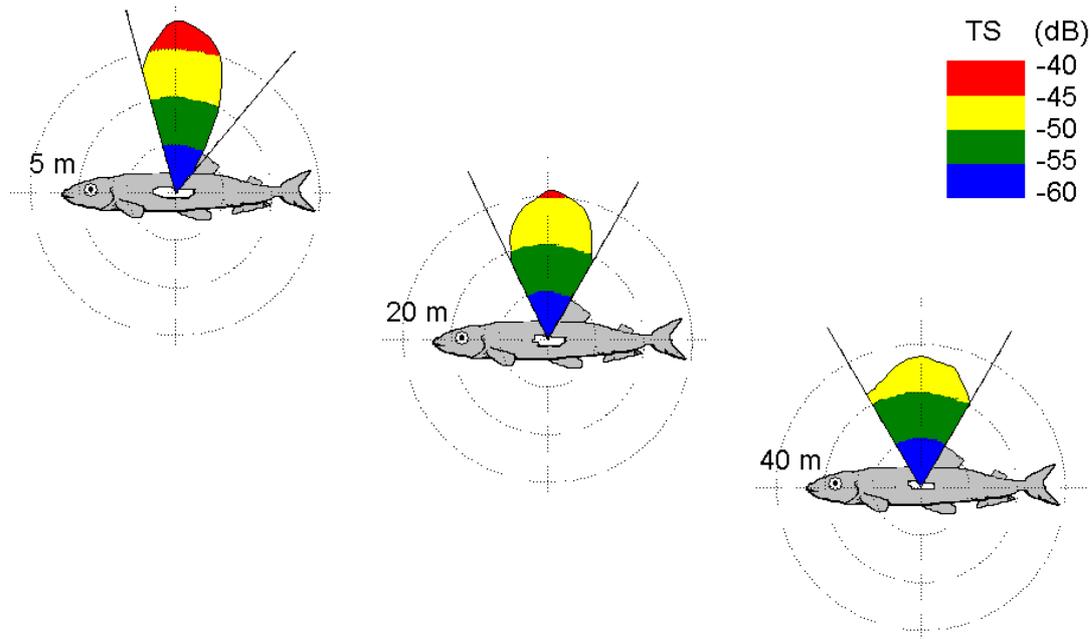


Figure 3: TS plotted against tilt angle for a 19.6-cm capelin at 5 m depth (left), 20 m depth (middle) and 40 m depth (right). The TS values are based on σ_{bs} smoothed by using a probability density function (PDF) with a rather narrow tilt-angle distribution ($s\theta = 2.5^\circ$) around each tilt angle.

$$\sigma_{bs z} = L^{2.33} 10^{-7.43} (P_z)^{-0.49}, \quad (3)$$

$$TS_z = 23.3 \log_{10}(L) - 74.3 - 4.9 \log_{10}(P_z), \quad (4)$$

where P_z is the ambient pressure in atm.

The maximum TS is, however, higher than the mean TS, and the pressure-dependent change in maximum TS may be slightly different than for mean TS. In the case of capelin, we use the contraction rate $\gamma_{\max} = -0.57$ for maximum TS (see Paper IV), and a $23.3 \log_{10}(L)$ length dependence would give:

