SWIMMING BEHAVIOUR OF SCHOOLS RELATED TO FISH CAPTURE AND ACOUSTIC ABUNDANCE ESTIMATION

by

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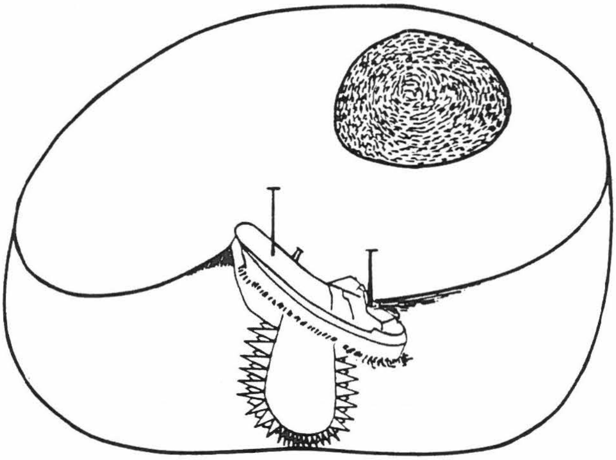

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PREFACE

Discussions about the schooling of fishes is known back to Aristoteles about 2400 years ago. Still, observers are astonished by the amazing regularity and synchrony of schooling individuals. During the last decades much effort has been devoted to reveal the behavioural rules of schooling. There has been significant progress in investigating the functions of schooling behaviour and describing and quantifying school structure. Especially the approach of behavioural ecology of the ways in which behaviour is influenced by natural selection in relation to ecological conditions has been fruitful. Most of the work has been conducted in artificial environments in small aquarias and tanks with a small number of fish. However, due to practical limitations and lack of adequate methods for field observations, there is limited knowledge on the behaviour of large, free-swimming schools.

Capture of schooling, pelagic fish is the basis of major worldwide fisheries, and the fishing methods developed are so effective that without effective regulations pelagic stocks may be depleted. Still, capture of sensitive, fast-swimming schools is a challenge that encourage development of new methods and technology. Likewise, there is a need for improvement in in the methodology for acoustic abundance estimation of schooling fish that are avoiding vessels and swimming close to surface. Better knowledge about the swimming behaviour of schools is therefore fundamental, both to improve the catching efficiency and acoustic abundance estimation.

This thesis is the result of participation in research activities in which the study of how freeswimming schools are behaving was an important aspect. The projects were conducted by the Institute of Fisheries Technology (FTFI), Fishing Gear and Methods Division, Bergen, and the Institute of Marine Research (IMR), Bergen, from 1985 to 1990. The first two years I was a student at the Department of Fisheries Biology, University of Bergen, and from 1987-1990, I recieved a scholarship from the Norwegian Fisheries Research Council. During the whole period, I have enjoyed the stimulating atmosphere at the Fishing Gear and Methods Division that are now a part of IMR.

Motivated by a curiosity on the behaviour of schooling fish obtained as a crew member on board the purse seiner M/S "Nybo" for several periods in the years 1973 - 1980, it has been my intention that the work presented in this thesis may contribute to increased knowlegde of the behaviour of the large, free-swimming schools.

Several persons have had major influence on the fullfillment of this thesis. I am particularly grateful to Prof. Steinar Olsen for giving me the opportunity to study and work at FTFI, supporting my work through professional guidance and critisism, and encourage participation in stimulating symposias and meetings abroad. Through his lectures and challenging discussions, Dr. Anders Fernø has been an inspiring teacher of behavioural biology, and his careful reviews and critisism of the manuscripts have improved this thesis substantially.

I owe special thank to Mr. Arvid K. Beltestad and Dr. Asgeir Aglen for their cooperation during most of this work, and my other co-authors are thanked for stimulating discussions. I have appreciated the social atmosphere and go-ahead spirit at the Fishing Gear and Methods Division, and the staff are thanked for help and encouragement during the long process of finishing this thesis.

Two of the papers are based on studies conducted on board the purse seiners M/S "Libas" and M/S "Klaring", and the skippers and crews of these vessels are thanked for their good cooperation.

I express special acknowledgement to Elen Hals who kindly prepared the thesis and Anders Brettingen who corrected the English text.

