

Cross-scale observations on distribution and behavioural dynamics of ocean feeding Norwegian spring-spawning herring (*Clupea harengus* L.)

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Interpretation of the behavioural dynamics and distribution of herring requires explicit consideration of spatial and temporal scales since no single mechanism can explain the pattern on all scales. High resolution sonar and echosounders were used as our observation tools. The cluster ratio, mean Nearest Neighbour Distance (mean ISD); mean of the average Inter-school Distance (mean ISD) provides a descriptive index linking scales of distribution pattern within and between clusters of schools. It can be used to compare school clustering patterns for surveys made at different places and seasons. Two mesoscale patterns of school clustering were observed, as indicated by the distribution of nearest neighbour distances; one at 0.05–0.3 km revealed by sonar and another at 0.8–2.5 km revealed by echosounder. In general, schools were tightly aggregated, whilst school clusters were patchily distributed. Heightened feeding motivation explains the predominance of relatively small schools and their tendency to be found closer together and more clustered than large schools. Differences in distribution and density of food patches and predators may account to some degree for the observations (1) schools were distributed according to their size; both small and large schools had nearest neighbours of similar size more often than expected, (2) splitting and joining of schools were the most frequently recorded behavioural events. A considerable amount of variation in distribution and dynamics can be accounted for by changes in behaviour associated with diurnal vertical migrations. Some schools apparently did not perform diurnal vertical migrations. We suggest that when profitable, some herring may “dip in to the fridge” (feed in deep, cold water) during the day rather than pursue food on potentially high energy migrations.

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Introduction

Processes that result in the observed distribution pattern and structure of herring schools can be viewed as being derived from a hierarchical complex of space–time events. At the lowest spatial level (micro-scale, cm to m), individual fish execute second-to-second trade-offs, evaluating the profitability of joining, leaving, or staying with other fish (Pitcher and Parrish, 1993). Such decisions generate the internal dynamics of herring schools,

which are characterized by changes in internal (packing density) and external (shape) structure (Pitcher and Partridge, 1979; Misund *et al.*, 1995). At the next level (small meso-scale, 10s m to 100s m), we observe school movements and interaction among schools such as joining and splitting. These actions can also be extremely dynamic, occurring within a short-time scale (minutes) and often in response to specific events (Pitcher *et al.*, 1996). The large natural variability of school size testifies to this dynamic situation (Misund, 1993). It is at the

small meso-scale that many of the interactions between predators and pelagic prey takes place (Schneider and Piatt, 1986; Vabø and Nøttestad, 1997). The next two higher levels (large meso-scale, 100s m to 10s km; and macro-scale, 10s to 100s km) focus our observations on distribution patterns between schools or school clusters and the range occupied by a stock, with the associated temporal scale of interest spanning days to weeks, and months to years, respectively. Large meso and macro-scale distribution may vary in a characteristic manner during different life history phases (Fernö *et al.*, 1998), and has been shown to be directly linked to spatial and temporal distribution patterns of oceanographic features and conditions (Reid *et al.*, 1993; Maravelias *et al.*, 1996). To gain insight to the basic mechanisms and processes that govern the repertoire of herring behaviour, and how this relates to distribution pattern of schools, requires that our studies traverse spatial and temporal scales.

During April, Norwegian spring-spawning herring migrate in schools (*sensu* Pitcher, 1983) from the coast northwards to the region of a cold front, a rich feeding ground which they follow north and eastwards throughout the summer (Røttingen, 1992; Dragesund *et al.*, 1997). Motivation to feed is considered to be the primary driving force governing the migration although intense predation at the Norwegian coast may also be important (Fernö *et al.*, 1998). Previous surveys of the *Mare Cognitum* programme (see IMR, 1997) have revealed that during the ocean feeding period the macro-scale distribution of herring is closely linked to that of food (Melle *et al.*, 1994), but may potentially be modified by competitive interaction with other pelagic planktivores such as blue whiting, and also by predation pressure from a variety of species including saithe, cod, haddock, fin whales, false killer whales, white sided dolphins, killer whales (Christensen *et al.*, 1992; Haug *et al.*, 1995; Similä *et al.*, 1996; IMR, 1997), and sea birds (Anker-Nilsson and Barret, 1991; IMR, 1997; Fernö *et al.*, 1998).

Although fish in larger shoals may gain benefits through sampling behaviour (Pitcher and Magurran, 1983), for hungry fish it is suggested that smaller, less cohesive schools are better for optimum foraging, a reduced overlap of perceptive field resulting in less competition and less interference of individual feeding acts (Blaxter, 1985). Laboratory and field observations have revealed that feeding fish have a tendency to spread out and are often horizontally flattened in shape (Nøttestad *et al.*, 1996). They choose to be in smaller schools, are less cohesive (Morgan, 1988), have a reduced packing density, and display increased behavioural activity (Robinson, 1995). In the absence of predators, shoaling fish congregate according to the profitability of food patches (Milinski, 1979; Godin and Keenleyside, 1984) or where food patches are found

(Robinson *et al.*, 1995). Diurnal vertical migrations may track that of prey species.

Experiments demonstrate clearly that prey animals measure risk when deciding whether to forage (Morgan and Colgan, 1987; Lima and Dill, 1990; Milinski, 1993). In herring, the shoaling rules (and consequently shoal structure and distribution) are modified when fish are forced to make trade-offs between foraging and avoiding predation. Since risk of predation has evolutionary priority over feeding (Life-dinner principle, Dawkins and Krebs, 1979), in the face of potential predation, individuals will behave according to perceived risk. For example, when fish are well fed and food is abundant, reduced competition and the desire to maintain anti-predator advantages of larger shoals may result in the joining of shoals.

Although a considerable knowledge of changes in structural characteristics of schools has amassed, there is very limited understanding of meso-scale distribution characteristics; changes in the pattern within and between school clusters. Our analysis of the herring schools in the Norwegian Sea has two objectives; (1) to characterize the large meso-scale spatial distribution and changes in diurnal distribution of schools using a descriptive index (Cluster Ratio) that compares clustering patterns of schools between locations and seasons; (2) to link large and small meso-scale observations based on the pre-supposition that the structure, dynamics and distribution is a consequence of evolutionary adaptive behaviour associated with feeding and avoiding being eaten. Based on previous lab and field studies on schooling fish, we specifically hypothesize that during this period of ocean feeding that on average, school size will be small, packing density low, and vertical and horizontal distribution of schools will be related to feeding activity. Moreover, school dynamics ought to reflect a dynamic regime of adjustments according to trade-offs associated with feeding and predation risk.

