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SCHOOLING BEHAVIOUR OF SARDINE *SARDINOPS SAGAX* IN FALSE BAY, SOUTH AFRICA

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The schooling behaviour of sardine *Sardinops sagax* in False Bay on the south coast of South Africa was studied in October 1995 using high-resolution sonar and a hull-mounted, echo-integration unit. School formation and disintegration were studied, and school shape, packing density, swimming behaviour and inter- and intra-school event rates were quantified. Mean fish density was 29.5 fish m^{-3} (*SD* 46 fish m^{-3}), but it varied between schools by a factor of about 100 (from 2 to 233 fish m^{-3}). Tracked schools moved at average speeds of 0.67–1.59 m s^{-3}. Schools changed shape on average every 2.08 minutes, and underwent either splits or merges with other schools on average every 5 minutes. Relationships between the geometric dimensions and biomass of the schools were established.

Key words: sardine, schooling behaviour, sonar, South Africa

The southern African sardine *Sardinops sagax* supports major purse-seine fisheries in South Africa, Namibia and Angola (Crawford *et al*. 1987). Fishing is conducted on both dense daytime schools and more dispersed night shoals, so that schooling behaviour may have an impact on the efficiency of purse-seine operations.

Sardine fisheries in southern African are managed mainly on the basis of acoustic surveys (Hampton 1992, Barange *et al.* 1999, Boyer *et al.* 2001). Abundance estimates from these surveys are highly sensitive to biases caused by fish behaviour, which may influence the acoustic detection of the fish (MacLennan and Simmonds 1992, Fréon and Misund 1999). For conventional echo-integration with hull-mounted transducers, both vessel avoidance (Olsen 1990) and near-surface schooling (Misund *et al*. 1996) may cause substantial underestimation of fish density. During the past two decades, growing attention has been paid to the study of school characteristics and school behaviour in relation to fishery management based on acoustic surveys in order to improve the precision of abundance estimates, survey design and species identification (e.g. Fréon *et al*. 1992, Haralabous and Georgakarakos 1996, Petitgas and Levenez 1996, Scalabrin *et al*. 1996, Bahri and Fréon 2000, Coetzee 2000, Reid *et al*. 2000, Lawson *et al*. 2001, Muiño *et al*. 2003).

The aim of this study was to map and quantify aspects of the schooling behaviour of sardine that are relevant to acoustic estimation of abundance. The study focuses on school formation and disintegration, school shape, packing density, relationships between geometric school dimensions and biomass, and swimming behaviour. The variations in school characteristics can be caused by environmental factors such as light level and currents, as well as by hunger, fear of predation or disturbance by vessels or fishing gears (Fréon and Misund 1999).

MATERIAL AND METHODS

Survey and equipment

The study was conducted in False Bay on the southwest coast of South Africa from 10 to 17 October 1995 on board the Norwegian research vessel R.V. *Dr Fridtjof Nansen*. During the first two days, the area was surveyed twice using sonar and conventional echo-integration; four pelagic trawls were done to identify acoustic targets (Misund and Coetzee 2000). During the following six days, the vessel conducted experimental studies, such as acoustic determination of