Bergen, June 1991
Ole Arve Misund

To Synøve,
our daugthers Kristine and Marie,
and my mother.

1 LIST OF PAPERS

This thesis is based on the following papers:

I Misund, O. A. 1990. Sonarobservations of schooling herring. School dimensions, swimming behaviour, and avoidance of vessel and purse seine. Rapp. P.-v. Réun. Cons. int. Explor. Mer, (in press)

II Misund, O. A., W. Dickson and A. K. Beltestad. Optimization of purse seines by large meshed sections and low lead weight; theoretical considerations, sinking speed measurements, and fishing trials. Submitted to Fish. Res.

III Misund, O.A. Predictable swimming behaviour of schools in purse seine capture situations. Submitted to Fish. Res.

IV Misund, O.A. and A. Aglen. Swimming behaviour of fish schools in the North Sea during acoustic surveying and pelagic trawl sampling. Submitted to J. Cons. int. Explor. Mer.

V Engås, A., O. A. Misund, A. V. Soldal, B. Horvei and A. Solstad. Fish behaviour and vessel noise; Catch data comparisons, noise analysis, and playback experiments. Submitted to Can. J. Fish. Aquat. Sci.

VI Misund, O.A., A. Aglen, A. K. Beltestad and J. Dalen. Relationships between the geometric dimensions and biomass of schools. Submitted to J. Cons. int. Explor. Mer.

VII Misund, O. A. Dynamics of moving masses; variability in packing density, shape and size among pelagic schools. Submitted to Anim. Behav.

2 SYNTHESIS

2.1. Introduction

Schooling fishes, such as most of the clupeoids, scombroids, and carangids are the foundation of major worldwide fisheries and fishing industries. Fishing for sensitive and fastswimming schools is still a special challenge to the fishermen, and catching techniques based on surrounding or towed nets develop continously (von Brandt 1984). Likewise, acoustic abundance estimation of schooling species may be rather uncertain (Aglen 1989), and special methodology must be applied to compensate for vessel avoidance and distribution close to the surface (Hewitt et al. 1976).

Computerized sonar equipment has become an indispensable tool for school fishing. Its function is not just to detect underwater fish concentrations, but also to reveal the swimming behaviour of schools. Exact and favourable positioning of the gear relative to the avoiding schools is practically totally dependent on such instruments. True motion, multibeam sonars are also excellent tools for quantification of size, swimming behaviour, and vessel avoidance of schools (Bodholdt and Olsen 1977). The most sophisticated instruments project the school area and display the movements of both vessel and school (Bodholdt 1982).

Being in motion is a prerequisite for the existence of schools (Partridge 1982a, Pitcher 1983). Knowledge and understanding of the school movements are therefore necessary for developing gears and tactics for fish school catching (Pitcher 1979). Information about swimming behaviour is also fundamental to acoustic methods for estimating school biomass (Foote 1989). The first objective of this thesis was therefore to quantify the movements of schools when influenced by vessels during fishing and acoustic surveying. Secondly, the fish-to-gear reactions are mapped when purse seining and pelagic trawling. The investigations have been carried out by the use of true motion sonars onboard survey and commercial fishing vessels for herring (*Clupea harengus*), mackerel (*Scomber scombrus*), and sprat (*Sprattus sprattus*) in different season and geographical locations. Based on these studies, considerations and experiments have been carried out to optimize the construction of purse seines, and a tactical school positioning method has been developed. An attempt has also been made to determine the characteristics of vessel-generated sound that may elicit avoidance reactions.

Due to acoustic shaddowing, the directivity of the fish backscattering strength and considerable noise reverberation in horizontal guided beams, estimation of school biomass by sonar echo integration is complicated (Mitson 1983). To establish an alternative based on the principle that school volume is proportional to the number of individuals and the cube of their length (Pitcher and Partridge 1979), relationships between the geometric dimensions and biomass of schools have been studied. Special attention has been paid to investigate the variation in internal packing density and shape of schools.

2.2 Swimming behaviour: A basic element in the definitions, structure and functions of schools

Schooling behaviour is quite common among fishes. Shaw (1978) has estimated that about 25% of the approximately 20000 fish species are schoolers. Moreover, about 80% of all fish species exhibit a schooling phase in their life cycle (Burgess and Shaw 1979). Schooling as juveniles is especially prevalent. Other aquatic organisms such as squids (Hurley 1978), tadpoles (Wasserzug et al. 1981), and krill (Strand and Hamner 1990) may also form schools. In addition, the behaviour of airborne bird flocks during migrations is a close analogy to fish schooling (Major and Dill 1978).