$$TS_{\max} = 23.3 \log_{10}(L) - 70.3 - 5.7 \log_{10}(P_z), \quad (5)$$

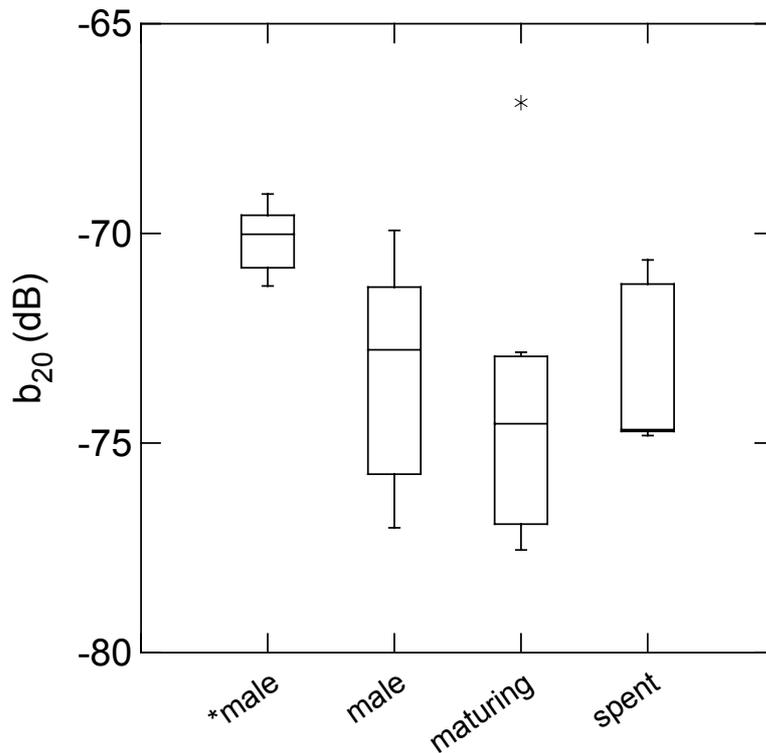


Figure 4: TS normalised by $20 \log_{10}(L)$ is called b_{20} . Results on males from the rig experiment are computed with an assumed tilt-angle distribution of $N(-3, 13)$, and are labelled “*male” ($n=10$). Results from males in the net pen experiment are labelled “male” ($n = 12$). Results on maturing ($n = 10$) and spent females ($n=5$) are from the net pen experiment.

3.1.3 Physiological aspects

The measured swimbladder lengths of mature Barents Sea capelin ranged from 1.3 to 3.0 cm in the net pen experiment (Paper II), and from 2.6 to 3.8 cm in the rig experiment (Paper IV). The swimbladder lengths of capelin observed in the net pen experiment were significantly lower than observed in the rig experiment (Mann-Whitney test, $p=0.001$, $n=20$).

Variation in physiological state may influence the swimbladder shape and thus influence the echo returned from the fish (Ona, 1990). Among female capelin within a length of 15.5 to 18 cm, mean TS was significantly negatively related to fish weight (Paper II), indicating that increasing condition leads to lower mean TS. Maturing females have eggs in the body cavity that may possibly squeeze the swimbladder. There were, however, no significant differences in the normalised backscattering cross section, $\sigma_{bs} L^{-2}$ (Haslett, 1965; Horne

and Clay, 1998) between maturing females, spent females and males at the rather low sampling sizes in Paper II. Even though no significant differences were observed, it can be noted that the maturing females tended to have lower normalised TS (b_{20}) than spent females and males, and that the results on males from the rig experiment support this trend (Figure 4).

Another possible explanation of the variation in swimbladder length could be that when the enclosed net pen was slowly lowered, some capelin ejected a substantial amount of gas in panic, as has previously been observed in panic reactions among salmon (Fänge, 1983) and herring (Nøttestad, 1998; Wahlberg and Westerberg, 2003). Even though gas ejection was not observed during the net pen experiments, it would, however, have consisted of a few rather small gas bubbles that are somewhat difficult to observe with the bare eye.

The maximum TS of capelin observed in a net pen (Papers I and II) and in a submersible rig (Paper IV) were always lower (0.5 to 10 dB) than the maximum TS for clupeiform fish as predicted by Dalen *et al.* (1976). This is probably due to the fact that Dalen *et al.* (1976), in addition to capelin, included TS from herring, salmon (*Salmo salar*) and sprat in their equation. Herring and sprat also have a higher maximum TS than capelin (Nakken and Olsen, 1977; Ona, 2003; Papers I, II and IV).

Present studies (Papers II and IV) and Dalen *et al.* (1976) observed mature capelin with a rather narrow range in length (15 to 20 cm), and found rather large variations in maximum TS. A major part of the variation in TS is explained by variations in swimbladder length (Paper II and IV). The strong correlation between the logarithm of swimbladder length and maximum TS also applies when data from the physoclistous fish species saithe and pollack are merged with the capelin data (see Figure 5).