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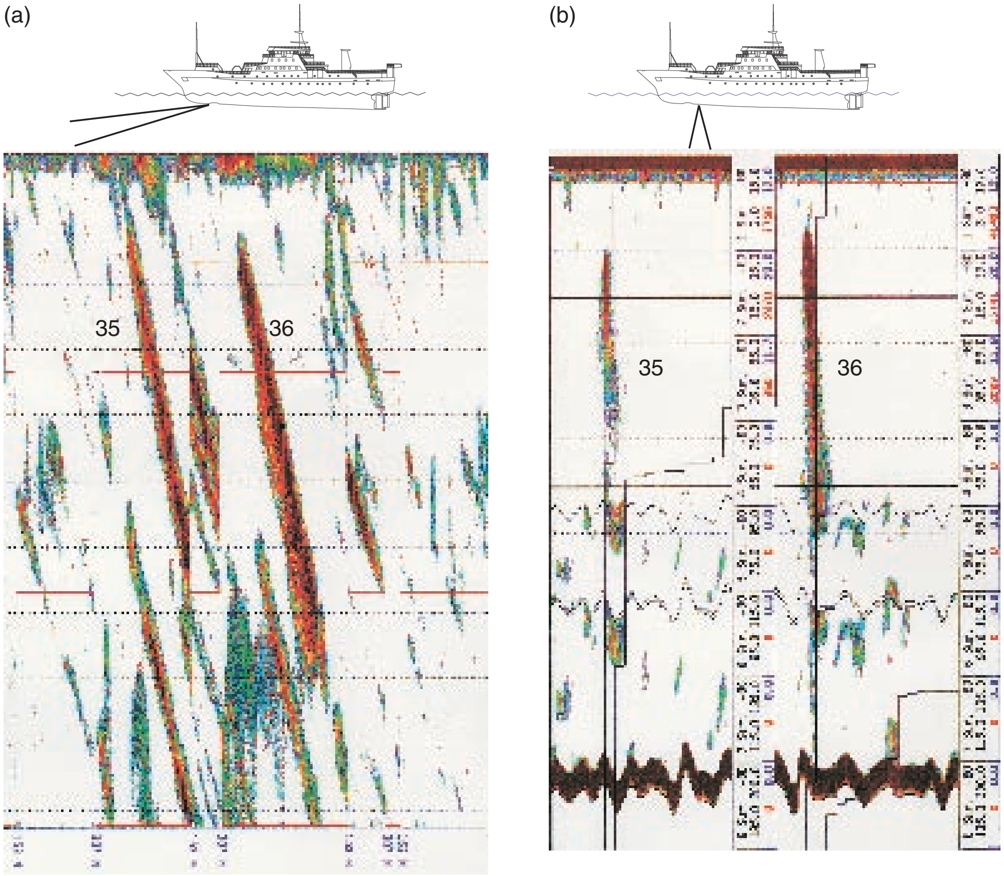

Fig. 1: Southern African sardine schools imaged by (a) the SIMRAD SA950 sonar and printed by the school detection programme and (b) the SIMRAD EK500 echo-sounder

school dimension, school-tracking, side-scan sonar imaging of schools, and horizontal and vertical avoidance experiments. Four additional trawl stations were conducted to identify the acoustic recordings.

Fish schools were recorded using a 95 kHz, high-resolution SIMRAD SA950 sector-scanning sonar covering a sector of 45° in the horizontal plane (Misund *et al*. 1995). A HP 720/9000 workstation with customized software for computer-based detection and area measurement of school recordings (Misund *et al.* 1994) was connected to the sonar. Only distinct, high-intensity, pelagic recordings were accepted as fish schools (Fig. 1). This categorization aimed to accommodate Pitcher's (1983) formal definition of a fish school, i.e. many fish in polarized, synchronized movements.

For conventional echo-integration, a 38 kHz SIMRAD EK500 system was used, and calibrated according to standard procedure (Foote *et al.* 1987). To improve the recordings in bad weather, the transducer is mounted on a protrudable keel, which can extend 2.5 m under the keel, to about 8.5 m below the surface (Ona 1994). For scrutinizing the echo recordings, the echo-integration system was connected to a Bergen Echo-Integrator post-processing system (Foote *et al.* 1991). The SIMRAD SA950 sonar was operated with the following settings: gain function at Step 9, noise-reduction filters at weak, and with frequency modulated transmission at FM-3. The school-detection programme of the HP workstation was run with the following settings: minimum of 25 m range vessel-to-school, maximum of 300 m range vessel-to-school, colour threshold of 15, minimum range interval of 8 m, minimum 10 m width of each school, minimum 5 m gap, ping-to-ping movement of school maximally 30 m, and a minimum of four detection counts for each school (Misund *et al*. 1994).