Schooling is regarded as an efficient way of conducting underwater movements, and is beneficial to the individual participants. Effects of schooling such as reduced detection probability, attack dilution and a repertoire of cooperative anti-predator tactics enhance a higher survival towards predation (Godin 1986, Pitcher 1986). Higher aggregated search rate results in faster food localization for fish in larger schools (Pitcher et al. 1982), and feeding sites are more effectively sampled (Pitcher and Magurran 1983). Similarly, reduced timidity in larger groups enables the individuals to allocate more time to feeding, even when predators are present (Magurran and Pitcher 1983). Likewise, since the mean direction route of a migrating group is likely to be more precise than each individual's choice (Larkin and Walton 1969), schools also migrate more accurately. Hydrodynamic advantages, proposed on a theoretical basis by Weihs (1975), have been disputed by results from empirical studies (Partridge and Pitcher 1979). Nevertheless, indications are accumulating that schooling individuals do benefit hydrodynamically from the motions of their neighbours (Pitcher et al. 1982, Partridge et al. 1983, Pitcher et al. 1985, Abrahams and Colgan 1985, 1987).

It is the movements, and how the movements are organized, that is the unique feature of schooling behaviour. Pitcher (1983) defines schooling simply as fishes in polarized and syncronized swimming, while fish shoals are more loosely organized. Older definitions of school definitions generally emphasised the group element. Parr (1927) considered schools as fish herds which have an apparently permanent character and being a habitual spatial relationship between individuals. The schools were claimed to exist on a diurnal basis and to result from visual, mutual attraction and subsequent adjustments of directions to parallell swimming. Both Parr (1927) and Spooner (1931) distinguished the less regular fish groupings formed by influence of external stimuli from the consistent schools formed by mutual attraction. Breder and Halpern (1946) defined schools as groups of fish that were equally orientated, regularly spaced and swimming at the same speed. Breder (1959) added that school formation must not be caused by environmental influence. Breder (1967) suggested the term 'obligate schoolers' for species swimming most of their lives in coherently polarized and permanent groups, while species forming such groups temporarily were called 'facultative schoolers'. Finding the various school definitions partly overlapping, Shaw (1969) found none of them explicit enough to be generally accepted. Later a group of researchers agreed to define a school simply as a group of mutually attracted fish (Shaw 1970). To russian scientists the term 'school' meant just a group of fish swimming together (Radakov 1973). Shaw (1978) ended the group-emphazing tradition stating that groups of fish united by mutual attraction, which may be either polarized or nonpolarized, should be considered schools.

Illustrating that it is the individuals own decision to join, stay with, or leave a group of companions, Partridge (1982a) argues that schools should be characterized by independent measures of time spent schooling and degree of organization. This view was developed further to the statement that a school is a group of three or more fish in which each member constantly adjusts its speed and direction to match those of the other members of the school (Partridge 1982b). Clearly, this definition is analogous to the heuristic one proposed by Pitcher (1983), with syncronized and polarized motion as the main characteristics. The element of organized motion accomplished by the participation of each individual is the basic criterion in both these definitions of school.

The function of an internal school structure is to enable the individuals to take up positions that maximise the flow of information about the swimming movements of their neighbours (Partridge et al. 1980). In this manner, well coordinated school manoeuvres can be performed. Schooling fishes therefore tend to organize at certain distances and directions to each other (Partridge et al. 1980). Herring prefer to swim at 45° or 135° relative to its neighbour horizontally and 30° above or below. Saithe (*Pollachius virens*) school more alongside its neighbour horizontally, but with the same elevation tendency. Schooling cod (*Gadus morhua*) are more randomly spaced. The individuals may swim less than one bodylength apart (Cullen et.al. 1965, Smith 1970, Graves 1977, Pitcher and Partridge 1979), but interfish distance of free-swimming schools is often much larger (Radakov 1973, Serebrov 1976, 1984, Cushing 1977, Paper VII).

