

Distribution and behavioural dynamics of ocean feeding Norwegian spring  
spawning herring: observations across spatio-temporal scales

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# Distribution and behavioural dynamics of ocean feeding Norwegian spring spawning herring: observations across spatio-temporal scales

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## Abstract

Interpretation of 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. A protocol for the meso-scale mapping of herring schools is outlined. Two mesoscale patterns of school clustering was observed as indicated by distribution of nearest neighbour distances; one at 0.05-0.2 km revealed by sonar and another at 0.8-2.5 km revealed by echosounder. The cluster ratio (mean nearest neighbour distance: mean of the average inter-school distance) provides a descriptive index linking scales of distribution pattern within and between clusters of schools. In general, schools were found to be tightly clustered, whilst clusters were patchily distributed. Heightened feeding motivation appears to play the most important role in determining behaviour during this life phase. Specifically, it 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 or predators account to some degree for the observations (i) schools were found to be distributed according to their size; both small and large schools having nearest neighbours of similar size more often than expected, (ii) splitting and joining of schools was the most frequently recorded behavioural event. A considerable amount of variation in distribution and dynamics can be accounted for by changes in activity associated with diurnal vertical migrations. Some schools did not perform diurnal vertical migrations. We suggest that when profitable, some herring may 'dip in to the fridge' during the day rather than pursue food on such high energy migrations.

## Introduction

Description of pattern is synonymous with description of variation. Accordingly, concepts of scale and pattern are inevitably fused since determination of scales is a prerequisite to understanding variation (Denman and Powell 1984). Lack of explicit consideration of spatial and temporal variation often occurs because simple patterns are more easily observed from 'homogenisation' of the data spatially or temporally. Yet, since each species observes the environment on its own unique suite of scales of space and time (Weins 1976), variability is not an absolute and only has meaning relative to a particular scale of observation (Levin 1992). Moreover, since variation in local density of marine organisms reaches high values at some spatial scales and low at others, parameters characterising local density dependence may only apply at certain spatial scales (Schnieder 1989). Consequently, particular ecological processes may be better studied by explicit simultaneous consideration of spatial and temporal components (Resh and Rosenburg 1989).

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

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 characterised by changes in internal (packing density) and external (shape) structure (Pitcher and Partridge 1979). At the next level (small meso scale, 10's m to 100's 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 huge 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 take place (Schneider and Piatt 1986). The next two higher levels (large meso, 100's m to 10's km; and macro scale, 10's to 100's km) focus our observations on distribution patterns between schools or school clusters and the range occupied by a stock. Large meso and macro scale distribution vary during different life history phases (Fernö et al. 1998), and have been shown to be directly linked to spatial and temporal distribution patterns of oceanographic features and conditions (Reid 1993, Maravelias et al. 1996). To gain insight to the fundamental 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. In this research, a deliberate attempt is made to achieve the end.

During April, Norwegian spring spawning herring migrate in schools (*sensu*, Pitcher 1983) north-west to the region of the Polar front, a rich feeding ground which they follow north and eastwards throughout the summer (Røttingen 1992). Motivation to feed is considered to be the primary driving force governing the migration (Fernö et al. 1998). During this period, the herring are subject to significant predation pressure from a variety of species (Fernö et al. 1998). We conjecture that the observed behaviour dynamics, school structure and school distribution pattern of herring during this period is the consequence of evolutionary adaptive behaviour and trade-offs associated with feeding and avoiding being eaten. With reference to previous theoretical, experimental and field observations, we use this presupposition to focus our analysis and discussions towards interpreting; (i) macro-scale distribution of herring, (ii) meso-scale pattern of school clustering, (iii) medium-term temporal changes in the shape, packing density and size of schools, (iv) short term dynamics of individual schools.

## Material and Methods

Biological, physical and acoustical data were recorded from a scientific cruise in the Norwegian Sea during 6<sup>th</sup> –22<sup>nd</sup> April 1997, onboard the research vessel R/V "G.O.Sars". Continuous acoustic recordings of fish and plankton were made by a calibrated integration unit consisting of a 38 kHz Simrad EK500, connected to a Bergen Echo Integrator (BEI) for post-processing. A 95 kHz Simrad SA950 sonar was used to determine the spatial distribution of schools, and to track selected herring schools for periods of up to one hour. During tracking, behavioural events of schools were noted continuously by a reporter and also recorded on video for later analysis. Behaviours were classified in three categories; predator, intra- and inter-school events. Pitcher et al. (1996) provide detailed descriptions of the interpreted events in each category.

All recording of schools was conducted within a range of 50-300 m either side of the vessel and output to computer file and colour coded paper echogram. Accurate vessel position was obtained from a differential global positioning system. Migration speed, depth and direction of schools recorded by sonar was calculated with specific software on a HP 9000 workstation

connected to the sonar system. Appendix 1 provides technical details on acoustic settings. Fish schools of all species recorded by echosounder were identified using the BEI system which filters echo data on the basis of strength of signal and amount of contiguous pings with such a signal. From the filtered data, those schools deemed to be herring were determined on the basis of the proportion of different species caught at trawl stations, target strength distribution, and fish behaviour. For sonar data, 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.

Pelagic trawl samples (Akra-trawl) were taken to identify fish species. 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). Sub-samples 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 1).

During the cruise, a new protocol was devised for conducting small meso-scale surveys of school distribution. Immediately after an individual school was tracked, the vessel surveyed the surrounding area by running a cruise track of increasing concentric rings. The radius of the outermost ring was approximately 1.2 km. Although it is possible to use way points plotted on the automatic navigation system to aid control of the cruise track, we consider in hindsight that it is more convenient to run straight cruise tracks creating squares of increasing width (Figure 1). Three meso-scale surveys were completed, but due to poor weather conditions for sonar operation the mapping was unsuccessful. Description here serves to outline the new protocol.

