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# Evidence for a clustered spatial distribution of clupeid fish schools in the Norwegian Sea and off the coast of southwest Africa

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To quantify and characterize the spatial distribution of clupeid fish schools, sonar data were collected during surveys off the coast of Namibia in 1994 (pilchard (*Sardinops sagax*), anchovy (*Engraulis capensis*), and round herring (*Etrumeus whiteheadi*)), off Angola in 1995 (sardinella (*Sardinella* sp.)) and in the Norwegian Sea in 1997 and 1998 (Norwegian spring-spawning herring (*Clupea harengus* L.)). The two-dimensional distances between clupeid schools were calculated in the order that the different schools were observed along the survey vessels transect lines. In all four surveys, two different modes (frequency distribution maximums) were observed. The first mode, representing the most usual interschool distance, was about 60 m. The second mode, around 1600 m, probably represented the distances between different clusters. The distances between clupeid schools and between different clusters were found to be about the same for separate pelagic clupeid species, locations, and years of observation. The mean diameters of the school clusters were estimated to vary between 450 and 1450 m.

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# Introduction

To understand fish schooling, there has been much focus on quantifying the internal structure and function of fish schools (Cullen *et al.*, 1965; Pitcher, 1973; Shaw, 1978; Burgess and Shaw, 1979; Partridge, 1982). During the past decade, the perspective has changed to include studies of large-scale spatial distribution of schools (Swartzman, 1997; Fernø *et al.*, 1998; Mackinson *et al.*, 1999; Mason and Brandt, 1999). Reid *et al.* (2000) and Petitgas (2003) both introduced standard, but different, procedures/analysing protocols for fish school characteristics and spatial distribution that may compute reproducible results from different echosounder surveys. By meta-analysis of different acoustic surveys on a number of pelagic stocks, Petitgas *et al.* (2001) considered how stock abundance influences the spatial distribution of schools.

Schools in nature are seldom observed one by one. Usually they occur in larger groups or clusters of several schools (Mackinson *et al.*, 1999; Petitgas *et al.*, 2001; Petitgas, 2003), but our knowledge of the relation between schools and clusters of schools is still relatively scarce. School aggregation pattern is a key factor during abundance estimation surveys and also influences fish catchability (Parrish, 1999; Coetzee *et al.*, 2001). In this paper we use a meta-analytic approach to examine the distribution of fish schools and school clusters of five pelagic clupeid schooling species in three different habitats and between different years of observation. On the basis of sonar recordings, we quantified the horizontal distance between pelagic schools in a cluster and between different clusters; we also estimated the diameter of school clusters.

# Material and methods

We analyse sonar recordings from four surveys carried out on clupeid pelagic schooling species in the northern and southern Atlantic. RV "G. O. Sars" recorded Norwegian spring-spawning herring (Clupea harengus L.) in the Norwegian Sea in May 1997 and in May 1998, and RV "Dr. Fridtjof Nansen" recorded pilchard (Sardinops sagax), anchovy (Engraulis capensis), and round herring (Etrumeus whiteheadi) off Namibia in November/December 1994 and sardinella (Sardinella sp.) off Angola in April 1995. The recordings on both vessels were made using a 95-kHz high-resolution SIMRAD SA950 horizontally guided narrow beam sector scanning sonar (see Haugland and Misund, in press). The sonar recordings were postprocessed by applications developed in SAS (SAS, 1988). The standard range for recordings was set from 50 to 300 m to the side of the vessel. An elementary sampling distance unit (ESDU) of 5 nautical miles (1 nautical mile = 1852 m) was used to compare mean school number in the different surveys. The total useable length of the surveys varied from 195 ESDUs in the Norwegian Sea in 1997 to 611 ESDUs off Namibia in 1994.