This indicates that the packing structure of schools is rather dynamic. Considerable internal school movements have been observed, but the syncrony and polarization were maintained as individuals match changes in swimming speed and headings of their neighbours within time lags of about 0.1 s (Hunter 1969, Partridge 1981). The individuals pack denser when the swimming speed increase (Pitcher and Partridge 1979, Partridge 1981). Therefore internal movements may create short-term differences in speed and consequently interfish distance among various school regions. Since relatively small changes in distance among the individuals may give large changes in number of fish per unit of volume, such moving-mass dynamics may result in the great variations in internal packing density recorded in large, free-swimming herring schools (Paper VII). The internal movements may result in temporarily high-density regions, empty lacunas and also cause formation of short-lived subgroups (Paper VII). The size of the individuals also influences the packing structure, as juveniles prefer relatively greater interfish distances than larger fish (Van Olst and Hunter 1970). Similarly, individuals prefer to swim alongside school members of similar size (Pitcher et al. 1982, Pitcher et al. 1984).

The structure of schools is also affected by external factors such as presence of predators (Seghers 1974, Major 1978, Pitcher and Wyche

1983, Abrahams and Colgan 1985), level of background noise (Moulton 1960), vessel noise (Freon et al. 1990), and amount of dissolved oxygen (MacFarland and Moss 1967). Furthermore, the feeding motivation of the individuals greatly influences the school organization. Hunger loosens the school structure as the individuals tend towards individual food-search behaviour (Morgan 1988, Robinson and Pitcher 1989a, b). The influence of these factors may explain variations in packing density observed seasonally, geographically and even between nearby schools (Paper VII).

Adopting a certain external school structure may reduce the probability of being detected by searching predators. This would be obtained by adopting a spherical school shape, which minimizes the area-to-volume proportion (Breder 1959, 1976, Cushing and Harden Jones 1968, Radakov 1973). Pitcher and Partridge (1979) argues for the commonly observed discoid shape. However, the external school shape seems very dependent on vertical position, with quite spherical schools midwater and flattened discoids close to the sea surface or the bottom (Paper VII). This indicates that the sherical school shape is the principal, and that influence of the sea surface or sea floor modifies the school shape towards discoids. A steadily changing external structure with appendages and inward bends are probably caused by the internal school dynamics (Papers I and VII).

2.3. Swimming behaviour of schools during vessel influence, purse seining and pelagic trawling

When surveying, purse seining or pelagic trawling, the vessel is actively operated and generates stimuli that may constitute an important part of the total stimulation by which nearby fish are influenced. Fishing and survey vessels generate low-frequency sounds with peak energy in the hearing range of teleosts (Chapman and Hawkins 1969, Olsen 1969a). The swimming behaviour of schools in the vicinity of such vessels is therefore claimed to be the outcome of interactions between vessel sound stimuli and natural stimuli acting on the schooling individuals (Balchen 1984).

The swimming speed of schooling herring and mackerel larger than 20 cm averages 2.5–3.0 bodylengths/s in purse-seine capture situations (Paper I, Paper III). This may indicate that swimming speed increases in the presence of active vessels, as Harden Jones (1962) and Devold (1969), from following vessels, estimated migrating, large herring to swim at 1.0–2.0 bodylengths/s. The reaction to a directly approaching or pelagic trawling vessel is even more conspisous as herring larger than 20 cm swam with an average speed of about 4 bodylengths/s in such situations (Paper I, Paper IV). However, there were great variation in swimming speed among schools, indicating varying influence of natural stimuli stronger than that of the nearby vessel (Schwarz 1985).

Olsen et al. (1983a) argues that avoidance reactions are elicited by an instantaneous increase in the pressure gradients of low-frequency sound emitted from an approaching vessel. This is probably the case for fish with a swimbladder since this organ transforms scalar pressure to particle motions that can be sensed by the otholith organs (Hawkins 1986). Blaxter et al. (1981) found that herring showed avoidance reactions to low-frequency sound pressure stimuli alone. Fish without swimbladder, such as mackerel, can detect the particle motion only of vessel- generated sound, and are therefore less sensitive than fish with swimbladder by a factor of about 10 dB (Hawkins 1986). This difference in hearing ability seems not, however, to influence the reactions to fishing vessels, as herring and mackerel performed quite similar avoidance reactions to circling purse seiners (Misund 1988, Paper III). Probably, the vessel sound level at the actual distance was well above the reaction threshold for both species.