Materials and methods

Biological, physical, and acoustical data were recorded from a scientific cruise in the Norwegian Sea during 6–22 April 1997, on board the research vessel “G. O. Sars”. The survey consisted of one diagonal and four parallel transects spaced 30 nmi apart north–south between 66–67°30'N and 2°E–4°W. Continuous acoustic recordings of fish and plankton were made by a calibrated (after Foote, 1987) echo integration unit consisting of a 38 kHz Simrad EK500, connected to a Bergen Echo Integrator (BEI) (Knudsen, 1990) for post-processing of the recordings and allocation of back-scattering strength (S_A) to species, on the basis of the proportion of different species caught at trawl stations, target strength distribution, and fish behaviour. The S_A

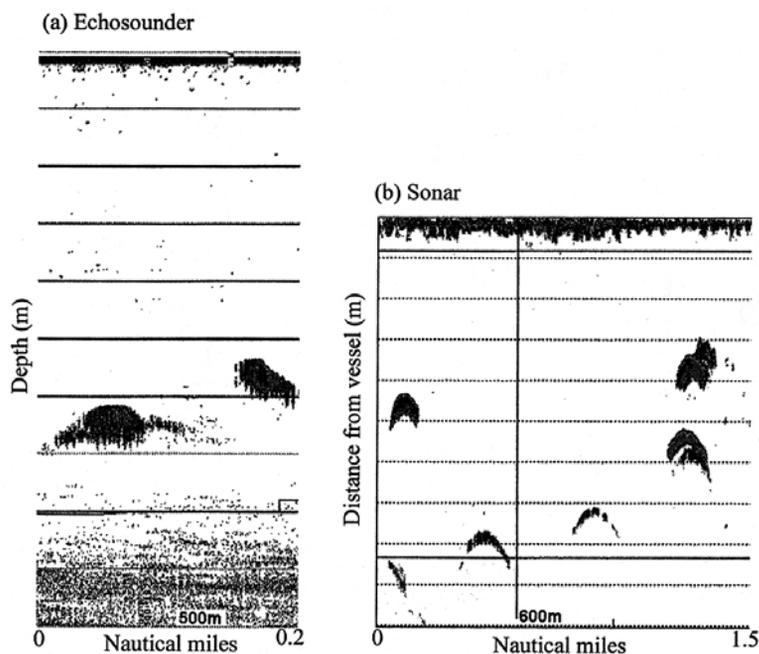


Figure 1. Recordings of herring schools by the (a) EK-500 echosounder: vertical axis is water depth, distance between solid horizontal lines is 50 m and maximum depth is 500 m. (b) SIMRAD SA950 sonar: The sonar is tilted -5° and directed 90° port. The dotted horizontal lines are spaced 60 m apart with the highest part of the figure closest to the ship. Only schools falling between 50 and 500 m (solid horizontal lines) were recorded for the survey, since beyond that reliability of measurements become limited. There is no relation between the signals and the actual school shape. The shape of the signals is due to the change in distance between the vessel and the school when the vessel passes the school.

(used as a proxy for relative school size) of individual herring schools was determined by using the school box option in the BEI system (Fig. 1a). Appendix 1 provides technical details on settings of acoustic instruments.

A 95 kHz Simrad SA950 sonar was used to determine the spatial distribution of schools at a range 50–500 m to the side of the vessel, and to track selected herring schools for periods of up to 1 h (Fig. 1b). Data was output to computer file and colour coded paper echogram. The sonar was connected to a HP 9000 workstation with software for the detection and measurements of school area (m^2) and relative density (measured as colour sum units; an expression of the relative echo intensity (Misund *et al.*, 1997) that is directly related to the relative density of a school (Misund, pers. comm.). Only those data log periods previously judged as herring from echosounder data, were used for analysis. Four periods of recordings were identified, for each of which confirmation of individual schools was later obtained by visual judging of paper echograms. During tracking, behavioural events of schools were noted continuously by a reporter and also recorded on video for later analysis. Behaviours were classified into two categories; intra- and inter-school events using the descriptions according to Pitcher *et al.* (1996) (Appendix 2).

Pelagic trawl samples (Åkra-trawl) were taken to identify acoustic targets. By modification of bridle and warp length and use of large floats on the doors, the trawl can be rigged to catch deep (100–400 m) or shallow (0–50 m) schools (Valdemarsen and Misund, 1994). Subsamples of up to 100 specimens of herring were taken from each trawl catch. Length, weight, age (from scales), sex, maturation stage, and stomach content were recorded using standard procedures and notation of Institute of Marine Research (IMR), Bergen (Appendix 3).

The ratio of mean nearest neighbour distance (NND; two-dimensional distance from a school to its closest neighbour school) to the mean average inter-school distance (mean \overline{ISD} ; where \overline{ISD} = average two-dimensional distance of a school to all other schools) serves as a useful descriptive index providing information on the meso-scale pattern of school clustering, viz:

“Cluster Ratio” is the comparison of meanNND:mean \overline{ISD}

where, $\text{meanNND} = \frac{\sum_{i=1}^n \text{NND}}{n}$ and $\text{mean}\overline{ISD} = \frac{\sum_{i=1}^n \overline{ISD}}{n}$
and n = number of schools

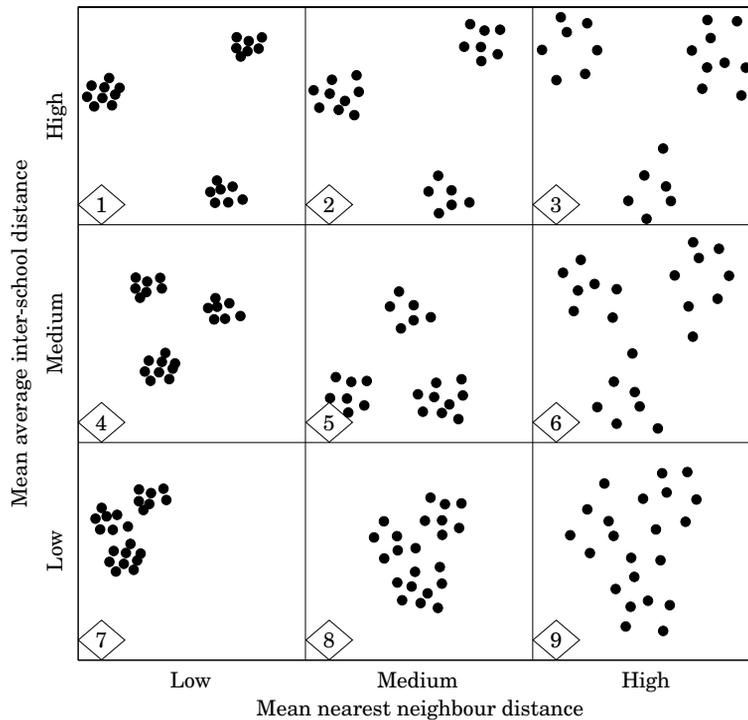


Figure 2. Schematic representation of hypothetical patterns of school clustering indicated by relationships between mean NND (distance to closest neighbour school) and mean ISD (mean of the average distance among all schools). Both parameters measure two-dimensional distance between schools.