Fish were sampled using a four-panel, 320-m circumference pelagic trawl with 3.2-m stretched mesh in the front. The gear was rigged with 180 m sweeps and 7.8 m^2 (1 670 kg) Tyborøn trawl doors. When sampling shallower than about 25 m, two large floats were attached to the upper sweeps near the wings of the trawl.

Temperature, salinity and oxygen were measured at six CTD stations in the bay, and ADCP current profiles were recorded at the last three stations.

Sizing of schools

The primary task, from the point of view of estimating abundance from sonar data, was developing and assessing a relationship between school area and biomass. This was achieved by recording and measuring schools using the sonar system, and having the ship pass over them so that they were recorded by the EK500 echo-integration system (Fig. 1). During these measurements, ship's speed varied between about 2 and 3 m s^{-1} (4–6 knots).

The horizontal area of the schools was measured by the sonar system, ping by ping as the ship approached. The instrument operator noted the allocated school number on the sonar echogram, with the corresponding detection school number given by the school detection programme on the HP workstation (Fig. 1). This permitted specific identification of the respective schools in the data files produced by the school detection programme (Misund *et al*. 1994). During post-processing of the sonar data (using SAS software), the respective schools were identified by their detection school number. The maximum area measured by the school detection programme 50–200 m ahead of the ship was then determined and recorded for each school.

The allocated school number was also noted on the EK500 echogram. For each school, the s_A value, i.e. nautical area scattering coefficient (NASC, m^2 nm^{-2}), was estimated using the school window function of the BEI post-processing system (Foote *et al*. 1991), and its height and length were measured by means of a ruler on the echogram and scaled to real dimensions (Misund 1993). The density of the schools was calculated using the target strength (*TS*) equation: $TS = 20 \log$ total length $(TL) - 70.5$, measured for southern African sardine by Barange *et al.* (1996). The schools were assumed to be ellipsoid, and their volume was calculated by multiplying the maximum school area measured by the sonar by the height of the school recorded by the echo-sounder. The school biomass was then calculated by multiplying fish density, school volume and average fish weight.

School shape imaging

In addition to the SIMRAD SA950 sonar, an EG&G 260, 100 kHz side-scan sonar (horizontal beam width 1.2° vertical beam width 50°, inclination 20°) was used for accurate imaging of schools. The tow-fish was towed at a depth of about 5 m from the surface, initially slightly aft of the ship and later (16 October) just ahead of the ship's propeller. In the former, the port beam was transmitted through the wake, and in the latter underneath the hull. Towing speed was between 1.5 and 2.0 m s^{-1} (3–4 knots). Time-marked data from both channels were captured on tape for re-analysis. During all experiments, the SIMRAD SA950 sonar (trained either 90° to starboard or straight ahead) and the SIMRAD EK500 echo-sounder were operated simultaneously. Attempts were made to relate SIMRAD EK500 and side-scan recordings through time signatures on the echochart and the data-capture tape.

The side-scan sonar gave useful recordings to about 100 m, the port channel giving somewhat better recordings than the starboard channel. Recordings made from the water column were usually better than those from targets beyond the range of bottom depth, which varied between 30 and 70 m. The best, and most numerous recordings, were obtained on 16 October, a result of a combination of good weather, more-forward towing position, better performance of the starboard channel and abundance of suitable schools in the area.

School tracking

The swimming behaviour of fish schools was investigated by tracking 19 schools (presumed to be sardine) over a period of 4–74 minutes using the SIMRAD SA950. The school chosen for tracking appeared as quite large, red spots on the sonar screen. Speed was reduced gently and the ship was manoeuvred to within a distance of about 50–250 m from the schools. Tracking was possible in adverse weather conditions (in wind speeds of up to 35 m s^{-1}), because of the noise reduction capability of the SA950 sonar and good stability properties of the ship. During the observations, the school detection programme was run continuously, and the sonar data were stored on separate files for later analysis. Events, with drawings of changing school shapes, were

Table I: Results of a nested linear model with fish density of the schools as dependent variable and time of day as continuous effect ($n = 60$)

Parameter	*df*	Mean square	*F*-value	*p*	r^2
Model	4	6 400	3.55	<0.05	0.21
Weather	1	3 467	1.92	0.1713	
Depth (weather)	2	140	0.08	0.9250	
Time	1	20 721	11.48	<0.001	

noted continuously during the observations. An intra-school event rate (Pitcher *et al.* 1996) was calculated for each school as the number of occasions when the school changed shape or reorganized divided by the total observation time. Similarly, an inter-school event rate (Pitcher *et al.* 1996) was calculated as the number of times schools split or joined divided by the total observation time.