When fish density is estimated using echo integration, a species-specific relationship is usually used to estimate mean TS from fish length distributions sampled, e.g. by pelagic trawl (MacLennan and Simmonds, 1992). Even though the relationship between maximum TS and fish length also tends to be species specific (McClatchie *et al.*, 1996), the results in this thesis suggest that there might be a more general species independent relationship between maximum TS and the swimbladder length.

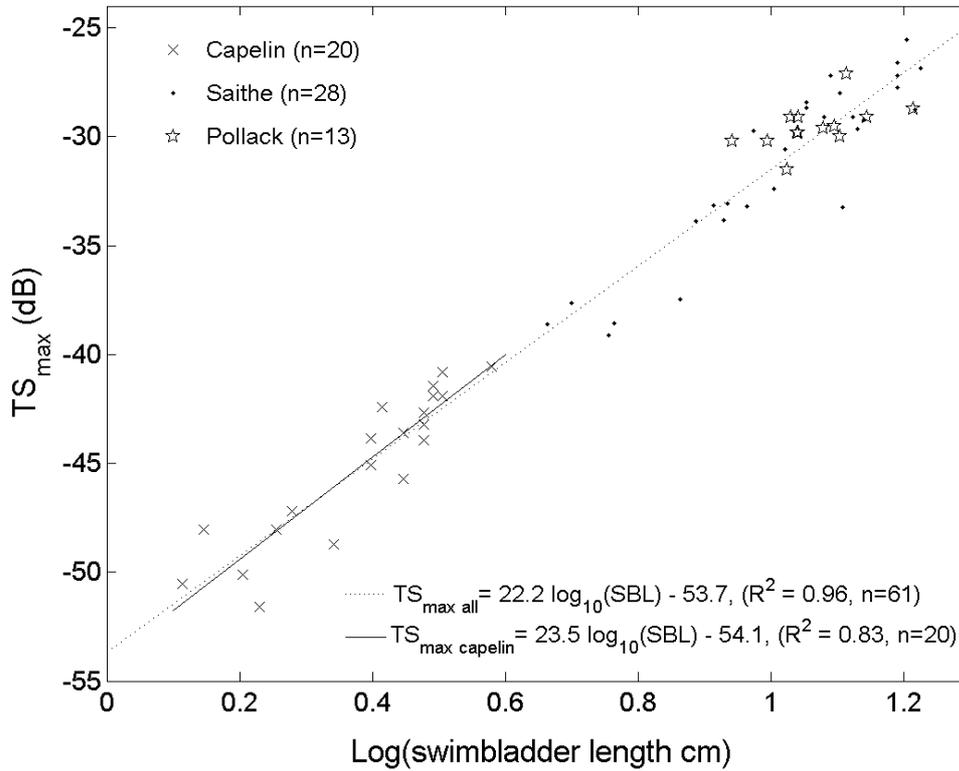


Figure 5: Maximal TS plotted against the logarithm of swimbladder length (SBL). TS data from capelin with intact swimbladders measured in net pen (n=12) and in submersible rig (n=8). TS measurements on live saithe in submersible rig at 5 m depth from Paper IV (n=5), Jørgensen (1998) (n=19), and Jørgensen and Olsen, unpublished data (n=2). TS measurements on two stunned saithe and 13 pollack at 2 m depth from Foote and Ona (1985).

The variation in maximum TS that is not explained by variations in swimbladder length may be due to variation of volume, width or curvature of the swimbladder, and methodological aspects (different freezing techniques and calibration procedures). Linear regression shown with the logarithm of swimbladder length as independent variable and maximum TS (TS_{\max}) as dependent variable gives a strong argument that TS data from capelin and other fish species are comparable in terms of swimbladder length rather than total length (Paper IV). Data on swimbladder length and TS_{\max} for capelin from the net pen and the rig experiment gave:

$$TS_{\max \text{ capelin}} = 23.5 \log_{10}(\text{SBL}) - 54.1, (R^2 = 0.83, n=20), \quad (6)$$

and for merged data from capelin, saithe and pollack at 38 kHz gave:

$$TS_{\max \text{ all}} = 22.2 \log_{10}(\text{SBL}) - 53.7, (R^2 = 0.96, n=61), \quad (7)$$