Figure 1 near here

## 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 south western area (IMR cruise report 1997). Within all samples, herring were recovering from spawning (mean gonad score: 7.8, spent to recovering), actively feeding (mean gut fullness index: 3.3, medium to full) and with a low fat content (mean fat index: 1.2, non to little). Most schools were migrating in a westerly direction with average migration speeds of between 0.05-1.8 m/s (equivalent: 0.16 to 5.6 body lengths/sec for a 32 cm herring).

### Large meso-scale observations

#### *School structure characteristics*

A total of 285 herring schools were recorded by echosounder (Figure 2), 52 percent 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 2 near here

Using the area back-scattering strength ( $S_A$  -value) as a proxy for relative school size, individual schools were grouped into relative size categories (Figure 3). Very small, small and medium sized school were most numerous (83%) but only accounted for approximately one third of the total relative size.

Figure 3 near here

Of those school recorded by sonar, most were between 50 and 200 m<sup>2</sup> with a low relative density of approximately 500 colour sum units (Figure 4 and 5). Colour sum units is an expression of the relative echo intensity (Misund et al. 1997), and is directly related to the relative density of a school (Misund pers. comm). Using an approximate conversion to calculate fish biomass based on school area recorded by sonar (Misund 1996), the average school size was estimated to be 1969 kg, approximately 2 metric tons.

Figure 4 near here

Figure 5 near here

*Spatial distribution pattern*

Nearest neighbour distance (NND) distributions suggest two spatial scales of clustering; i) Echosounder data indicates a high occurrence of schools within 0.8-2.5 km of each other (Figure 6a), ii) Sonar data shows a high number of schools with NND between 0.05-0.3 km (Figure 6b). 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 8-35km 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 7 linkage of schools by nearest neighbour reveals most clustering occurs on a scale of 1 to 2 km.

Figure 7 near here

The ratio of mean nearest neighbour distance to the mean average inter-school distance (mean ISD; where ISD = average 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 = *meanNND* : *meanISD*

where, 
$$meanNND = \frac{\sum_1^n NND}{n} \quad \text{and} \quad meanISD = \frac{\sum_1^n ISD}{n}$$

and *n* = number of schools

Alone, each statistic tells us small pieces of information. The mean ISD tells us about the scale of observation; the area over which schools are distributed together with an indication of the survey extent and the equipment used. Mean NND tells us how close schools in a cluster are. But together as a ratio, the mean NND: mean ISD provides us with a more powerful 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 (Figure 8).

If we reduce the ratio to the coefficient;

$$\text{Cluster coefficient} = \frac{\text{meanNND}}{\text{meanISD}}$$

we lose the information on scale but still retain an impression of what the overall pattern and degree of clustering is like. Cluster coefficient values can range from 0 to 1 but are likely to be the lower end of this scale, since it is rare that mean ISD distance would be close or equal mean NND. A low CC value (mean NND low and mean ISD high) would suggest that individual schools in close proximity are tightly clustered whilst those clusters are dispersed (Box 1, Figure 8). A CC close to 1 suggests many schools are diffuse, not forming strong clusters (Box 9, Figure 8).

Figure 8 near here

The distribution of NND/ISD 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 (Figure 6) 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, Figure 8). Furthermore, comparison of the sonar and echosounder mean NND, mean ISD and cluster coefficient values confirms that despite differences in detection capabilities of sonar and echosounder, there is similarity in the pattern of school clustering across scales (Table 1).

Figure 9 near here

Table 1 near here

### *Spatial distribution by size*

Both frequency of occurrence with, and average distance to other surrounding schools were found to be different for different size of schools. Firstly, for certain school sizes there was significant difference in frequencies of occurrence with neighbour schools of a particular size ( $\chi^2=41.37$ ,  $df=16$ ,  $p<0.001$ , Table 2). In particular, small schools had other small and very small schools as nearest neighbour more often than expected, whilst medium and large schools were neighbours less often than expected. Large and medium schools occurred as neighbours more than two times more frequently than expected (although note that the total frequency was low). Secondly, average distance between schools increased with school size, small schools being closer to other schools than large schools were ( $\chi^2=11.82$ ,  $df=4$ ,  $p<0.02$ ) i.e. small schools were more tightly clustered than large ones (Figure 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 ( $\chi^2=60.7$ ,  $df=48$ ,  $p>0.11$ ).

Table 2 near here

Figure 10 near here

#### *Diurnal temporal variation in pattern and distribution*

An attempt was made to see if there was any difference in clustering pattern of schools between day and night. To remove differences due to spatial variation we focused the analysis on small data periods in which schools were continuously recorded and where there were approximately the same number of schools recorded during day and night. Schools were found to be significantly more tightly clustered during the night than day (Table 3), and as schools became more clustered at night, the extent or range of these clusters (indicated by mean ISD) declined significantly also (Table 3). The implication of the result that the cluster coefficient is no different between day and night for the echosounder, whilst it is more than double for the sonar, is that changes in the pattern of clustering was only observed on the finer scale. At this scale, schools are closer together at night, whilst distribution of clusters is more diffuse than in the day.

Table 3 near here

Within individual 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 (Figure 11a). Both echosounder and sonar data showed depth of schools was significantly deeper during the day than night; i) Echosounder: (One tailed t-test,  $t=15.13$ ,  $df=260$ ,  $p<0.0001$ ; Figure 11b), ii) Sonar: many more schools were detected during the night (78%) and were significantly shallower than daytime schools (One tailed t-test,  $t=15.6$ ,  $df=147$ ,  $p<0.0001$ , Figure 12). Although not 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 of schools (mean area =  $107 \text{ m}^2$ , both night and day), or the relative size (Sa Value). Daytime schools were also found across a greater depth ranges.