The vessel-generated sound spectrum is composed of discrete, engine-created line frequencies superimposed on a continous spectrum generated by propeller cavitation (Urick 1967). The amplitude of the vessel sound within the sensitive frequency band was the main determinant for provoking avoidance reactions of cod and herring (Paper V), but the temporal structure of the sound seemed also to be of importance. For saithe, a trawler with a high sound level in the 60–300 Hz band obtained lower catch rates than similar, but more silent vessels (Paper V). Tuna vessels generating sound spectra with distinct line frequencies rising more than 3 dB above the spectral level, clearly obtained lower catch rates than vessels emitting smooth sound spectra (Ericksson 1979, Bercy and Bordeau 1987).

Olsen et al. (1983a) proposed an avoidance behaviour model assuming that schooling fishes pack more closely and polarize strictly when responding to vessel-generated sound. Such behaviour has been observed for shoaling herring and cod when exposed to low-frequency sound or vessel noise playback (Hering 1968, Olsen 1976, Schwarz and Greer 1984, Paper V). As the vessel approaches, the model predicts that the fish increase the speed, and swim radially with a downward component away from the vessel. This linearity in the reaction pattern is not supported by sonar observations of schooling herring, mackerel and sprat (Misund 1988, Papers I, III, and IV) or penned herring and cod exposed to vessel sound playback (Paper V). As the vessel-to-school distance diminished from about 600 m to about 50 m no increase in the swimming speed of herring has been recorded (Papers I and IV). Similarly, penned cod and herring seemed to not increase the swimming speed during reaction to playbacks of trawler noise. There was, however, clear evidence of radial horizontal swimming away from both circling and approaching vessels (Papers I and IV). This means that schools tend to be guided in inner loops by circling vessels (Misund 1988, Paper I) and in front of and in the same direction as directly approaching vessels (Papers I and IV).

The vessel-generated sound is directive with lobes of higher intensity to the sides and a sound intensity minimum in front of the vessel (Urick 1967). This is also reflected in the spectral distribution from a trawler with very low frequencies (<50 Hz) dominating in front, while the medium frequencies (50–1000 Hz) reach the highest levels to the side of the vessel (Paper V). That schools are guided in an inner circle by a surrounding vessel and in front of a directly approaching vessel may therefore be explained by fish orientation to the gradients of the emitted sound and swimming for positions with lower vessel-sound stimulation (Paper I, Paper IV). Such a gradient is quite steep to the side of the vessel but much weaker in front (Urick 1967). Still, fish are able to discriminate small variations in amplitude, and cod and haddock (*Melanogrammus aeglefinus*) detect variations of as little as 1.3 dB (Hawkins 1986).

Fish can detect the direction of (Olsen 1969b, Schuijf 1975, Hawkins and Sand 1977, Buwalda et.al. 1983) and probably also the distance to (Schuijf and Hawkins 1983) a low frequency sound source. The vessel avoidance patterns may therefore be the result of directional orientation also. In this case, the guiding in front of the vessel may alternatively be explained by an 'effect of pursuit' (Misund 1986). This means that the pursued animal does not avoid sideways, but move in the same direction as the pursuer.

That about 14% of the schools aimed at by a survey vessel was not recorded by the echo sounder indicates sideways horizontal avoidance close to the vessel (Paper IV). This seemed not to be that case for directly approaching purse seiners as about 5 % of the schools aimed at were not recorded by the vertical sounder of those vessels (Paper I). However, the swimming behaviour of schools closer than 50 m to the vessel has not been recorded due to a blind zone of the sonar (Paper I, Paper IV). Recently, omni directional sonars like the Simrad SR 240 have been developed, and the uncertainty about the swimming behaviour of schools in the near zone of vessels can be revealed by use of such instrumentation.

Downward swimming, as predicted by the avoidance behaviour model, is not a general pattern of behaviour towards approaching vessels (Ona and Godø 1990, Paper I, Paper IV). An exception is spawning-migrating herring that showed strong avoidance with clear diving when the vessel approached (Paper I). However, there is a substantial increase in the sound level close to and underneath the vessel, and schooling herring seemed to swim downwards when the vessel passed directly over (Olsen 1979, Olsen et al. 1983b, Paper I).