The level of maximum TS of capelin appears therefore to be explained mainly by the swimbladder length. If we assume that the SBL does not change significantly due to the change in pressure from the depth of the experiment ($P=1.5$ atm) to the surface where the capelin was frozen, it is possible to estimate the ratio of swimbladder length to total length of capelin at different ambient pressures. Combining equations 5 and 6 gives the average SBL/L at pressure P for the capelin in the rig experiment (Paper IV):

$$\text{SBL/L} \approx 0.20 P^{-0.24} \quad (8)$$

Equation 8 predicts SBL/L of 0.18 for capelin at 5 m, 0.14 at 40 m and 0.11 at 100 m depths. Thus, in the future it could be worthwhile to try to solve the problem of how to implement maximum TS, SBL/L and SBL/ λ from empirical measurements, as well as different tilt-angle distributions of the fish into models predicting the mean TS.

3.2 Behaviour and acoustic abundance estimation

Changes in tilt-angle distribution or changes in vertical distribution may occur as a result of natural behaviour (Olsen, 1971b; Huse and Ona, 1996). The vertical distribution may also affect whether or not all fish in an area are detected. When the fish are close to the bottom or near the sea surface, conditions for acoustic abundance estimation are unfavourable due to acoustic dead zones (Midttun and Nakken, 1977; MacLennan *et al.*, 2004). However, estimated fish density may also be affected by the capelin TS being dependent on changes in pressure and tilt-angle distribution during the vertical migration.

3.2.1 Vessel avoidance

Vessel avoidance and its effect on acoustic abundance estimates is well known for several species of fish, including herring (Olsen, 1990; Vabø, 1999; Ona and Korneliussen, 2000). The vessel avoidance experiments on capelin presented in Paper III did not demonstrate any significant influence of avoidance reactions to survey vessels on the volume scattering coefficient (estimated fish density), either in the feeding area or on the spawning grounds. There were, however, indications of changes in the centre of depth distribution (diving)

before the pass in dense concentrations at the spawning grounds. This is supported by observations made by Olsen *et al.* (1983a) at 70 kHz, which indicated that capelin even in deeper layers reacted to an approaching vessel by swimming downwards, although the total estimated density of fish in the water column was unaffected. Significant diving (changed tilt angle) might lead to changes in the mean volume backscattering coefficients due to changes in target strength. At 38 kHz, however, the drop in target strength attributable to moderate changes in tilt angle is expected to be rather small for capelin with the degree of polarisation in swimming behaviour that has been observed among free-swimming capelin (see Paper I, II and IV).

Barents Sea capelin are under the selective pressures of marine mammals (Sars, 1879; Christensen *et al.*, 1992; Gjørseter, 1998) that produce sounds within the frequency spectrum of vessel noise (Richardson *et al.*, 1995). When exposed to vessel noise, the capelin may choose a behavioural option that has maximised fitness for the species in similar situations throughout evolutionary time. In the cold waters of the Barents Sea, capelin have a rather low swimming speed (He, 1993; Misund *et al.*, 1993) as compared to the warm-blooded predators that might be associated with low frequency sound in a natural feeding situation (Whitehead and Carlson, 1986). Therefore, flight responses at somewhat short range in response to a large moving object producing low frequency sounds, like a fin whale (*Balaenoptera physalus*) or a survey vessel, may be less distinct for capelin than for faster swimmers like herring (Vabø and Nøttestad, 1997; Nøttestad *et al.*, 2002). Thus, in general, the selective process acting on capelin may for instance favour maximising its fitness by investing in feeding and reproduction rather than in predator (or vessel) avoidance.

The behavioural options that maximise the fitness of capelin at different life stages may, however, lead to different strategies in predator avoidance, and thus vessel avoidance. Capelin might avoid detection by predators by using more “passive” avoidance, such as horizontal or diurnal vertical migration in the feeding area (Gjørseter, 1998; Shackell *et al.*, 1994; Stensholt *et al.*, 2002). At the rather shallow spawning grounds in Varangerfjord, however, there were indications of changes in the centre of depth distribution (diving) of capelin in dense concentrations exposed to vessel noise (Paper III). This might be interpreted in terms of the capelin being a bit more vigilant on the spawning grounds than in the feeding area.