Alone, each statistic tells us small pieces of information. By quantifying the mean distance among all schools, the mean $\overline{\text{ISD}}$ tells us about the area over which all schools are distributed relative to the extent of the survey area; it provides information on the scale of observation and is dependent on the observation tool. Mean NND tells us how close schools in a cluster are. The ratio of the two descriptors, mean NND: mean $\overline{\text{ISD}}$, provides us with a more functional comparative distribution index. Not only does it allow us to deduce facts about spatial scale, it provides insight into the intensity and pattern of school clustering (Fig. 2).

If we reduce the ratio to the coefficient:

$$\text{Cluster coefficient} = \frac{\text{meanNND}}{\text{mean}\overline{\text{ISD}}}$$

we lose the information on scale but still retain an impression of what the overall pattern and degree of clustering is like. Cluster coefficient (CC) values can range from 0 to 1 but are likely to be the lower end of this scale, since it is rare that mean $\overline{\text{ISD}}$ distance would be close to or equal mean NND. A low CC value (mean NND low and mean $\overline{\text{ISD}}$ high) would suggest that individual schools in close proximity are tightly clustered whilst those clusters are dispersed (Box 1, Fig. 2).

A CC close to 1 suggests many schools are diffuse, not forming strong clusters (Box 9, Fig. 2).

Results

Herring were recorded mainly between 65°30'–67°30'N, 003°30'W–002°E as confirmed from samples of nine trawl stations. Average size ranged from 30.4 to 33.8 cm with a tendency for larger herring to be found in catches from the southwestern area (IMR, 1997). Within all samples, herring were recovering from spawning (mean gonad score: 7.8, spent to recovering), had a low fat content (mean fat index: 1.2, none to little) and were confirmed to be actively feeding (mean gut fullness index: 3.3, medium to full).

Large meso-scale observations

School structure characteristics

A total of 285 herring schools were recorded by echosounder (Fig. 3), 52% of which were recorded during darkness. In comparison, 604 schools were recorded by side-scan sonar over four short periods of observation, during which time the echosounder recorded only 62 schools.

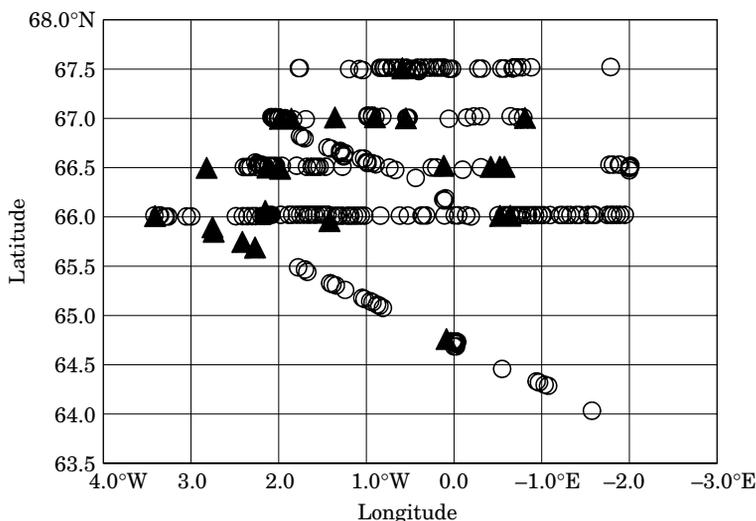


Figure 3. Distribution of herring schools in the Norwegian Sea recorded by EK500 echosounder (circles) (8/4/97–18/4/97) and locations of individual school tracking using sonar (solid triangles). After each tracking, trawl samples were taken to identify acoustic targets.

Using the area back-scattering strength (S_A -value) as a proxy for relative school size, individual schools were grouped into size categories (Fig. 4). Very small, small, and medium sized schools were most numerous (83%) but only accounted for approximately one-third of the total relative size (ΣS_A -values).

Of those schools recorded by sonar, the area of most was between 50 and 200 m^2 with a low relative density of approximately 500 colour sum units (Figs 5 and 6). Using an empirical relationship published by Misund *et al.* (1996) the biomass of herring shoals recorded by the SA950 sonar can be estimated from the area of the

school [Biomass (t) = $18.4 \times \text{Area (m}^2\text{)}$]. Using this formula, the average school biomass recorded during this survey was estimated to be 1969 kg, approximately 2 metric tonnes.

Spatial distribution pattern

Nearest neighbour distance (NND) distributions suggest two spatial scales of clustering; (1) Echosounder data indicates a high occurrence of schools within 0.8–2.5 km of each other (Fig. 7a), (2) sonar data shows a high number of schools with NND between 0.05 and 0.3 km (Fig. 7b). Based simply on detection capabilities (volume coverage), it is unsurprising that sonar results suggest a finer scale of spatial pattern. Also noteworthy is the occurrence of a few seemingly isolated schools with NND 8–35 km as detected by the echosounder. In addition to highlighting these isolated schools, cluster analysis of schools recorded by echosounder, provides supporting evidence for the scale of clustering determined from the NND distributions. From visual inspection of Figure 8, linkage of schools by nearest neighbour reveals most clustering occurs on a scale of 0.5 to 2 km.