Figure 11 near here

Figure 12 near here

### **Small meso-scale observations**

#### *Behavioural dynamics*

One hundred and four behavioural events were recorded from 31 herring schools tracked for an average of 40 min each, giving a total of 20 hours and 41 minutes total observation time. Some kind of change in school behaviour occurred every 11.9 min. ( $n=104$ , 95% CL:0-26). Behavioural events were classified in to three categories. *Inter-school* (between schools) events include approach, join, leave, split and occurred every 29 min ( $n=50$ ; 95% CL:5-54). *Intra-school* (within a school) events include shape and depth changes and occurred every 25 min ( $n=50$ ; 95% CL:0-52). *Predator events* (interactions interpreted as resulting from predators) occurred at night every 61 min ( $n=12$ ; 95% CL:63-143). We infer from sonar observations that attack from marine mammal predators occurred every 180 min ( $n=4$ ; 95% CL:90-270), while attacks from predatory fish were observed every 361 min ( $n=2$ ; 95% CL:241-481). The distribution of total events per hour (event rate) provides a guide for classifying the overall dynamics of the schools observed. This index, 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 (Figure 13). This point is born out in greater detail in Figure 14 b-d that 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. No predator events were recorded during the day. 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 the Polar front region mainly between  $65^{\circ}30' - 67^{\circ}30' \text{ N}$ ,  $003^{\circ}30' \text{ W} - 002^{\circ} \text{ E}$ . At the Polar front, warm Atlantic water rising northwards meets with cool polar water travelling south. The front is characterised by a sharp decline in temperature together with high concentrations of zooplankton. We presume the Polar front offers profitable foraging on zooplankton for actively feeding herring that are highly motivated by hunger following the non-feeding periods of overwintering and spawning (Slotte 1996, Nøttestad et al. 1996, Fernö et al. 1998). For similar reasons, potential predators of herring, including fish, birds (IMR cruise report 1997) and marine mammals (Christensen et al. 1992, Haug et al. 1995, Similä et al. 1996) are also abundant at the front.

Within the region, two levels of meso-scale distribution were observed, one at 0.05 to 0.3 km recorded by sonar and another at 0.8 to 2.5 km recorded by echosounder. Despite differences in detection capabilities (Misund et al. 1996, Misund 1997), pattern of distribution was similar between scales, as revealed by comparison of mean inter-school distance and mean nearest neighbour distance. Both scales indicated a patchy distribution of intensely clustered schools. The cluster ratio, mean NND:mean ISD is a relative measure of the intensity and pattern of clustering. By identifying and characterising changes in the dispersion pattern of schools, it offers a descriptive index to make comparisons between surveys conducted in different places and at different times.

Within clusters, the majority of schools (83%) recorded by echosounder were categorised as very small to medium size, and most of those recorded by sonar were between 50 to 200  $\text{m}^2$  (mean 107  $\text{m}^2$ ) with an equivalent biomass estimated at 0.9 to 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 1-20m and average height 2-7m, with the largest rarely extending >50m. Average school size for herring during overwintering and pre-spawning life history stages is generally much larger (Winters 1977, McCarter et al. 1994, Wood 1930, Nøttestad et al. 1996, Mackinson unpublished data).

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. 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 (Keenlyside 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 benefiting from foraging benefits associated with smaller schools (Pitcher and Parrish 1993). Indeed, our small meso-scale behavioural observations support the contention that dynamic adjustments among schools may aid transfer of information with respect to their surroundings. Inter-school events, the most frequent of which was joining and splitting, occurred on average every 29 mins. As previously observed (Pitcher et al. 1996), changes in shape and density of individual schools occurred more frequently than behavioural events among schools. Our observations of predator events are very limited, so despite evidence that risk of predation has been shown to be sufficient to cause significant changes in packing density within herring schools (Magurran 1990, Pitcher and Parrish 1993, Pitcher et al. 1996), we interpret the recorded variability as resulting primarily from the dynamics of a moving mass (Misund 1993).

The few recorded large schools occurred as neighbours more frequently than expected yet were more isolated with respect to other schools. Distance to nearest 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. 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 activity. 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 1980, 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 0.6-0.7 kg per m<sup>3</sup> (equivalent to approximately 2 fish per m<sup>3</sup> for 30 cm herring) in foraging Atlantic herring. Comparison of distribution of NND and ISD for individual schools indicate that on both scales, 0.05 to 0.3 km and 0.8 to 2.5 km, schools are more tightly clustered, 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 more patchy. 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 most likely account for the observed dynamics. Moreover, the observations support our hypothesis that the dynamics reflect individual behavioural decisions.

From our interpretations of school tracking we infer that no predator events occurred during the day, but occurred on average every 61 min at night. During this time, predators which rely on vision to detect and capture their prey may not present such a risk to herring when compared to marine mammals using sonar to detect their prey, and are known to be abundant at the Polar front (Pitcher et al. *in prep*). Behavioural studies on the Norwegian shelf region in May

1994 show predation pressure to be a powerful driving force giving rise to high dynamics within and between schools (some kind of events occurring every 5.5 min, Pitcher et al. 1996).

Given the significant energetic costs of performing diurnal vertical migrations, the adaptive benefit should necessarily exceed these costs. Several studies point to multiple causality with trade-offs occurring among factors including feeding, temperature optimisation 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 Sogard 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. Recognising 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. However it is important for us to understand the system description changes among scales. The use of fractals (Sugihara and May 1990) in our studies may take us in this direction in the future. At some scales, responses of herring occur to a narrow range of stimuli (e.g. predator attacks) and 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 our observations of predator events were limited, 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 May.

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## Appendix 1 – Acoustic settings

### 1. Echosounder

Range of 0-500 m  
 Max 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  
 3dB beamwidth: 7.0 dB  
 The  $S_A$  recordings per nautical mile were averaged over a five nautical miles distance. Echo sounder recordings were presented in echograms.