The horizontal areas of the fish schools and their density (Csum, integrated measure for echo energy) as well as their geographical coordinates were recorded automatically (Misund et al., 1994). The two-dimensional distance between the school centres (interschool distance, ISD) was calculated in the order in which the schools were detected along the survey vessel's transect lines (Figure 1). By studying the frequency distributions of ISD from the different surveys, spatial patterns such as the distance between schools included in clusters and distance between clusters will be revealed (Figure 2). A cluster was defined as a group of more than two schools closer than would be expected from an even distribution in the entire survey area. The intercluster distance (ICD) was defined as the distance between the centres of the outermost schools of two neighbouring clusters, so avoiding the effect of the cluster diameter. Because of the sonar recording range, the ICD would be measured parallel to the ship track inside the recording range. The ICD was estimated from the mode in the second high-frequency interval, by expanding this part of the histogram. On one occasion the mode was not obvious and a weighted mean was used to avoid subjectivity. The mode in the expanded part of the first high-frequency interval was interpreted as the most frequent distance between schools inside a cluster. A factorial analysis of variance model was used to test for statistical differences between the different surveys and high and low-frequency intervals. Differences in school characteristics between the Norwegian Sea and the southwest coast of Africa were tested for using ANOVA. All characteristics are reported as means  $\pm 1$  standard deviation (s.d.).

An estimation of the mean number of schools (R) in a cluster was calculated by the ratio of the percent of interschool distances regarded to be included in clusters (ISD  $\leq$  450 m) divided by the percent of interschool distances representing different clusters (1450 < ISD < 2050 m) (see Table 1).

$$R = \frac{\%(\le 450 \text{ m})}{\%(1450 - 2050 \text{ m})} \tag{1}$$

The sonar recorded horizontal school area automatically and the mean school area ( $\overline{A}$ ) was calculated from schools within clusters (ISD  $\leq 450$  m). The mean school diameter ( $\overline{D}$ ) was then estimated from the mean school area ( $\overline{A}$ ) by the equation:

$$\overline{\mathbf{D}} = 2\mathbf{r} = 2\sqrt{\frac{\overline{\mathbf{A}}}{\pi}} \tag{2}$$

The mean cluster diameter ( $\overline{CD}$ ) for the surveys with a mean of more than two schools (R > 2) in the clusters

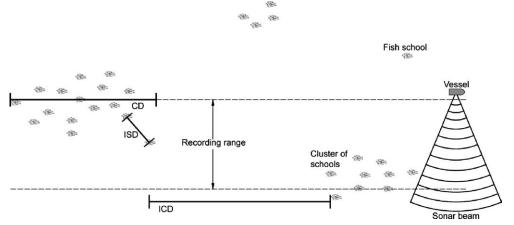


Figure 1. Conceptual model of spatial distribution of schools and cluster of schools. ISD (interschool distance) is the distance between the centres of two neighbour schools; ICD (intercluster distance) is the distance between the centres of the two outermost schools of two neighbour clusters and CD is the cluster diameter.

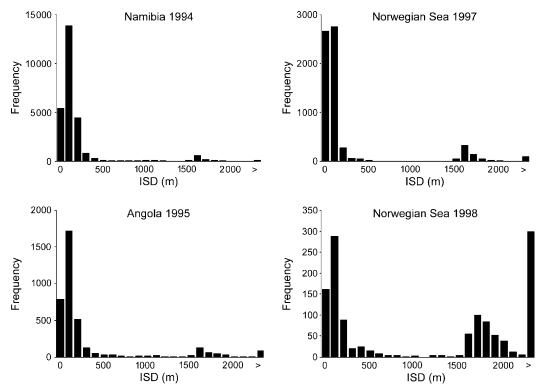


Figure 2. The frequency of interschool distances calculated for the four surveys. ">" indicates all observations above 2250 m.

was estimated based on information of the mean number of schools in a cluster and the average interschool distance:

$$\overline{\text{CD}} = R\overline{\text{D}} + (R-1)\text{ISD}(m) \tag{3}$$

where the ISD(m) refers to the first mode of the interschool distance distribution.