The distribution of cluster coefficient (NND/ISD) values for individual schools can be used to describe their intensity of clustering and thus is more informative than the distribution of NND alone. Giving consideration to the distribution of NND (Fig. 7) our interpretation of Figure 9 is that individual schools are aggregated into intense clusters and these clusters appear to be patchily distributed (a pattern similar to Box 1, Fig. 2). Furthermore, comparison of the sonar and echosounder mean NND, mean ISD and cluster coefficient values, confirms that despite differences in

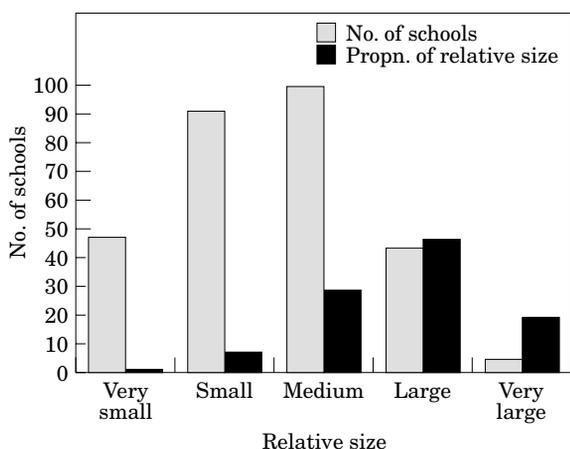


Figure 4. Size class frequencies and proportional contribution to total relative size (S_A -value) of echosounder recorded schools. Relative size classes based on area back-scattering coefficient (S_A -value): Very small <50, Small 50–250, Medium 251–1000, Large 1001–5000, Very Large >5000.

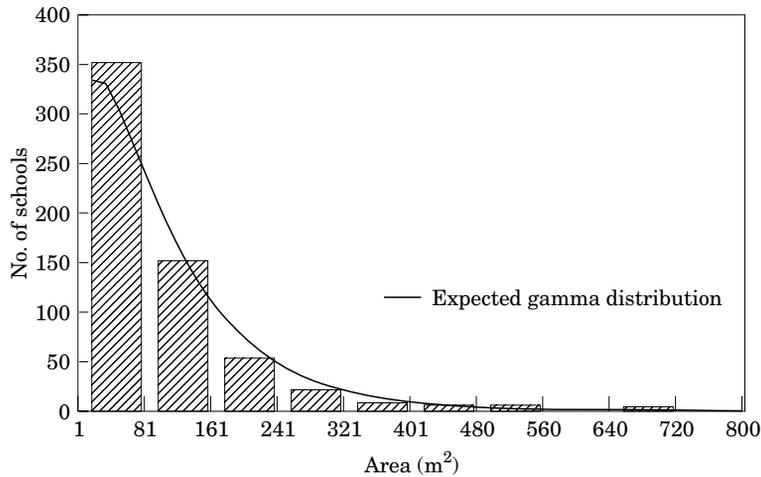


Figure 5. Frequency distribution of school area. A gamma distribution (scale parameter: 83, shape parameter: 1.28) is fitted to the data, although the observed data are significantly different from that expected ($\chi^2=32.55$, d.f.=3 (adjusted), $p<0.0001$).

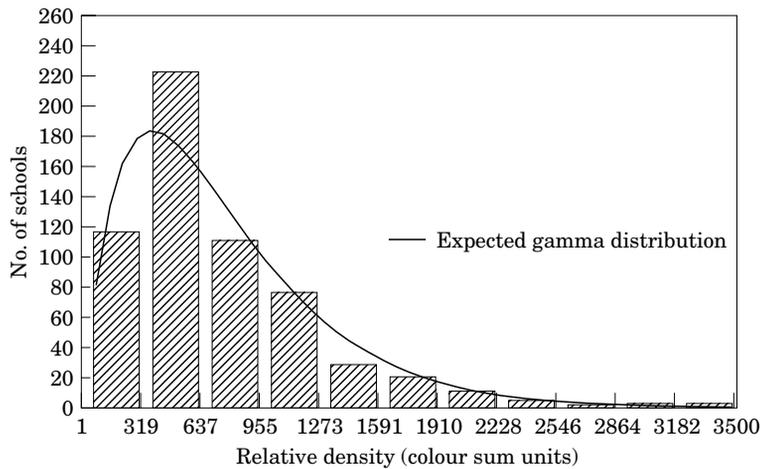


Figure 6. Frequency distribution of school relative density. Relative density scale runs from high on right hand side to low on left hand side. A gamma distribution (scale parameter: 389, shape parameter: 1.97) is fitted to the data, although the observed data are significantly different from that expected ($\chi^2=30.77$, d.f.=6 (adjusted), $p<0.0001$).

detection capabilities of sonar and echosounder, there is similarity in the pattern of school clustering across scales (Table 1).

Spatial distribution by size

Both frequency of occurrence with, and average distance to other surrounding schools were found to vary with school size. Firstly, for certain school sizes there was significant difference in frequencies of occurrence with neighbour schools of a particular size ($\chi^2=41.37$, d.f.=16, $p<0.001$, Table 2). In particular, small schools had other small and very small schools as nearest neighbour more often than expected by random chance, whilst medium and large schools were their neighbours less often than expected. Combinations of very large,

large, and medium schools occurred as neighbours appreciably more often than expected. Secondly, average distance between schools increased with school size, small schools being closer to other schools than large schools were ($\chi^2=11.82$, d.f.=4, $p<0.02$), i.e. small schools were more tightly clustered than large ones (Fig. 10). However, school size did not specifically determine the distance to nearest neighbour; when a size classified distribution of nearest neighbours was produced, it did not differ significantly from what may be expected by chance ($\chi^2=60.7$, d.f.=48, $p>0.11$).

Diurnal temporal variation in pattern and distribution

An attempt was made to see if there was any temporal difference in clustering pattern of schools between day

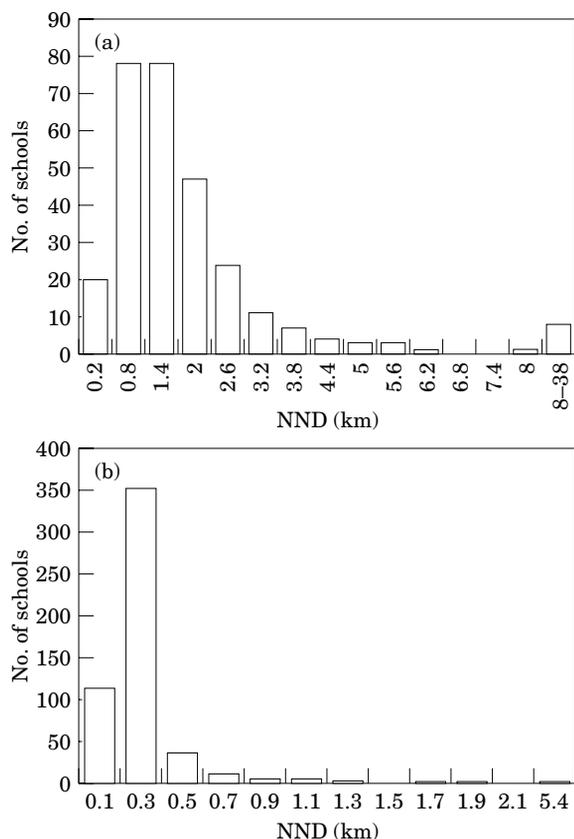


Figure 7. Distribution of NND; (a) Echosounder, (b) Sonar.