School formation and disintegration

To study the formation and disintegration of schools, four transition periods were recorded using the SIMRAD SA950 sonar and the SIMRAD EK500 echosounder. There were two night-to-day exercises (14 October, 03:00–04:50 GMT, and 17 October, 03:10–04:10 GMT), and two day-to-night exercises (15 October, 16:30–19:00 GMT, and 16 October, 15:40–19:00 GMT). During these periods, the ship drifted or tracked fish aggregations (layers or clusters of schools) at low speed (<1.0 m s^{-1}). The sonar was trained and tilted to record the aggregations optimally, and the school detection programme was run continuously. The sonar display was recorded by a video camera using High 8 VHS tapes.

RESULTS

Temperature was 15°C in the upper 20 m and decreased to 12°C at 50 m throughout most of the study area. The current at 35 m varied between 0.25 and 0.35 m s^{-1} and changed in direction from south to north-east, indicative of a clockwise gyre.

Sardine was the main pelagic species and contributed by weight to about 94% of the total catch from eight trawl stations during the surveys. Anchovy *Engraulis capensis* contributed most of the remainder of the catch, round herring *Etrumeus whiteheadi* being present sporadically. Sardine averaged 15.1 cm (range 11–23 cm) in total length and 33 g in weight.

During the two night-to-day transition period studies, sardine were initially (from about 03:00) concentrated in a continuous subsurface layer, which gradually became more structured at about 30 m deep. In both studies, the mean area of the individual school units, as recorded by sonar, increased significantly with time ($r = 0.58$, $p < 0.001$; and $r = 0.33$, $p < 0.001$). However, the number of school units and their relative densities showed no consistent trends with time. Distinct small schools were recorded 10–30 m deep after sunrise (around 06:00) during both night-to-day studies, and several instances of neighbouring schools merging were observed.

During the two day-to-night studies, schools located 30 m deep changed their shape, split into several smaller units and dispersed in layers at a depth of 30–40 m just after sunset. During both studies, however, dense and dynamic schools were still observed near the surface, from about 30 minutes after sunset (17:30) to 19:00 (the end of the study period). These schools moved quickly, changed shape frequently, and split and joined rapidly.

The density of the 60 schools of sardine whose dimensions were obtained acoustically during daylight averaged 29.5 fish m^{-3} ($SD = 46$ fish m^{-3}). However, densities among schools varied by a factor of about 100, ranging from 2 to 233 fish m^{-3}. The density of the fish schools was not significantly different whether it was recorded in good or bad weather or at different depths (surface, midwater or bottom; Table I). A significant correlation between time of day and fish density ($r^2 = 0.39$, $p < 0.001$) indicated that schools recorded in the afternoon tended to be more dense than those recorded in the morning.

The average biomass per unit area of school was estimated to be 8.38 kg m^{-2} ($SD = 17.0$ kg m^{-2}). There was a poor, but significant correlation ($r^2 = 0.19$, $p < 0.001$) between the area and biomass of schools in the linear scale (Fig. 2a), expressed as

$$\text{School biomass} = 10.4 \times \text{school area} \quad . \quad (1)$$

If log-transformed (Fig. 2b), the regression between the area and biomass of schools improved considerably ($r^2 = 0.96$, $p < 0.001$) and had the relationship:

$$\text{Log (school biomass)} = 1.18 \times \text{log (school area)} \; . \; (2)$$