#### Results

The mean number of recorded schools per ESDU varied from five in the Norwegian Sea 98 to 45 in Namibia 94 (p < 0.10, ANOVA). The school areas were larger for the two surveys off the coast of southwest Africa ( $144 \pm 258 \text{ m}^2$  in Namibia 94 and 116  $\pm$  203 m<sup>2</sup> in Angola 95) than for the two Norwegian Sea surveys (97  $\pm$  106 m<sup>2</sup> in Norwegian Sea 97 and 79  $\pm$  63 m<sup>2</sup> in Norwegian Sea 98; p < 0.10, ANOVA). School density (Csum), however, was nearly twice as large for the Norwegian Sea surveys (794  $\pm$  747 in Norwegian Sea 97 and 783  $\pm$  716 in Norwegian Sea 98) compared to the southwest African surveys (416  $\pm$  594 in Namibia 94 and 396  $\pm$  736 in Angola 95; p < 0.05, ANOVA). This indicates that the herring schools in the Norwegian Sea were generally smaller and denser than the clupeid schools off the coast of southwest Africa.

For surveys off Namibia in 1994, Angola in 1995, and in the Norwegian Sea in 1997 between 85.0% and 91.6% of the ISDs were 450 m or less, while in the Norwegian Sea in

Table 1. Estimated cluster diameter (CD) for the four surveys. See Material and methods for further explanation.

		% of obs. distances							
		No. of schools	ISD*: ≤450 m	ISD**: 1450—2050 m	Ratio (R): ISD* (ISD**) <sup>-1</sup>	Area $(m^2) \pm s.d.$ ISD $\leq 450 m$		Mode of ISD: 1450–2050 m	
Namibia	1994	27 27 1	91.6	4.5	20.4	$149 \pm 266$	60	1 580	1 4 50
Angola	1995	3 767	85.0	10.4	8.2	$122 \pm 212$	60	1 580	530
Norwegian Sea	1997	6612	88.2	9.3	9.5	$97 \pm 105$	40	1 580	450
Norwegian Sea	1998	1 2 5 4	46.6	25.5	1.8	$81 \pm 64$	60	1 700	_

1091

1998 only 46.6% of the ISDs were at 450 m or below. These first high-frequency intervals had modes at about 60 m off Namibia in 1994, Angola in 1995, and in the Norwegian Sea in 1998, while in the Norwegian Sea in 1997 the mode was about 40 m (Figure 2, Table 1). The frequency of ISDs between 450 m and 1450 m was scarce (Figure 2), ranging from 0.7% to 4.2% of the total frequencies. A second highfrequency interval was observed between 1450 m and 2050 m, which was interpreted as distances between clusters. In the different surveys, between 4.5% and 25.5% of the total number of observations were found in this interval. The highest value of 25.5% was found in the Norwegian Sea in 1998, indicating that the clusters were smaller than in the other surveys (Table 1, Figure 2). The modes were around 1580 m off Namibia and Angola and in the Norwegian Sea in 1997, while in the Norwegian Sea in 1998 the weighted mean was 1700 m. Weighted mean was used to avoid subjectivity because the number of observations was relatively low and the mode was not obvious. Fewer than 2.6% of the distances were above 2250 m for the surveys off Namibia, Angola, and in the Norwegian Sea in 1997. In the Norwegian Sea in 1998, 24.4% of the ISDs were above 2250 m. The higher percentage of distances above 2250 m in Norwegian Sea 1998 indicates that schools were more widely dispersed compared with the other surveys, and these data showed two additional high-frequency intervals, one around 3200-4000 m and the other around 5200-6000 m. Summing up the ISD results from all four surveys, most observations added up to two major high-frequency intervals with modes around 60 m and 1600 m, separated by a low-frequency interval with few observations and followed by a lowfrequency interval just above 2250 m (Figure 2, p < 0.05, factorial model). There was no significant interaction between the different surveys and the different highfrequency and low-frequency intervals (p > 0.05, factorial model), indicating that the frequency distribution between the different surveys was not significantly different. We interpret the first mode as representing the most frequent interschool distance (ISD) for schools included in clusters. The second frequency peak we interpret as representing a grouping on a larger scale, the intercluster distances.

The estimated cluster diameter varied from 450 m in Norwegian Sea 97 to 1450 m in Namibia 94 (Table 1). In Norwegian Sea 98, the cluster diameter was not calculated because of a small mean number of schools in the clusters.