and night. To do so, it is necessary to remove as far as possible the differences due to spatial variation. Accordingly, we focused the analysis on discrete data periods in which schools were continuously recorded and where there were approximately the same number of schools recorded during day and night. Individual schools were found to be significantly more tightly aggregated during the night than day (Table 3), and as schools became more clustered at night, the extent or range of school clusters (indicated by mean \bar{ISD}) declined significantly also (Table 3). The cluster coefficient is no different between day and night for the echosounder, whilst it is more than double for the sonar. This implies that changes in the pattern of clustering was only observed on the finer scale; individual schools being closer together at night, whilst clusters were less patchy than in the day.

Within clusters, a typical strong diurnal vertical migration was observed, the majority of schools rising to shallow water during the night and diving to deep water during the day (Fig. 11a). Both echosounder and sonar data showed depth of schools was significantly deeper during the day than night; (1) Echosounder: (One tailed t-test, $t=15.13$, $d.f.=260$, $p<0.0001$; Fig. 11b), (2) sonar:

many more schools were detected during the night (78%) and were significantly shallower than daytime schools (One tailed t-test, $t=15.6$, $d.f.=147$, $p<0.0001$, Fig. 12).

Although not statistically significant, mean relative density of night schools (746 colour sum units) was appreciably lower than daytime schools (848 colour sum units). No difference was detected in the area or the relative size of schools. Daytime schools were also distributed through a greater depth range.

Small meso-scale observations

Behavioural dynamics

One hundred and four behavioural events were recorded from 31 herring schools tracked by sonar for an average of 40 min each, giving a total of 20 h and 41 min total observation time. Some kind of change in school behaviour occurred every 11.9 min ($n=104$, 95% CL:0–26). Behavioural events (Appendix 2) were classified into two categories. *Inter-school* (between schools) events occurred every 29 min ($n=50$; 95% CL:5–54). *Intra-school* (within a school) events occurred every 25 min ($n=50$; 95% CL:0–52). The distribution of total events per hour (event rate) provides a guide for classifying the overall dynamics of the schools observed. This descriptor, which we have called dynamic tendency, is a measure of the propensity for schools to move, split, join, or change shape. Note that the dynamic tendency is significantly higher during the night than day (Fig. 13). This point is borne out in greater detail in Figure 14b,c which show intervals between behavioural events within each category. Most events occurred more frequently during the night than day. In particular, schools were observed more frequently changing shape, surfacing, joining, leaving, and splitting. Although the data do not support close scrutiny it is noteworthy that dusk appears to be a very active period. Of those intra-school events occurring at night only 15% of joins occurred at dusk, whereas 54% of splits and 100% of leaves were observed in this period.

Discussion

During April 1997, macro-scale distribution of ocean-feeding Norwegian spring-spawning herring was centred around a cold front region mainly between $65^{\circ}30'–67^{\circ}30'N$, $003^{\circ}30'W–002^{\circ}E$. At the cold front, warm Atlantic water rising northwards meets with cool polar water travelling south. The front is characterized by a sharp decline in temperature together with high concentrations of zooplankton (Blindheim, 1989). We presume the cold front offers profitable foraging on zooplankton for actively feeding herring that are highly

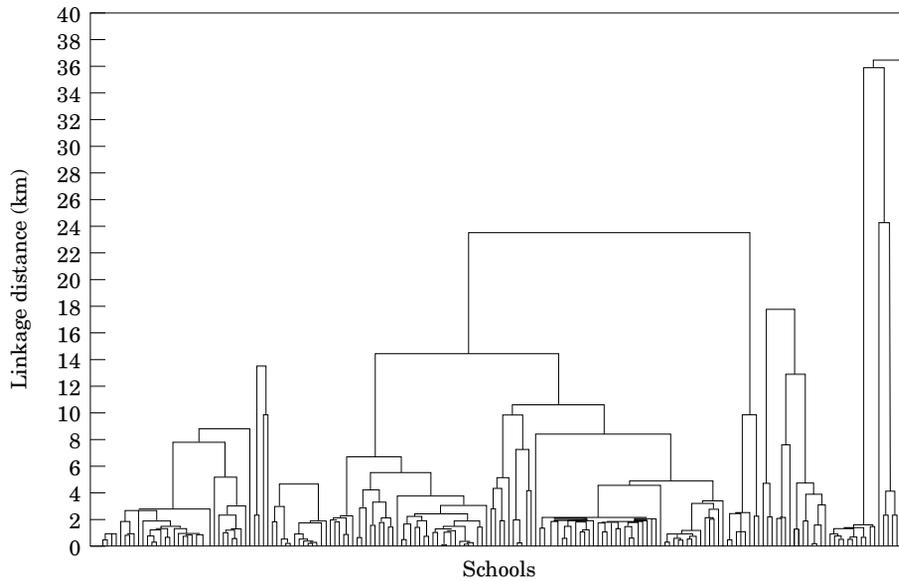


Figure 8. Cluster analysis tree, derived from a matrix of distances between schools recorded by echosounder. Linked using single linkage (nearest neighbour) basis. Many linkages occur at low distances (0.5–2 km) indicating tight clustering of schools at this scale. Schools on extreme right have highest linkage distance, being more isolated from other clusters.

motivated by hunger following the non-feeding periods of over-wintering and spawning (Slotte, 1996; Nøttestad et al., 1996; Fernö et al., 1998).

Within the region, two levels of meso-scale distribution were observed, one at 0.05–0.3 km recorded by sonar and another at 0.8–2.5 km recorded by echosounder. According to the cluster ratio (mean NND:mean ISD; a

relative measure of the intensity and pattern of clustering), both scales indicated a patchy distribution of intensely clustered schools. Furthermore, despite differences in detection capabilities of sonar and echosounders as a result differences in sampling volume (Misund et al., 1996; Misund, 1997), pattern of distribution was similar between scales, as revealed by comparison of cluster coefficients. By identifying and characterizing changes in the dispersion pattern of schools, the cluster ratio offers a descriptive index to make comparisons between surveys conducted in different places and at different seasons.