In accordance with linear response predictions of the avoidance behaviour model, Olsen (1979), and Olsen et al. (1983b) recorded stronger avoidance the higher the vessel speed and the lesser the swimming depth of the fish. This was not the case for schooling herring, however, as the speed of the vessel when both circling and passing over did not influence the swimming behaviour (Paper I). An important deviation from the model is also that the deepest swimming herring schools seemed to perform the strongest vessel avoidance (Paper IV).

The effect of sound as a biological stimulus is dependent on the conditions for sound propagation (Rogers and Cox 1988). In areas with linear sound propagation, schooling herring avoided weakly when probably detecting the approaching vessel at long range (Paper IV). Strong avoidance reactions were elicited when the herring schools probably did not detect the approaching vessel until at close range due to downward bending of the emitted sound (Paper IV).

When operating active gear such as purse seine or trawl, the noise field surrounding the vessels may be altered. Often there is a sudden change in pitch and revolution of the propeller when starting to shoot the purse seine. Additional noise may be generated when the leads run overboard, and from the line running through the purse rings. A change in the sound stimuli may therefore explain the tendencies towards more turning and a certain diving of schools during purse seine shooting (Paper I, Paper III). Olsen (1971) reported that purse seine vessels often had great problems even to come in shooting position before herring schools escaped downwards. In certain occasions, changes in swimming behaviour may also be induced by the free-running part of the purse line as it cuts through the sea (Paper III).

Towing a pelagic trawl increases the sound level generated by the vessel due to a heavier strain on the propeller (Chapman and Hawkins 1969, Buerkle 1977). This results in more radial swimming of herring schools in front of the vessel, and usually fast downward swimming of schools passed over (Paper IV). Ona and Chruickshank (1986) and Ona and Godø (1990) recorded similar behaviour of shoaling cod and haddock. Ona and Toresen (1988b) observed stronger sideways avoidance of shoaling herring when passed over during pelagic trawling than when just passed over by the vessel during night-time.

If properly encircled, the outcome of the purse-seine capture situations depends on the swimming behaviour of schools during pursing. In this phase the fish may come in close contact with the gear at the same time as the sound level rise due to intensive vessel manoeuvring and as the purse line runs through the rings (Maniwa 1971). However, in some occasions the schools escape during pursing by swimming towards and out under the noisy vessel (Misund 1986, 1988, Paper I). Probably, the schools orient to the gear visually and are hearded out by the moving net. At night, shoaling herring seldom escape capture by purse seine (Paper I).

Herring schools often react strongly to an approaching midwater trawl long before the fish can see the trawl body itself (Mohr 1971). At a distance of 100–150 m infront of the trawl mouth, herring schools swam quite precisely in the same direction as the moving trawl (Paper IV). In this position, the schools probably orient visually to the trawl warps, doors and the sweeps. Another possibility is that vibrations in the trawl generate sound of very low frequency which the herring can detect and orient away from (Blaxter and Hoss 1981, Blaxter et al. 1981, Blaxter and Batty 1985). However, high levels of background noise for such frequencies, (Wenz 1962), in addition to the vessel-generated noise, probably masks the gear- generated noise.

The escape of schools under the noisy vessel during pursing (Paper I) and the precise orientation in the trawl door area (Paper IV) supports that visual stimuli by moving gear have stronger effects than vessel- and gear-generated sound stimuli (Wardle 1983, 1986). This is especially apparent, since in the absence of visual stimuli during night-time, shoaling herring seldom escape capture by purse seine (Paper I). Engås and Ona (1990) argue that similarity between day-time and night-time vertical distribution of cod and haddock in the net mouth of bottom trawls is caused by orientation to gear-generated low-frequency sounds. Visual sensing of the trawl, at night enabled by biolumniscence, may also explain such similarity. Class and Wardle (1989) showed that the characteristic, ordered reaction pattern to approaching net ceased at low light levels.