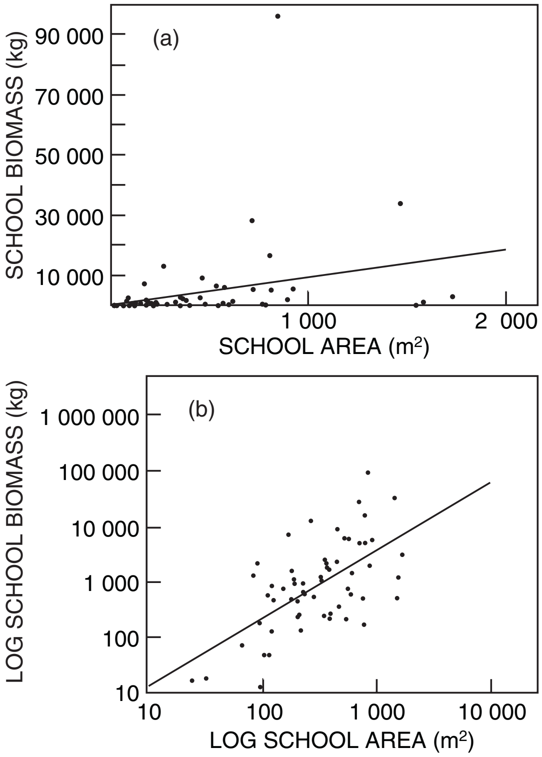

Fig. 2: Relationship between area and biomass of schools of sardine in (a) geometric and (b) logarithmic scale

If weighted by the school biomass, the regression ($r^2 = 0.99$, $p < 0.001$) is expressed as

$$\text{Log (school biomass)} = 1.54 \times \log \text{(school area)}\ . \quad (3)$$

Similarly, there were significant regressions between school volume and school biomass. In the linear scale, the regression ($r^2 = 0.37$, $p < 0.001$) followed the relationship

$$\text{School biomass} = 1.49 \times \text{school volume}\ . \quad (4)$$

If log-transformed, the regression improved markedly ($r^2 = 0.97$, $p < 0.001$) and is expressed as

$$\text{Log (school biomass)} = 0.9 \times \log \text{(school volume)}\ . \quad (5)$$

The average biomass per unit school volume was 0.97 kg m^{-3} (SD = 1.52 kg m^{-3}).