3.2.2 Implications of vertical migration for acoustic abundance estimation

In Figure 6 are shown TS of capelin for 5, 10, 15 and 20 cm fish size calculated by the TS equation used in the Barents Sea capelin surveys today expressed as horizontal dotted lines and compared with the pressure dependent TS given by equation 4 (page 14). The difference in TS between small (Paper I) and large (Paper II) mature capelin tend to be smaller when normalized with the use of a $23.3 \log_{10}(L)$ length dependence as suggested by O’Driscoll and Rose (2001), than with $19.1 \log_{10}(L)$, thus supports the use of the former. However, TS predicted from equation 4 is 1.5 to 1.8 dB higher than measured for small (Paper I) and large (Paper II) mature capelin, and 2.3 dB higher than measured for immature capelin (Jørgensen *et al.*, 2002). In contrary TS predicted by equation 4 tend to be 0.2 to 1.0 dB lower than the measurements of O’Driscoll and Rose (2001) and Olsen and Angell (1983). Halldorsson and Reynisson (1983) measured capelin TS 4 to 10 dB lower than predicted by equation 4. The results of Halldorsson and Reynisson (1983) are closest to TS of capelin individuals with very low swimbladder length and volume in Paper II.

For capelin with a length on about 5 cm (0-group) the commonly used TS equation (TS_{survey} , see equation 2 page 7), gives TS_{survey} values equal to equation 4 at about 25 m depth. Capelin with about 10 cm length (1-group) will be given a “correct” TS_{survey} at about 50 m depth, while older capelin (2-, 3- and 4-groups) as the length increases will be given a “correct” survey TS at greater depths (50 to 100 m). Below the depths (D_{lim}) where equation 4 and the TS_{survey} for a certain fish size are equal, the fish density estimated by using TS_{survey} may be underestimated due to the pressure effects on TS, while above D_{lim} the corresponding fish density may be overestimated.