### 2. Sonar

TX power: max  
 Range: 300 m  
 Pulse: FM auto  
 Gain: 9  
 Display gain: 9  
 Time Varied Gain: 30 log R  
 AGC: weak  
 Normalization: weak  
 Ping-ton-ping filter: weak.

### 3. HP 9000 workstation school detection system

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

### 4. 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	

### Appendix 3 – School tracking

#### School 6 10:4:97

Video:2.36.35-3.44.04

Start 01:24. 2 distinct schools, depth 153m Range 130m. Several small dense targets visible close to the school. Area 800-900m<sup>2</sup>. Other small schools in close vicinity

01:28 A school joins. School structure seems to be looser now. Larger area but lower density. School fragmenting whereas nearby school seems to be increasing. Pseudopodium visible. Joining. First school now dispersed. New school very elongated. School heading north



01:34 A different school appears on the echosounder

01:38 Depth 163m. School fragmenting? Maybe change in direction is causing poor aspect angle for visibility

01:41 Found again, 167m deep

01:43 Fairly circular. Dense, 15m deep. This is a different school

01:53 Turning vessel to improve the aspect angle. Now have a better view of the school

01:56 Back to the larger elongated school. It is about 50m from the other. Depth 167m

01:59 School joined from below. Original school becoming more elongated. Depth range 115-185m

02:04 2 schools appear on top right of the screen. Now there are three schools close together. Top 2 found to be connected.

02:16 Appeared to fragment - changed boat direction and school appeared clearly again

02:29 End. Travelled 500m in 1 hr = 0.14 m/s

## TABLES

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.

<i>Observed frequencies</i>					
	V.small	Small	Medium	Large	V.Large
V.small	7				
Small	43	40			
Medium	25	53	39		
Large	9	10	37	12	
V.Large	1	0	5	3	0

<i>Expected frequencies</i>					
	V.small	Small	Medium	Large	V.Large
V.small	7				
Small	30	30			
Medium	32	65	35		
Large	13	27	29	6	
V.Large	2	3	3	1	0.1

Table 3. Differences in diurnal distribution pattern. Standard errors are given in brackets. Note: <sup>a</sup> one tailed t-test with unequal variances; <sup>b</sup> one tailed t-tests with equal variances

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

**FIGURES**

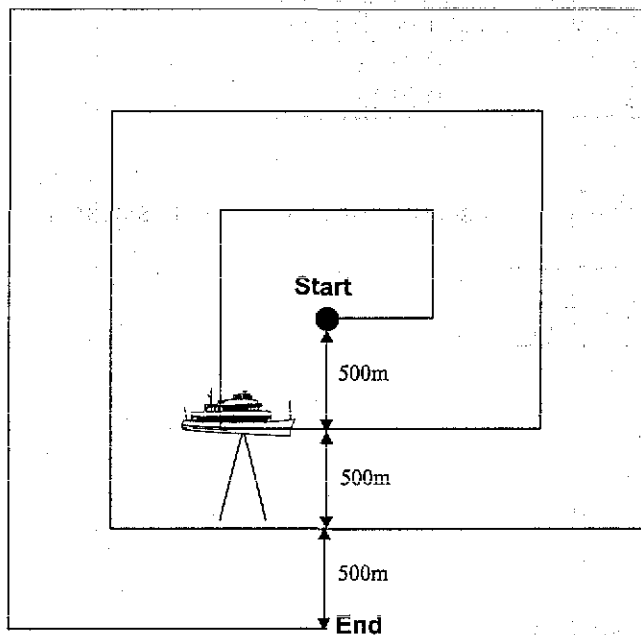


Figure 1. Meso-scale mapping of herring schools

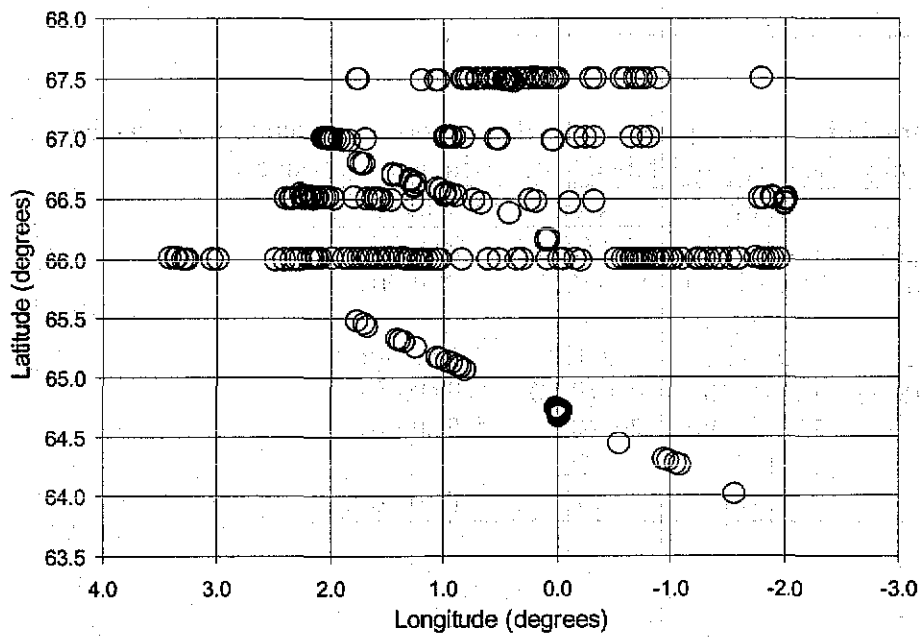


Figure 2. Distribution of herring schools in the Norwegian Sea recorded by EK500 echosounder (8/4/97-18/4/97)