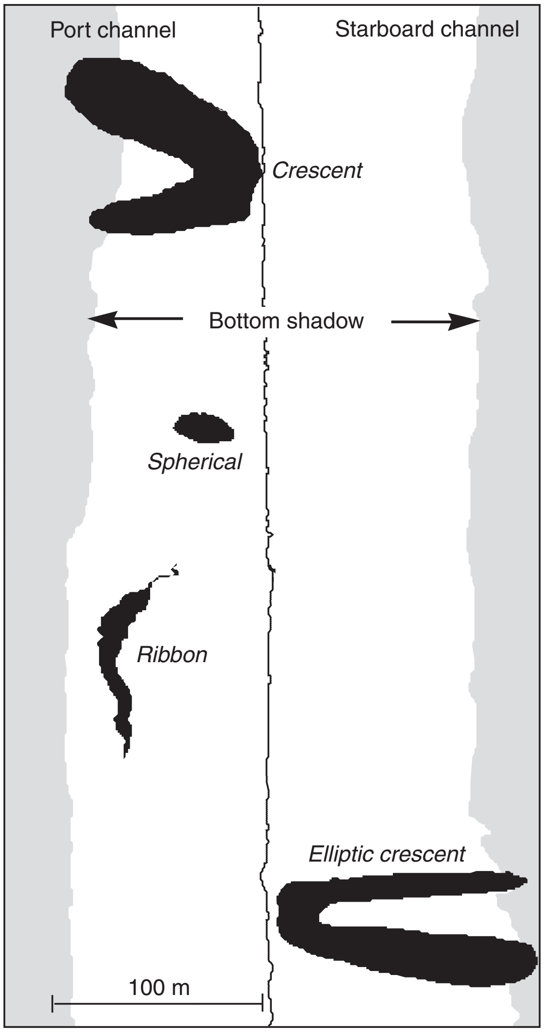

Fig. 3: Images of sardine schools redrawn from the side-scan sonar recordings

There was large variation in the size and shape of schools. They ranged from small spots no more than several metres across to spherical, elliptic or crescent-shaped (particularly common) schools of a few tens of metres in the longest dimension to amorphous or ribbon-shaped aggregations of more than 100 m in the longest dimension (Fig. 3). There was a tendency for the ribbon-shaped schools to be orientated with their

Table II: Summary of information on various parameters during the tracking of sardine schools in False Bay, October 1995

School number	Observation time (min)	Swimming speed (m s^{-1})		Average depth (m)	Average heading (°)	School area (m^2)		Event rate (min^{-1})	
		Average	*SD*			Average	*SD*	Inter-school	Intra-school
1	16	1.59	1.03	24	153	67	57	0.13	0.44
2	19	1.02	0.67	32	199	73	53	0.42	0.84
3	10	1.89	1.12	20	177	59	34	–	–
4	31	1.16	0.9	32	134	122	86	0.16	0.2
5	17	0.87	0.44	34	166	143	62	0.12	0.35
6	51	0.96	0.56	26	211	138	72	0.14	0.3
7	20	0.67	0.37	26	152	159	66	0.3	0.8
8	33	0.81	0.52	32	209	187	93	0.09	0.7
9	4	0.80	0.61	43	144	67	68	–	–
10	22	1.05	0.64	35	123	90	51	0.23	0.23
11	62	1.05	0.68	23	192	101	75	0.02	0.26
12	74	0.76	0.4	33	129	210	101	0.14	0.19
13	30	0.79	0.47	38	167	135	68	0.14	0.38
14	8	0.87	0.34	35	196	167	139	0.14	0.38
15	43	1.07	0.58	35	194	160	86	0.37	0.4
16	6	0.56	0.39	48	214	112	56	0.29	0.8
17	6	1.24	0.76	43	226	196	215	0.14	0.71
18	11	1.53	0.81	40	164	112	47	0.1	0.6
19	9	0.86	0.33	44	252	156	74	0.44	0.5

longest axis more or less parallel with the vessel – possibly indicating active orientation to the vessel. An impression, but one that was difficult to quantify, was that the detection rate on the SIMRAD SA950 was greater than on the side-scan sonar, either because of the lower detection threshold of the former or because of avoidance out of the path between the two transducers. Generally, the best correspondence was observed when the school passed under the vessel, but even then many schools detected on the EK500 were not detected on the side-scan sonar.

The tracked schools moved at average speeds of 0.56–1.89 m s^{-1}, at average depths of 20–48 m (Table II). All 19 schools moved southwards, between south-east and south-west. The average area of the tracked schools ranged between 59 and 210 m^2. The tracking of school number 12 (Table II), which moved in a south-east direction at an average speed of about 0.76 m s^{-1}, is illustrated in Figure 4. Swimming speed varied greatly during the tracking, possibly as a result of random GPS error, and the area of the school varied considerably during tracking (Fig. 4).

The average intra-school (change of shape) event rate was 0.48 min^{-1}, which indicates a change of shape every second minute. The average inter-school event was 0.2 min^{-1}, which suggests that schools split or joined every 5 minutes on average. On one occasion, Cape gannets *Morus capensis* dived on the schools. During the last tracking, in good weather conditions, small echoes that possibly originated from Cape fur seals *Arctocephalus p. pusillus* were occasionally recorded by the sonar near the schools. On 16 October, many schools were at the surface and seals were feeding on them.

DISCUSSION

The formation and disintegration of schools of southern African sardine were highly dynamic during the transition periods (night-to-day and day-to-night), despite some large schools remaining packed at high density for a long time after sunset. Similar observations were made in the Mediterranean Sea and interpreted as an active process to maintain schooling, even at low light intensity (Fréon *et al*. 1996).