Within clusters, the majority of schools (83%) recorded by echosounder were categorized as very small to medium size, and most of those recorded by sonar were between 50 to 200 m² (mean 107 m²) with an equivalent biomass estimated at 0.9–3.7 t (mean 1.96 t). Tokarev (1958 in Radakov, 1973) similarly noted that foraging Atlantic herring occurred predominantly as small schools with diameter 1–20 m and average height 2–7 m, with the largest rarely extending >50 m. Average school size for herring during over-wintering and pre-spawning life history stages is generally much larger (Winters, 1977; McCarter et al., 1994; Wood, 1930; Nøttestad et al., 1996; Mackinson, 1999).

The school area-to-school biomass relationship used to convert the sonar recording to biomass (Misund et al., 1996) was established for North Sea herring schooling shallower than 150 m, and to use the same relationship for the deep-swimming schools in the Norwegian Sea may not be valid. This is especially because the sonar projection of the schools at great

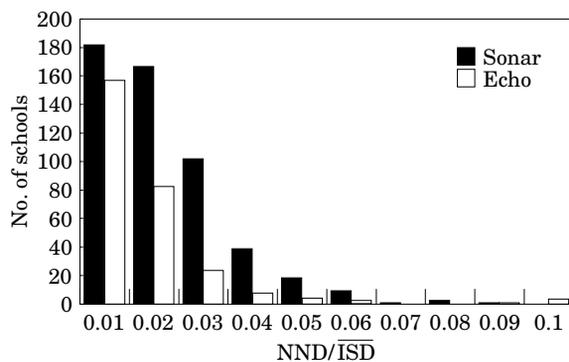


Figure 9. Distribution of cluster coefficient values.

Table 1. Comparison of school distribution parameters.

	Mean NND (km)	Mean ISD (km)	Cluster coefficient
Echosounder	1.83	127.8	0.0141
Sonar	0.163	11.62	0.0143

Table 2. Observed and expected frequencies of occurrence of schools of certain sizes as nearest neighbours.

	Very small	Small	Medium	Large	Very large
	Observed frequencies (expected frequencies)				
Very small	7 (7)				
Small	43 (30)	40 (30)			
Medium	25 (32)	53 (65)	39 (35)		
Large	9 (13)	10 (27)	37 (29)	12 (6)	
Very large	1 (2)	0 (3)	5 (3)	3 (1)	0 (0.1)

depth in daytime (down to about 350 m) may be a substantial underestimate of the true horizontal extent.

Small and very small schools were more tightly clustered than medium or large schools and occurred as neighbours more frequently than would be expected by chance alone. Close proximity provides small schools possibilities for rapid size adjustment through splitting and joining, and thus individuals achieve benefits of flexibility of responses to their dynamic environment.

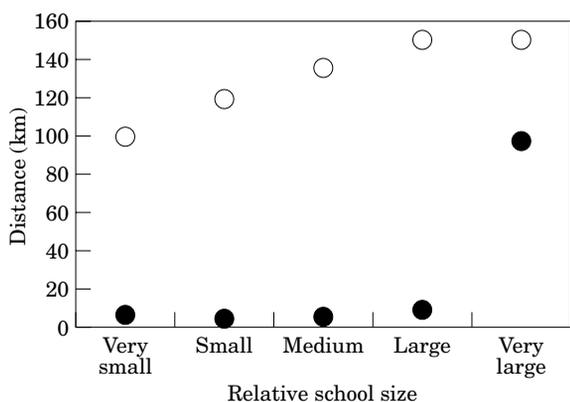


Figure 10. Relationship between average nearest neighbour distance (●, mean NND), mean average inter-school distance (○, mean ISD) and school size for echosounder data.

Whilst hunger reduces school cohesiveness (Morgan, 1988; Robinson and Pitcher, 1989) and active feeding may result in complete splitting of schools in to smaller units (Keenleyside, 1955), anti-predator advantages associated with larger school size (in particular dilution) are diminished (Magurran, 1990). However, intense clustering of schools combined with a dynamic adjustment regime may enable schools to maintain “collective” vigilance whilst simultaneously receiving the foraging benefits associated with smaller schools (Pitcher and Parrish, 1993). Indeed, our small meso-scale behavioural observations support the contention that observed dynamic adjustments among schools may aid transfer of information about their surroundings. Inter-school events, the most frequent of which was joining and splitting, occurred on average every 29 min.

As might be expected and as previously observed by Pitcher *et al.* (1996), intra-school events including changes in shape and density of individual schools occurred more frequently than behavioural events among schools. Although in this survey we did not observe any direct evidence of herring predators (in part due to exceptionally poor surface observation conditions), they are known to abound in the survey region. If herring opt for a precautionary approach and behave as if attack from predators likely (Lima and Dill, 1990) even if it seldom occurs, this may have an important effect on distribution, school size, and behaviour dynamics.

Table 3. Differences in diurnal distribution pattern. Standard errors are given in parentheses. Note: ^aone-tailed t-test with unequal variances; ^bone-tailed t-tests with equal variances.

	Day	Night	Significance
Echosounder			
Mean NND (km)	4.5 (0.75)	2.8 (0.33)	^a p<0.05
Mean ISD (km)	95.6 (4.55)	56.5 (2.37)	^a p<0.001
n	54	35	
Cluster coeff.	0.047	0.050	^b Not signif.
Sonar			
Mean NND (km)	0.4 (0.06)	0.1 (0.004)	^a p<0.001
Mean ISD (km)	33.5 (1.08)	2.9 (0.06)	^a p<0.001
n	132	138	
Cluster coeff.	0.011	0.024	^b p<0.001

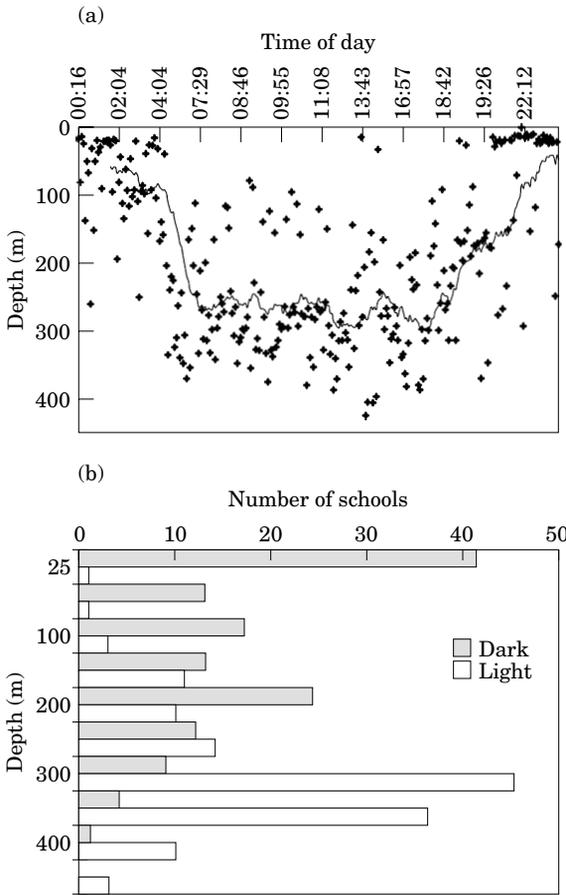


Figure 11. Diurnal changes in vertical distribution recorded by echosounder; (a) depth distribution with running average line plotted on figure, (b) number of shoals recorded at each depth.