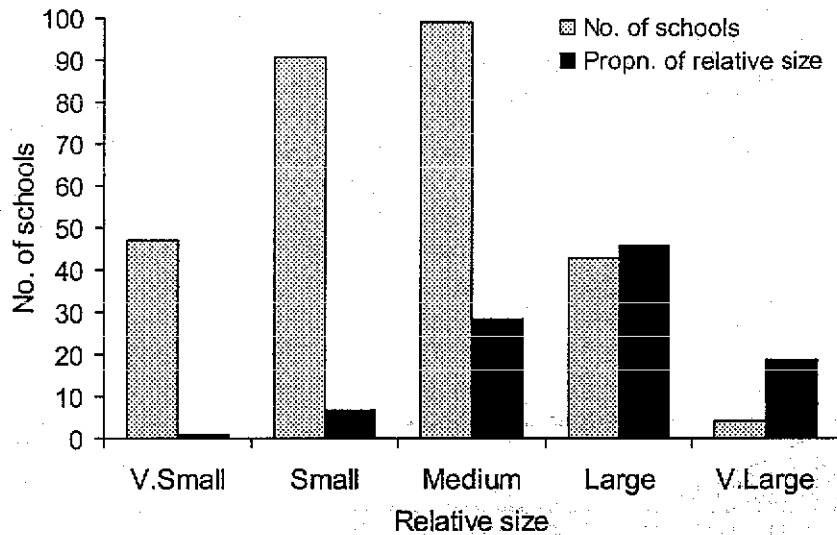


Figure 3. Size class frequencies and proportion contribution to total relative size (Sa value) of echosounder recorded schools. Relative size classes based on area back-scattering coefficient (Sa value): Very small <50, Small 50-250, Medium 251-1000, Large 1001-5000, Very Large >5000.

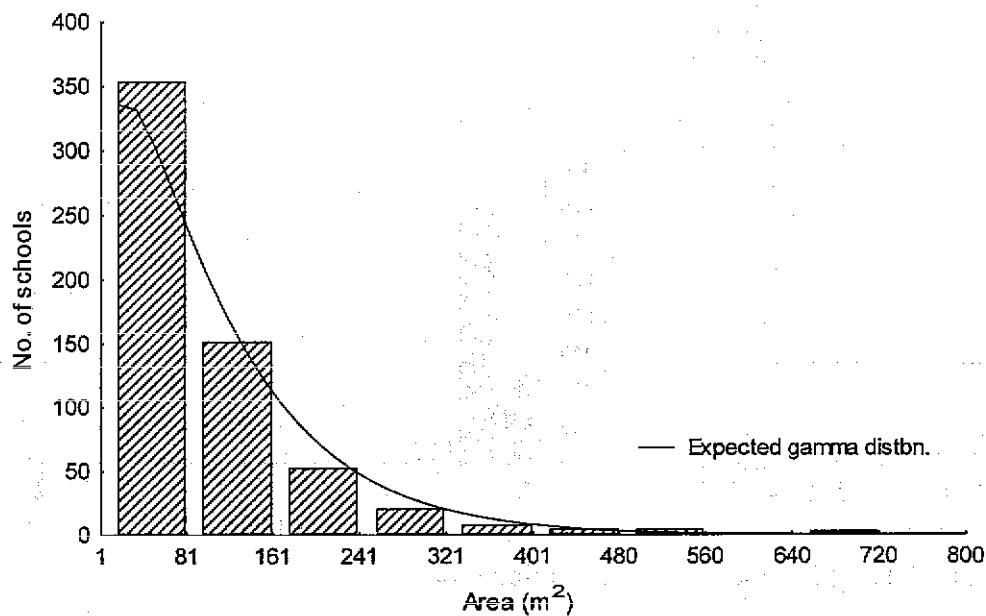


Figure 4. Frequency distribution of school area. A gamma distribution (scale parameter: 83, shape parameter: 1.28) is fitted to the data, although the observed data are significantly different from that expected ( $\chi^2=32.55$ ,  $df = 3$  (adjusted),  $p < 0.0001$ ).

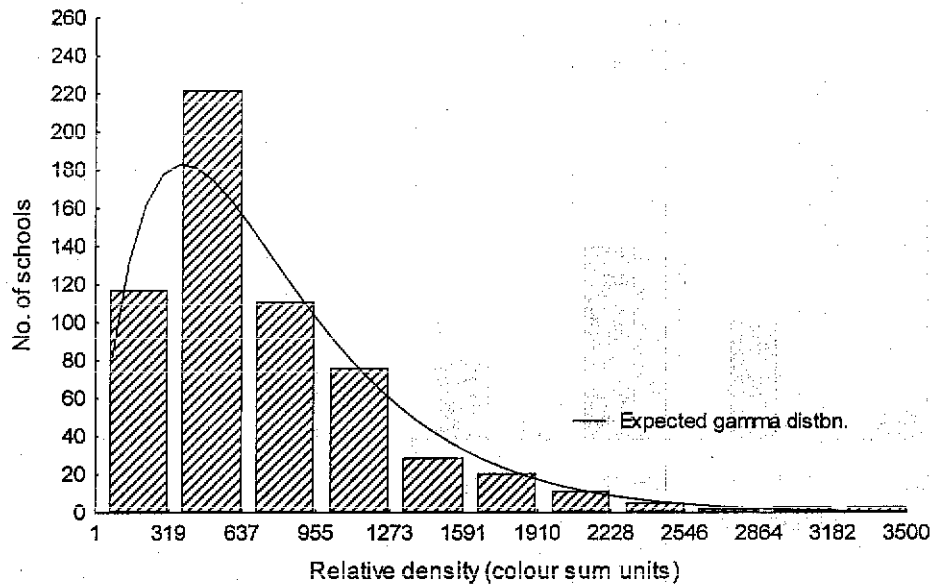


Figure 5. Frequency distribution of school relative density. Relative density scale runs from high on right hand side to low on left hand side. A gamma distribution (scale parameter: 389, shape parameter: 1.97) is fitted to the data, although the observed data are significantly different from that expected ( $\chi^2=30.77$ ,  $df = 6$  (adjusted),  $p = <0.0001$ ).