Significant relationships between school geometry and school biomass have been established for herring *Clupea harengus* in the northern Atlantic (Wheeler and Winters 1990, Misund *et al*. 1992). Relationships between school area and school biomass allow conversion of sonar measurements of these parameters, with a certain degree of error. This enables surveys combining sonar and echo-integration recordings to be conducted. A horizontally tilted sonar will cover a much larger near-surface area than a hull-mounted echosounder. Similarly, multi-beam sonar covering at least a sector of 90° can be used for scanning a vertical plane on one side of the vessel, even though the efficient range of existing sonar is currently limited to 100 m on account of the high frequency used (Gerlotto *et*

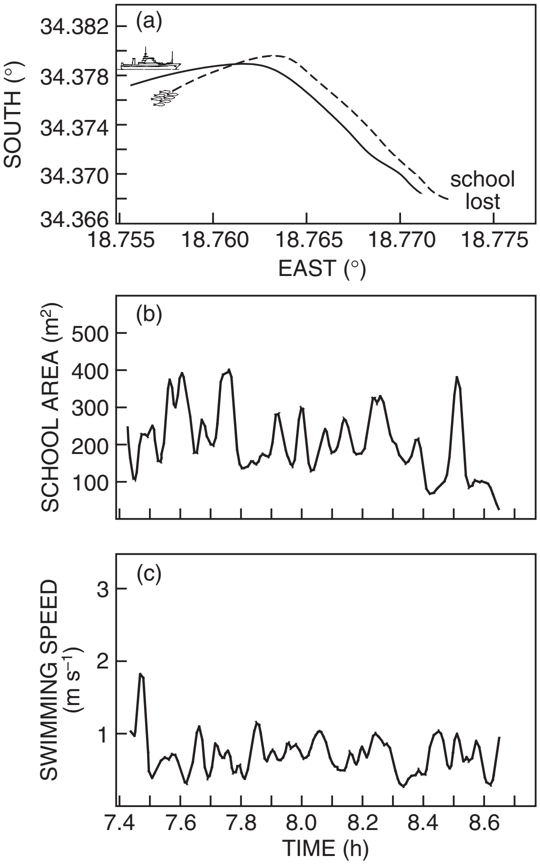

Fig. 4: Sonar tracking of a single southern African sardine school (number 12, Table II) in False Bay – (a) movement of fish school and vessel, (b) horizontal area of school as projected by the sonar and (c) swimming speed of the school

al. 1999). For technical reasons, echo-integration with hull-mounted echo-sounders normally starts at a depth of 10 m, leaving the upper margin of the water column as a blind zone. Multibeam sonar may, in addition, have an increased ability to record schools that are avoiding the vessel (Misund *et al.* 1995, Soria *et al.* 1996). Biomass estimation of fish schools near the surface may therefore be more accurate using sonar (Misund and Coetzee 2000).

There was a significant relationship between area and biomass of sardine schools, but it was weak using a linear scale. The relationship improved considerably using log-transformed data, but there was a scatter of about two orders of magnitude. This was also evident between volume and biomass of schools. For converting sonar measurements of school area to school biomass, the geometric relationship would give a biomass about three times that of the logarithmic relationship. This is because the dense and large schools would influence the relationship more in the geometric than in the logarithmic domain. The geometric relationship is additive, in that the summed area of all schools recorded within a particular distance can be converted to overall biomass. However, this cannot be achieved using the logarithmic relationship, whereby school recordings must be converted from area to biomass individually, or an approximation must be made (Hoyle 1968).

The considerable scatter in the relationships between the geometry and biomass of schools was induced by variation in the packing density of schools of about two orders of magnitude. Similar large variations in the packing density of clupeoid schools have been observed in the northern hemisphere (Misund 1993, Fréon *et al.* 1996). The variation may be caused by such activities as feeding, predator avoidance or the migratory behaviour of schools, which could partly reflect different motivational status of the individuals constituting the different schools.