2.4. Operation and gear optimization

Conducting active fishing such as purse seining or pelagic trawling requires exact positioning of the gear relative to the target schools. Dealing with slowly moving, nonreactive schools is usually rather straightforward, while conquering fast swimming, avoiding schools may be much more difficult. The latter situation requires tactics based on experience and the ability to forecast the movements of the schools. In purse seine capture situations, the swimming behaviour of herring, mackerel and sprat schools is relatively constant (Paper I, Paper III). The individual schools tend to swim at more or less the same speed, pattern of movement and swimming direction until the purse seine has been shot around them. There are large variations among the schools, however, and tendencies towards slightly more turning and downward swimming during shooting. Nevertheless, the consistency of swimming behaviour of individual schools has enabled development of a position prediction model that when implemented in true motion sonars can forecast the school position in real capture situations (Paper III).

The swimming behaviour of schools is also reflected in the purse seines designed and constructed to catch the actual species (von Brandt 1984). The faster the species swims, the longer the actual purse seine usually is. Similary, the deeper a species usually swims, the greater the depth and the lower the hanging ratio (greater bossom) of the corresponding purse seine. Another important aspect is the sinking speed, since purse seines work by fencing in schools that occasionally swim at substantial depth. Traditionally, it has been argued to use as much lead weight as can be handled to get the purse seine to sink as fast as possible (Itaka 1971).

However, the size and amount of lead weight of purse seines are usually constrained by practical limitations such as the vessel stability, space available in the net bins, and the power of the gear handling equipment (Hamre and Nakken 1971). Use of large meshes that acts as a herding net in the last part and along the ground of purse seine is therefore advantageous (Paper II). The amount of twine necessary to build a given piece of net declines inversely with mesh size, which gives substantial savings in both building costs and storing space required onboard when increasing the mesh size up to 150 mm. White coloured net of this mesh size seems to have the nesessary herding effect, since schooling herring, mackerel and saithe did not swim through (Beltestad 1990, Paper II). Since the sinking speed increases exponentially with mesh size (Paper II), satisfactory sinking speed may be obtained even when using reduced lead weight, by combining it with large-meshed sections. Sinking speed improvements are also obtained when using hexagonal meshes in small-meshed net (Beltestad 1980), or using net of fibres with high specific gravity such as polyester (Beltestad 1990).

Conventionally rigged, pelagic trawling for schooling herring and mackerel close to the surface usually gave low catch rates (Paper IV). To be operated near the surface, conventionally rigged pelagic trawls require shorth warp length. Consequently, the trawl will be moving close to the vessel and the propeller wake, an area with substantial avoidance (Ona and Toresen 1988b). Therefore, using floats to keep the trawl near surface even with extended warp lengths, manoeuvring the trawl out of the propeller wake, and taking advantage of the guiding effect increased the catch rates for schools near the surface substantially (Paper IV).

2.5. Swimming behaviour and estimation of school size

Individuals in syncronized and polarized swimming appear as a unit of high density (Partridge et. al 1980). The volume occupied is proportional to the number of individuals and the cube of the fish length (Pitcher and Partridge 1979). This indicates a relationship between the geometric dimensions and biomass of schools.

Such relationships between the geometric dimensions and biomass of schools have been confirmed by two methods which both are based on measurements of school area by multibeam sonar. Simply by relating sonar measurements of the school area to the biomass of whole schools caught by purse seine, clear school-area to school-biomass regressions were established (Misund 1986, 1988, Paper I). Strong relationships between both the area and volume of the school and the estimated school biomass have been found by acoustic dimensioning using sonar and echo sounder combined with density estimation by echo integration (Paper VI).

For herring schools, the sonar and echo integration method gave biomass estimates about one fifth of the sonar and purse-seine capture method. The accuracy of conventional echo integration is influenced by sources of errors like sound absorbtion (Røttingen 1976, Foote 1990, Toresen 1991), variation in fish backscattering strength (Foote 1987, Olsen and Ahlquist 1989), system saturation and bottom detection in schools (Aglen 1989), and vessel avoidance (Olsen et al.1983b, Paper I, Paper IV). By combining estimates for all these errors, Aglen (1989) simulated an average echo-integrated density to be about 2/3 of the real in a case study for North Sea herring. The sonar and purse-seine capture relationships were based on measurements of schools singled out for purse seining. Such schools are usually quite large and dense, whereas schools varying by a factor of 100 000 in size and nearly 100 in density were included in the sonar and echo-integration relationships. The discrepancy between estimates of the two methods may therefore be caused both by the different sampling strategies and by the sources of errors connected to echo integration.