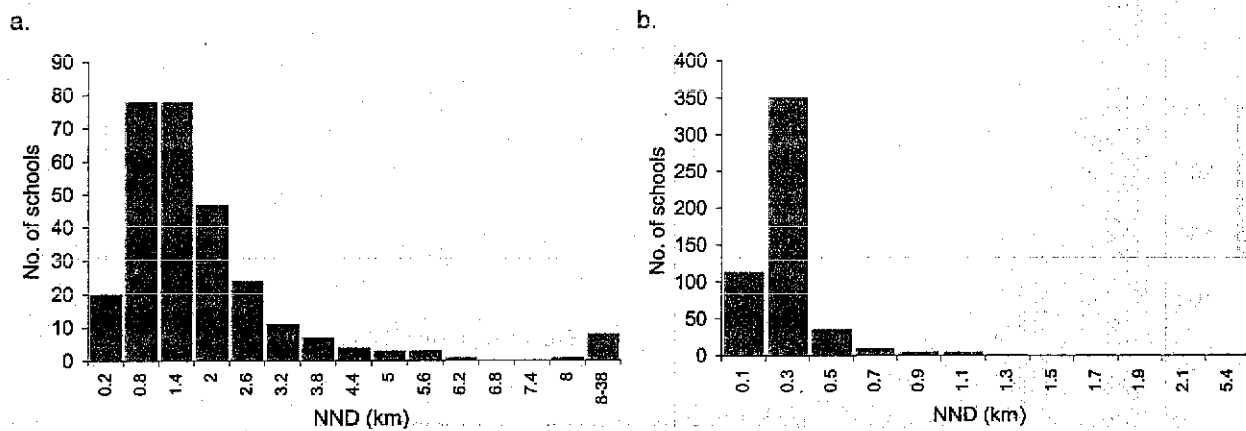


Figure 6. Distribution of NND. a) Echosounder data; b) Sonar data

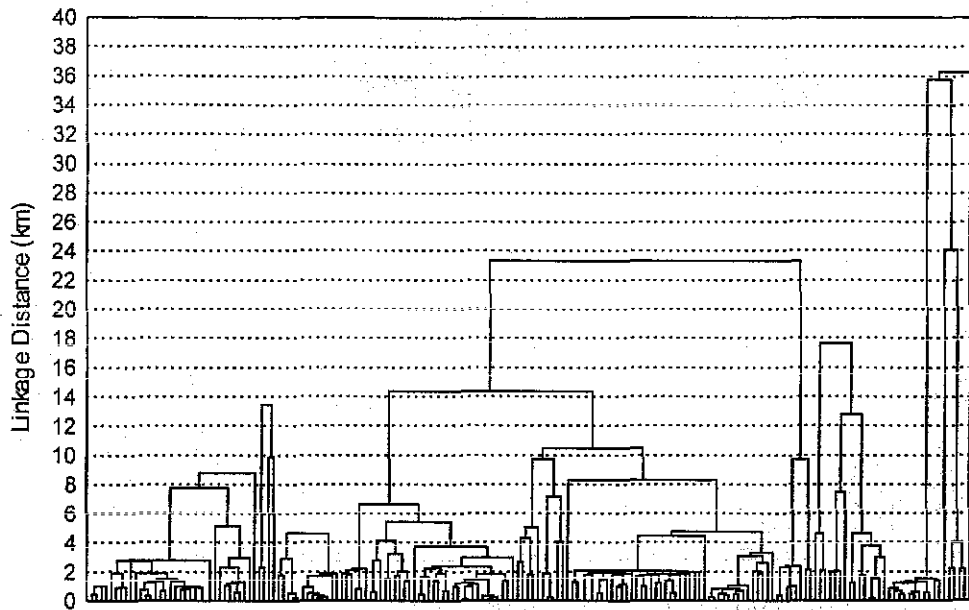


Figure 7. Cluster analysis tree, derived matrix of inter-school distance linked using single linkage (nearest neighbour) basis.

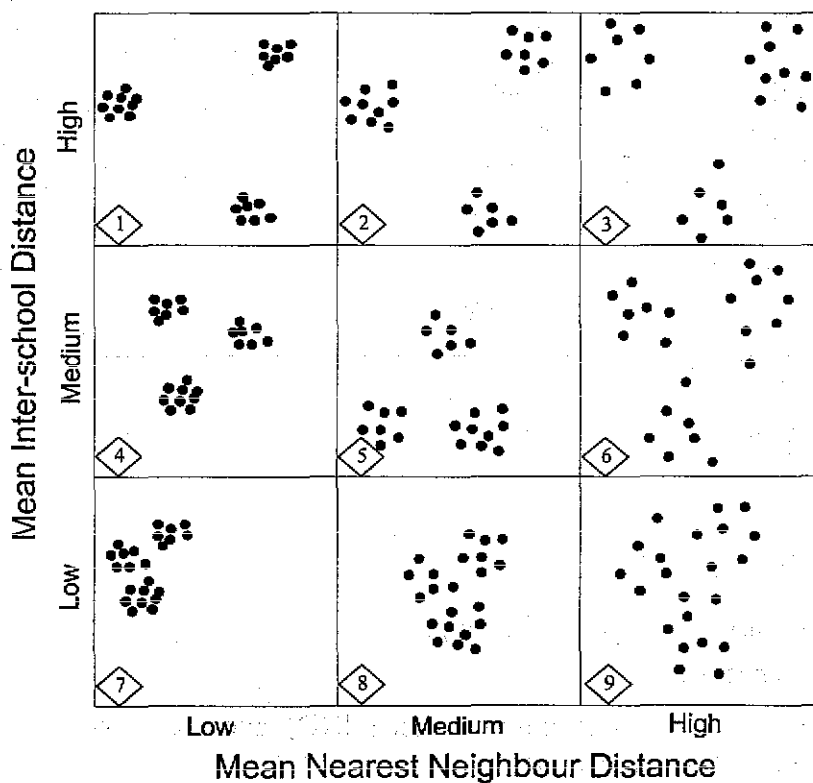


Figure 8. Patterns of school clustering indicated by relationships between mean NND and mean ISD