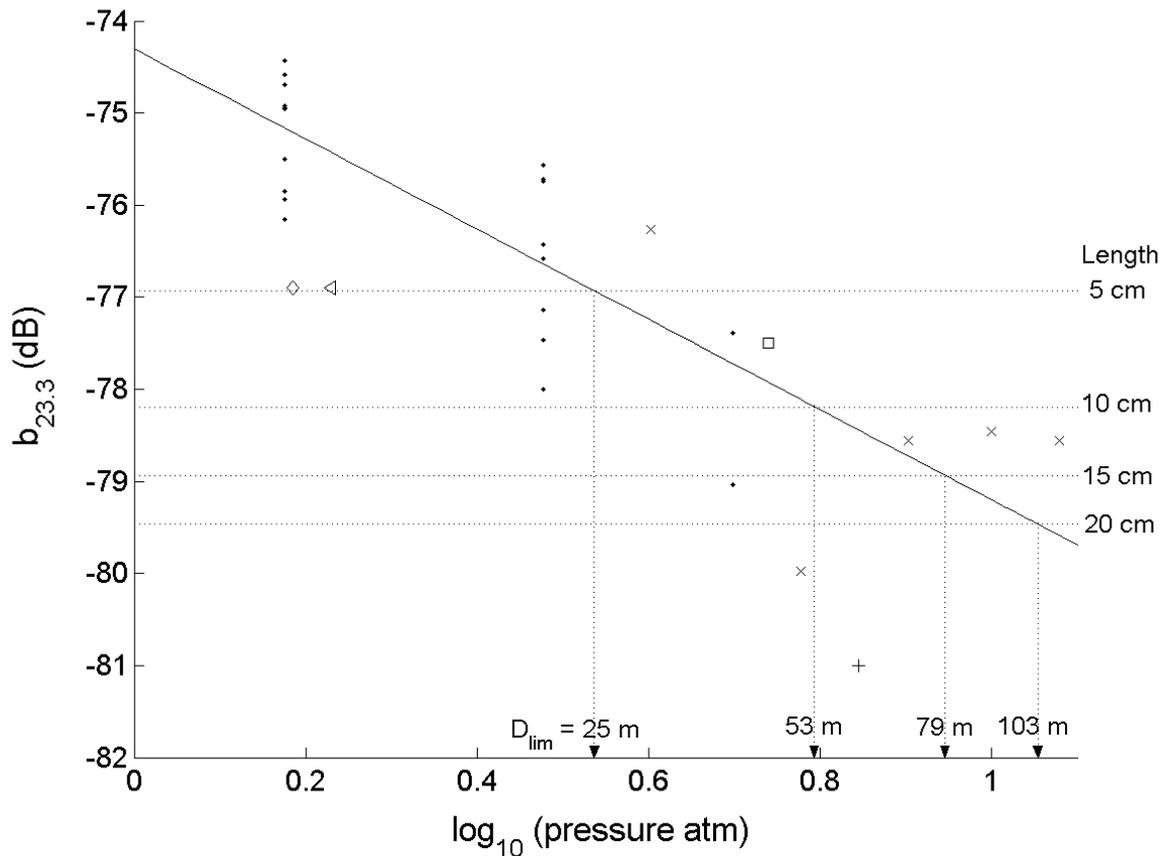


Figure 6: $b_{23.3}$ is mean TS normalised according to a length dependence of $23.3 \log_{10}(L)$ plotted against $\log_{10}(\text{pressure atm})$ from the sea surface to 110 m depth. The solid line shows $b_{23.3}$ estimated from measurements (points) in the submersible rig. The horizontal dotted lines show the level for TS from the survey equation used during the capelin survey today normalised according to a length dependence of $23.3 \log_{10}(L)$ for 5- to 20-cm capelin (lower). The arrows indicate the hypothetical depth under which the survey equation underestimates the biomass and above which the survey equation overestimates the biomass for different sizes of capelin. Also plotted are $b_{23.3}$ (calculated from mean $\sigma_{bs} L^{-2.33}$) from Paper I (triangle), Paper II (diamond), O'Driscoll and Rose (2001) (square), Jørgensen *et al.* (2002) (plus) and Olsen and Angell (1983) (cross).

When the acoustic survey of pelagic fish in the Barents Sea takes place in September, 0-group capelin are usually found close to the surface at daytime and at the depth of the thermocline (20-30 m) at dark (Beltestad *et al.*, 1975). According to Figure 6, the survey equation will give the best estimates at 25 m depth. 0-group densities at shallower depths might be underestimated due to the acoustic dead zone near the surface, but equation 4 points to the possibility of an underestimated TS outweighing some of the loss due to the acoustic dead zone.

The immature and adult capelin are known to make extensive vertical migration in the autumn (Gjøsæter, 1998) and winter (Stensholt *et al.*, 2002). In general, according to

equation 4 the estimated fish densities are likely to be correct or underestimated at nighttime during acoustic surveys of pelagic fish in the Barents Sea and underestimated during daytime. Adult capelin have frequently been observed to be densely packed near the bottom (125 to 175 m depths), especially in areas where humpback whales are present (Anon, 2002). Under these conditions, the estimated fish densities are likely to be underestimated both through using the too high TS_{survey} and because some fish are not detected due to the bottom dead zone.

4. Conclusions and future suggestions

The equations for capelin presented in this paper are based on measurements of fish with rather limited range in size and observed in a limited depth range. The results therefore ought to be verified by *in situ* and *ex situ* TS measurements that cover a range in fish length and depth representative of length distributions and the vertical distribution in acoustic surveys of the Barents Sea capelin. However, it is strongly recommended to include the effects of ambient pressure in the TS equation used in surveys in order to make the acoustic stock size estimate of capelin in the Barents Sea a better absolute estimate of the stock abundance. Differences in vertical distribution of capelin may occur in different areas and seasons, or between years with differences in oceanographic conditions or predation. As this may bias absolute estimates of stock abundance of capelin, more effort should be diverted towards these questions.

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Paper I

Paper II

Paper III

Paper IV



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