The level of the dimension-to-biomass relationships varies seasonally and between areas (Paper VI). This may be due to corresponding variations in fish backscattering strength (Foote 1987), in addition to varying predator exposure that influences the school structure. The relationships are independent of fish length (Paper VI), since the packing density is inversely proportional to the cube of the fish length (Paper VII), whereas fish weight is directly proportional to the cube of the fish length.

Acoustic abundance estimation using multibeam sonar and dimension-to-biomass conversion enables measurements of vessel-avoiding and surface-distributed schools. This method is therefore a usefull alternative to conventional echo integration by sonar (Hewitt et al. 1976). An attempt to use the method for abundance estimation of schooling mackerel has been conducted in the region of Skagerak and eastern North Sea (Misund 1991), and Misund and Beltestad (1989) used acoustic dimensioning and density prediction from length-to-density relationships to estimate the size of schools off Mozambique.

Complications such as the directivity of the fish backscattering strength (Nakken and Olsen 1977), noise reverberation in horizontal guided beams (Mitson 1983), and absorbtion of the emitted sound beam (Røttingen 1976, Foote 1978, Toresen 1991) probably have less influence on the dimension-to-biomass conversion method than the conventional one. For abundance estimation, dimension-to-biomass relationships established regionally and seasonally by sonar dimensioning and echo integration will be most appropriate. For this method it is easy to include all categories regarding size and density of schools within the actual population. The accuracy of the method may be improved using echo integration units that do not saturate (Bodholdt et al. 1988), correcting for the sound absorbtion within schools (Foote 1990, Toresen 1991, Paper VI), and using high resolution sonars with stochastic horizontal beam-width correction (Misund et al. 1989). When used for precapture school biomass estimation during purse seining, the level of the dimension-to-biomass relationships may be adjusted through experience (Simrad 1989).

2.6. Summary

Schooling individuals swim in positions relative to each other that maximize the flow of information about the movements of their neighbours. This enables the high syncrony and polarization that characterizes the motions of schools. There is great variation in the internal packing density of large free-swimming herring schools, however, due to the dynamics of moving masses. Schools tend towards flattened discoids when swimming near the surface or bottom, whereas the shape is more circular midwater.

Fish detect and respond to the low-frequency sounds generated by fishing and survey vessels. Amplitude and temporal structure in the sensitive low-frequency band of the sounds emitted from the vessels are important determinants for eliciting avoidance responses.

Schools usually avoid circling purse seiners and approaching survey vessels horizontally, and tend to swim downwards when passed over. Orientation to gradients in the emission pattern of vessel generated sound probably results in tendencies to in front of vessel guiding when approached and inner circle swimming when circled by the vessel.

Vessel avoidance increases during pelagic trawling. However, taking advantage of the guiding effect by operating the trawl with special floats and out of the propeller wake, increases the catch rates for schools near surface substantially.

When circled by a purse seiner, individual schools maintained a rather consistant swimming pattern, but there were great variations among schools. These results are the basis of a swimming behaviour model that when implemented in true motion sonars may enable position prediction of schools in real capture situations.

During pursing, schools may orient to the purse seine and thereby escape out under the noisy vessel. Similarly, when the front area of a pelagic trawl approaches, schools show precise orientation and swim in nearly the same direction as the vessel. This indicates that visual stimuli from moving gear such as pelagic trawls or purse seines may have stronger effects on fish behaviour than vessel- and gear-generated sound stimuli.

Use of large-meshed sections will improve purse seines. The material requirements, building costs, and net bin volume are reduced while the sinking speed is maintained, even with lower lead weight.

The structured swimming of schooling individuals results in relationships between the geometric dimensions and biomass of schools. Based on acoustic dimensioning by multibeam sonar, such relationships can be used for abundance estimation of schooling species and tactically for precapture prediction of school size.

2.7. References

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2.8 Erratum

The second proof of Misund (1990) is printed in this thesis, and the following errors have been detected:

- Urick (1983) on page 145 and in the references should be Urick (1967).
- Page 145: 'the leadline stated to rise' should be 'the leadline started to rise'.
- The abbrevataion for J. Cons. Perm. int. Explor. Mer, is misspelled in the reference for Bolster (1958) and Dow (1962).
- In the reference for Gjestland (1968), the word characteristica is misspelled