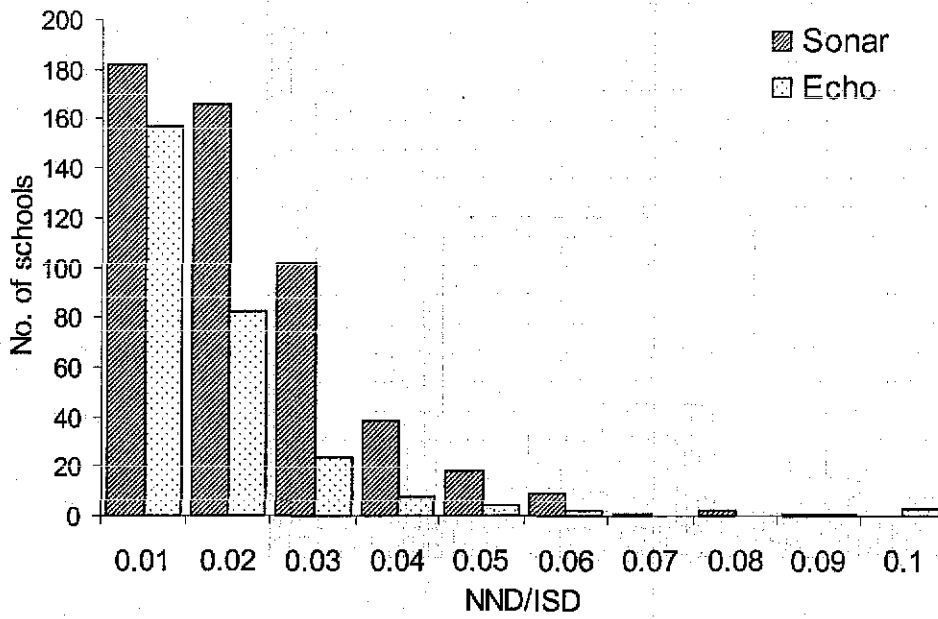


Figure 9. Distribution of cluster coefficient values

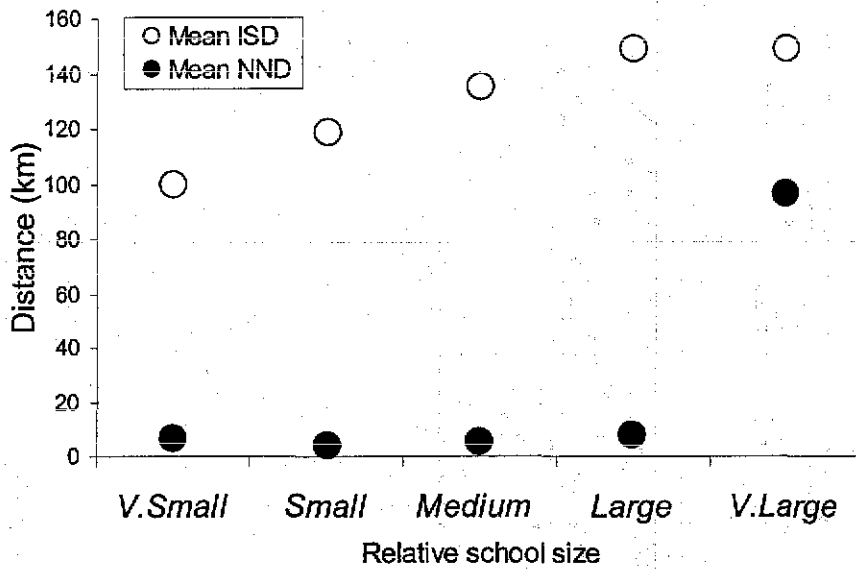
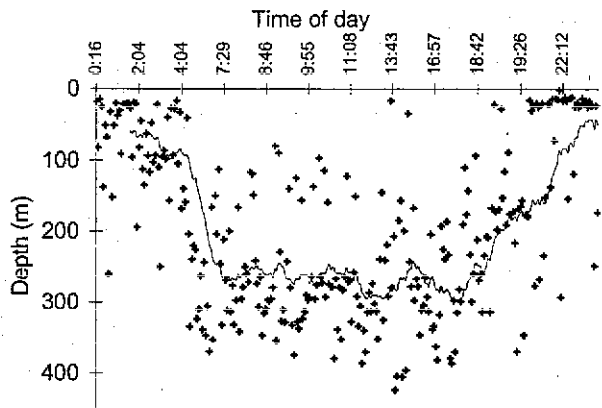


Figure 10. Relationships between average nearest neighbour distance (NND), average inter-school distance (ISD) and school size for echosounder data.

a.



b.