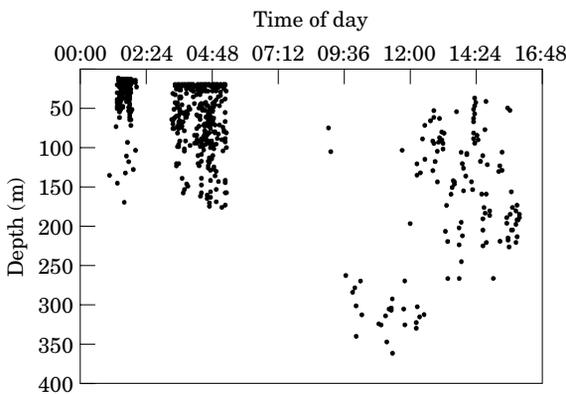


Figure 12. Diurnal depth of distribution of sonar recorded schools. Note: the four distinct groups relate to four separate data log periods.

The few recorded large schools occurred as neighbours more frequently than expected yet were more isolated with respect to other schools. Distance to near-

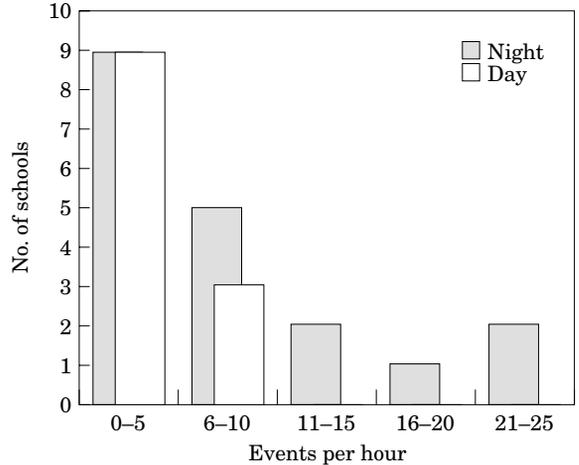


Figure 13. Distribution of behaviour events.

est neighbour was higher and their average distance to all other schools also higher. Occurrence of dense food patches may in part explain the more diffuse distribution of large schools. When food is very abundant there is likely a threshold beyond which no foraging benefit is gained from splitting and leaving a school. Reduced competition may allow for the persistence of larger schools. The range of school sizes observed lends supporting evidence to this. An alternative suggestion is that these larger schools are migrating schools that are somehow distinct from those classified as feeding as observed by Nøttestad *et al.* (1996). Larkin and Walton (1969) presented theoretical evidence suggesting large school size is more efficient for migrating to a specific point since the error in navigation is reduced.

A considerable amount of variation in structure and distribution of herring schools can be attributed to scale changes associated with diurnal migration. Changes in depth distribution of many schools displayed a typical vertical migration, presumably as herring moved with their food. However, some schools remained deep (300 m) even at night. Although there was no apparent difference in school size, density of schools was appreciably lower at night and we assume this to be a direct result of feeding activity (Pitcher and Partridge, 1979; Morgan, 1988; Robinson and Pitcher, 1989) and reduced light level (Radakov, 1973; Blaxter and Hunter, 1982). Yudovich (1954, in Radakov, 1973) recorded a packing density of $0.6\text{--}0.7\text{ kg m}^{-3}$ (equivalent to approximately 2 fish m^{-3} for 30 cm herring) in foraging Atlantic herring. Comparison of distribution of NND and \overline{ISD} for individual schools indicate that on both scales, 0.05–0.3 km and 0.8–2.5 km, schools are closer together, and the range of clusters is significantly reduced at night. The pattern of school clustering is also significantly different at the lower scale; clusters being relatively less patchy. The observation that many more

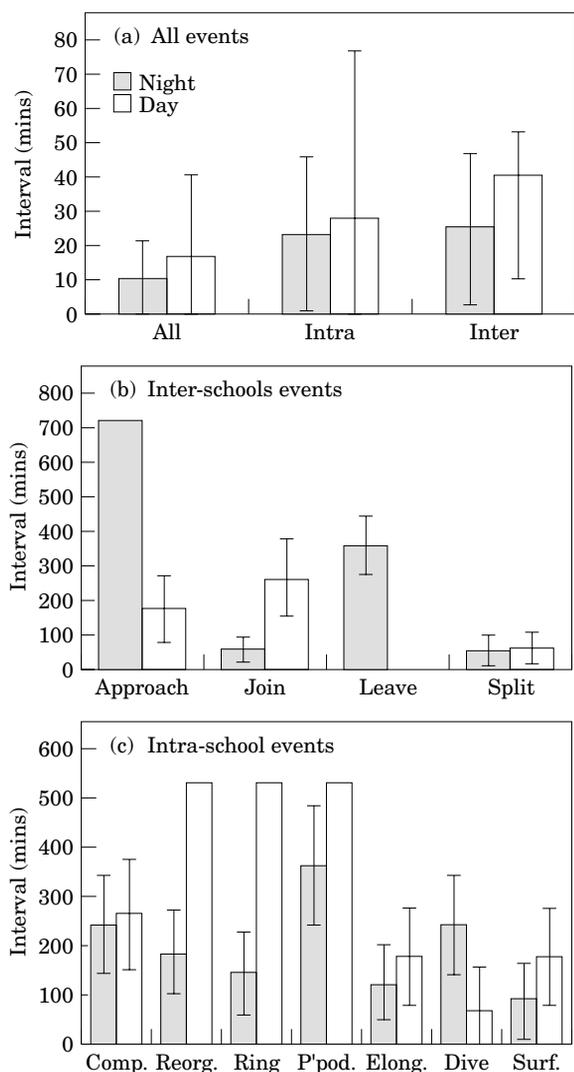


Figure 14. Behavioural event intervals of tracked schools. No error bars are displayed for events recorded less than twice. Abbreviations of behavioural events (see Appendix 2 for detailed descriptions): Comp., compact; Reorg., reorganize; P'pod., pseudopodium; Elong., elongate; Surf., surface; Ring, ring structure.

schools were detected by sonar during the night may in part be accounted for by the sonars' reduced detection of deep-swimming schools during daytime.