# Discussion

The frequency distribution of interschool distances for all four surveys shows similar trends, with two prevailing modes around 60 m and 1600 m. This indicates that pelagic schooling clupeids may have a preferred spatial organization.

In Namibia, Angola, and in the Norwegian Sea in 1997, between 85.0% and 91.6% of the calculated interschool distances were 450 m or less, which shows that most schools were found fairly close together, in clusters. Considering all four surveys the total mode of interschool distances was 60 m. We suggest that the similarities in spatial distribution may be a function of clupeid aggregation and communication, representing a comparable strategy to comparable challenges. Clustering clupeid fish may maintain a kind of active or passive information transfer between the schools and the schools can join to form larger schools when attacked by predators (Hoare and Krause, 2003). Information may be transferred between schools in clusters through sound production (Fish and Mowbray, 1970; Schwarz, 1985) or by exchange of individuals (Vabø and Nøttestad, 1997). For instance, feeding herring schools are dynamic by nature and split and join on average every 60 min in coastal areas (Pitcher et al., 1996). Mackinson et al. (1999) observed a high frequency of interschool distances, recorded by the sonar, in the interval 50-300 m for herring in the Norwegian Sea that is comparable with the first mode in our study. The spatial pattern of herring schools was also studied by Maravelias and Haralabous (1995), who, using geostatistics, found spatial structures on three different scales: large-scale - 17 nmi (accounted for 22% of total variance), meso-scale -9 nm (30%), and an unresolved dissolution on a small scale - less than 2.5 nm (48%). The high percent of unresolved small-scale spatial distribution indicates the existence of a spatial structure below 2.5 nm. This unresolved small-scale distribution could possibly be attributed to cluster and intercluster structures. Swartzman (1997) suggested that there could also be an interaction between gadoids schools in clusters.

There was a second but lower mode around 1600 m. We interpret this as the distance between the outermost schools included in different clusters. Mackinson *et al.* (1999) found indices of clustering for herring on a scale of 500-2000 m from echosounder recordings, but did not observe the same from their sonar recordings. Gerlotto *et al.* (1999) analysed sonar recordings which indicated that schools were distributed in patches surrounded by large empty areas. The weaker mode around 1600 m is related to the fact that the sum of schools inside a cluster is much higher than the number of different clusters in the sample area. Still, the tendency for clustering is clear for all surveys.

We found a comparable aggregation pattern among the surveys, despite variations in the number of schools per unit distance (ranging from five schools per ESDU in the Norwegian Sea in 1998 to 45 per ESDU off Namibia). Petitgas *et al.* (2001) found that an increase in the number of schools per area was linked to an increase in the number of clusters, which resulted in clusters occupying a greater proportion of the survey area as well as a higher density of the schools within the clusters. Marchal and Petitgas (1993) found that the probability of encountering a school with large biomass seems to increase when abundance of the school increased, but they found no correlation between the biomass in each school against the number of schools per ESDU. Comparably, we found the largest clusters and

largest areas for schools within clusters when the number of schools per ESDU was high.

The estimated cluster sizes varied from 450 to 1450 m. Because most of the school recordings are not of schools along the cluster diameter and since solitary schools with large interschool distances are also included in the analysis, our estimates probably represent minimum cluster sizes. This would agree better with the results of Petitgas (2003), who found a cluster structure of a few kilometres using an echosounder. Swartzman (1997) suggested that the size of clusters and size and density of schools included in those clusters were not significantly affected by environmental factors. Petitgas et al. (2001) found no correlation between stock abundance and clustering of schools, but instead that high fish abundance was associated with schools containing a larger biomass. They suggest that stock size was not the primary driving factor for school aggregation, but that the aggregation could be driven by factors such as behaviour or the environment. Our study suggests that the observed distributional similarities could be a function of clupeid aggregation and communication behaviour possibly as solutions to comparable environmental challenges. Similarities in the statistical characteristics of school organization have also been observed in tropical areas (Marchal and Petitgas, 1993) and in the North Sea (MacLennan and MacKenzie, 1988).

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