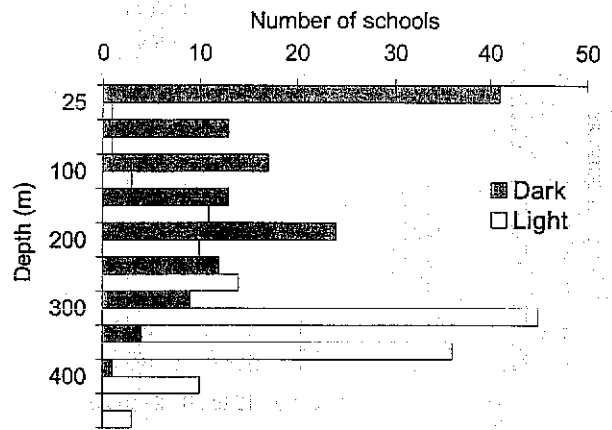


Figure 11. Diurnal changes in vertical distribution recorded by echosounder. a) depth distribution with running average line plotted on figure, b) number of shoals recorded at each depth

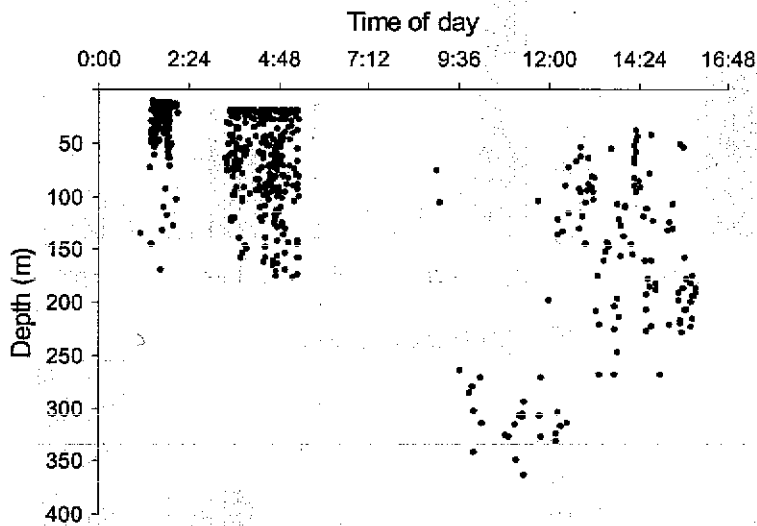


Figure 12. Diurnal depth of distribution of sonar recorded schools. Note: the four distinct groups relate to four separate data log periods.

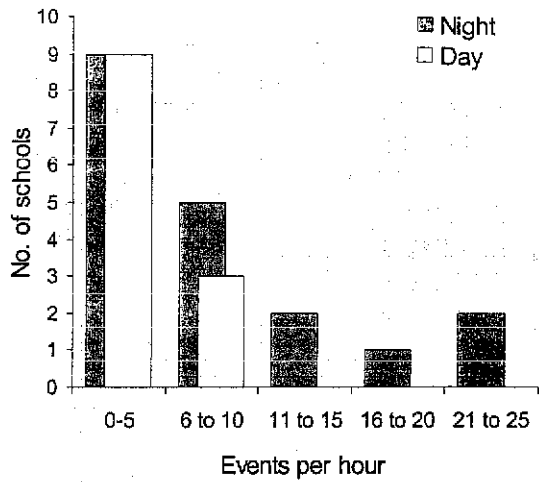


Figure 13. Distribution of behaviour events

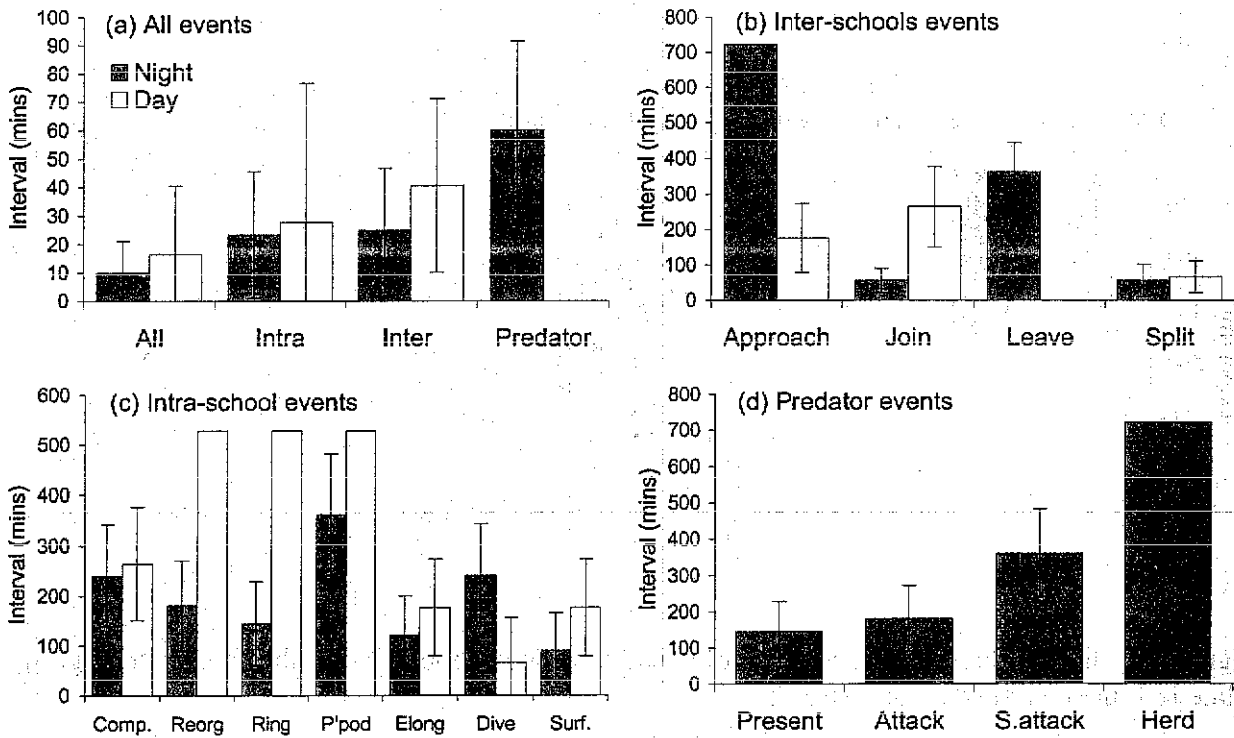


Figure 14. Behavioural event intervals of tracked schools. No error bars are displayed for events recorded less than twice.