The dynamic tendency of individual schools was significantly higher at night than during the day. In particular, shape of schools together with splitting and joining events occurred much more frequently at night, presumably reflecting the dynamics associated with active feeding. Much activity associated with change in school size occurred specifically at dusk. Although some of the events recorded by sonar can be attributed to varying degrees of distortion (Misund *et al.*, 1997), rapid changes

in tilt angle distribution associated with feeding might account for the observed dynamics, particularly changes in school shape. Moreover, the observations support our contention that the dynamics reflect a regime of rapidly changing individual behavioural decisions.

Although herring are known on occasion to exhibit strong avoidance reactions to near field vessel sounds (Olsen *et al.*, 1983; Misund, 1997), we do not consider this to have biased our observations for several reasons: (1) during daytime schools tend to swim at great depth (up to 500 m); (2) behavioural observations were made by sonar on schools at a considerable distance from the vessel and for relatively long observation periods; (3) low vessel speed (1–3 knots) and hence noise, is unlikely to elicit a strong avoidance response; (4) herring are known to display reduced reaction during this season (Mohr, 1971) probably as a result of heightened feeding motivation.

Given the significant energetic costs of performing diurnal vertical migrations, the benefit should necessarily exceed these costs. Several studies point to multiple causality with trade-offs occurring among factors including feeding, temperature optimization, and predator avoidance (Neilson and Perry, 1990; Olla and Davis, 1990; Sogard and Olla, 1993; Brodeur and Wilson, 1996). Herring that choose not to perform diurnal vertical migrations may have feeding opportunity in deep, cold water where food can also be abundant (Melle *et al.*, 1994). Vertical migration to below a thermocline can be stimulated by feeding opportunity (Brodeur and Wilson, 1996; Galaktionov, 1984), particularly if food is limited above the thermocline (Bailey, 1989). When prey availability was low, 0-group walleye pollock accrued an energetic advantage from diel migration to cold water since growth was enhanced through exposure to low temperatures (Smith *et al.*, 1986). Risk of predation may provide additional motivation for preventing the herring from performing vertical migration. In lab experiments, juvenile pollock generally remained above a thermocline but were motivated to go below when food was introduced below or a predator from above (Olla and Davis, 1990; Sogard and Olla, 1993). Furthermore, very deep water may present a physiological limit to potential predators, thus providing a safe haven for herring. For migrating fish, lower temperatures and deep currents may also confer energy saving advantages.

Spatial and temporal variation is partly a function of the size of window used to view the world (Levin, 1992), and thus our description of the system will vary with the choice of scales. In this study our tools, echosounder and sonar, provide the window. Recognizing limitations associated with both the use and interpretation of these methods (Misund, 1997), they have nevertheless provided insight to two scales of spatial pattern of herring schools and provided important understanding of how

the system description changes among scales. The use of fractals (e.g. Sugihara and May, 1990) may help provide fuller insight. At some scales, responses of herring occur to a narrow range of stimuli (e.g. predator attacks) while others are diffusely linked to a broad range of conditions such as food distribution and temperature gradients. Correlations of the distribution of avian predators and schooling fish have been shown to be scale-dependent, not simply a reflection of each others general distribution (Schneider and Piatt, 1986; Schneider, 1989). Since we have no direct evidence of predators, we conclude that for the most part, activity motivated by feeding opportunities is the primary behaviour giving rise to the observed variability in distribution, structure, and dynamics of herring schools in the Norwegian Sea during early spring.

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Appendix 1. Acoustic settings

Echosounder

Range of 0–500 m; Maximum power: 4000 W; Time Varied Gain; 20 logR; Pulse length: 1 ms; Bandwidth: wide; Angle sensitivity: 21.9; 2-way beam angle: – 21.0 dB; Sv transducer gain: – 25.0 dB; TS transducer gain: 24.9 dB; 3 dB beam width: 7.0 dB; S_A recordings per nautical mile were averaged over a 5 nmi distance. Echosounder recordings were presented in echograms.

Sonar

TX power: max; Range: 600 m; Pulse: FM auto; Gain: 9; Display gain: 9; Time Varied Gain: 30 log R; AGC: weak; Normalization: weak; Ping-to-ping filter: weak.

HP 9000 workstation school detection system

Minimum range: 50 m; Maximum range width 5 m; Minimum interval 5 m; Minimum detection pings: 4.

Appendix 2. Descriptions of behavioural events (from Pitcher *et al.*, 1996)

Behavioural events were defined as a change in school status and recorded when they became evident to the observer. Events were recorded in two categories: inter-school events and intra-school events. The seven intra-school behaviour events were as follows. *Compact*: an increase in density and reduction in area of a school, over a time span of 1–2 min. *Reorganize*: rapid internal re-arrangement of school subgroups over a time span of 2–5 min. *Ring*: annular school structure, with a vacuole, or up to 3/4 of a vacuole, in the centre. *Pseudopodium*: elongated school subgroup extending out from the main

body, often joining two globular school subgroups. *Elongate*: elongated main school, more than three times as long as broad, generally in the direction of swimming. *Dive*: rapid increase in school depth in less than 1 min. *Surface*: rapid decrease in school depth moving towards the surface. Four inter-school behaviour events were: *Approach*: continued move towards another school target by the focal school, or an approach by another school. *Join*: coalescence of two schools. *Leave*: small target, >10% of main group size (herring sub-group, or possibly predators) leaving focal school. *Split*: fission of one school into two, generally entailing two subgroups emerging as schools over a time frame of 1–3 min.

Appendix 3. Institute of Marine Research biology codes for fish data.

Parameter				
Scale	Fat	Sex	Stage	Stomach content
1	Nothing	Male		Empty
2	Small	Female	Immature	Small amount – open stomach to find it
3	More		Maturing	Medium – clearly see content
4	A lot		Maturing	Full
5	Can't see gut for fat		Maturing	Distended – food visible through lining
6			Spawning	Food expelled
7			Spent	
8			Recovering	