An important parameter in estimating the packing density of the schools under study was their length. This was measured from the echogram, which was scaled to real dimension and then corrected for beamwidth distortion by the echo-sounder. This correction assumes that the schools were recorded only to the -3dB points of the echo-sounder beam (Misund 1993). Dense schools close to the transducer were probably recorded beyond the -3 dB points of the echo-sounder beam. Consequently, the length would be systematically overestimated, and the packing density of the schools would be underestimated accordingly (Diner 2001). Extending the recording width of the echo-sounder beam from -3 to -12 dB points would increase the correction factor from 4.3 to 8.0 m for a school recorded at a depth of 35 m. For the sardine schools under study, this would decrease their average length from 15.3 to 11.6 m, and consequently increase the estimated packing density by 25% on average. The sonar recordings of the horizontal area of the schools have not been corrected, because the narrow and sharp horizontal beam (1.5° between -3 dB points) of the sonar is assumed to cause marginal distortion at a range <200 m.

There were rapid changes in the shape and structure of the sardine schools. This could reflect their feeding activity or predator avoidance behaviour in the presence of seals. The tendency of schools to be stretched out in a crescent or a ribbon shape is common in sardine, as revealed by aerial observation off Japan (Hara 1985) and Namibia (Hampton *et al.* 1979).

The average horizontal swimming speed of 0.76 m s^{-1} for the sardine under study equates to an average speed of about 5.9 body lengths s^{-1}. This value falls within the limit of sustained swimming speed for a 15 cm (*TL*) clupeoid at the temperature range for the study area (Viedeler and Wardle 1991), even when current speed is taken into account. However, several factors render the sonar measurements in this study as overestimates of the actual swimming speed of the schooling sardine. First, the measurements are based on GPS positions, which would have inherent random errors. This error was reduced by averaging the positions over 50 pings, and by discarding averaged observations when the school movement exceeded 60 m in north-south or east-west directions from the previous averaged observation. Second, movements of the schools were calculated on the basis of the distance between the geometric midpoints of successive recordings. These movements may be different from the real movements of the schooling sardine. Varying intensity in the backscattered strength, and therefore variations in the horizontal extent given by successive pings within the schools, may cause larger movements of the geometric midpoints of the school recordings than the real movements of the schooling sardine. The same averaging and filtering process applied to minimize the GPS error was used to reduce this geometric midpoint error.

The tracked schools changed shape and interacted with other schools frequently. This indicates that the schools were dynamic, with frequent inter- and intra-school events. This probably reflects feeding activity of the schooling sardine, which at the same time were being chased by feeding seals and gannets. During an aerial survey off Japan, Hara (1985) recorded splitting and joining of sardine schools every few minutes, but the observations were anecdotal. Pitcher *et al.* (1996) recorded intra- and inter-school event rates for a herring feeding migration in the Norwegian Sea, which were about three times lower than the present event rate, even though the herring were being chased by predators such as cod *Gadus morhua* and saithe *Pollachius virens*. To further support the hypothesis that high event rate between schools can be attributable to the presence of predators, Misund *et al.* (1998) found that herring schools feeding in a nearly predator-free environment along the cold-water front in the Norwegian Sea have very low intra- and inter-school event rates.

Although multi-sector sonars have been available for more than 15 years, few studies have used them for quantifying school behaviour. The instrument has the advantage over conventional vertical echo-sounders by limiting the effects of fish avoidance, especially at medium or low vessel speed. This is confirmed by similar findings of sardine school shape and school dynamics during aerial surveys, which do not disturb the fish (Hara 1985). These results may be useful as input to models of fish behaviour such as those proposed by Swartzman (1991) and Mackinson (2000). Combining the modelling approach with field observations should help to resolve unanswered questions, or conflicting results regarding the relationships between schools, clusters of schools and abundance of pelagic fish, which have crucial implications for stock assessment and fisheries management (Gerlotto *et al*. 1999, Mackinson *et al*. 1999, Petitgas *et al*. 2001).

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