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TRENDS IN THE ABUNDANCE AND DISTRIBUTION OF ANCHOVY AND SARDINE ON THE SOUTH AFRICAN CONTINENTAL SHELF IN THE 1990s, DEDUCED FROM ACOUSTIC SURVEYS

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The South African pelagic resources have been monitored acoustically since 1983. The results of these surveys are currently used to determine catch limits for anchovy *Engraulis capensis* and sardine *Sardinops sagax*. Two main surveys are conducted annually, in winter to determine the strength of the year's recruitment and in summer to estimate the size of the adult stock. The results of the surveys conducted between 1990 and 1997 are presented and discussed in the context of the time-series of stock abundance. Distribution patterns, size structure and biomass levels are related to general trends in the life-history strategies of anchovy and sardine, as well as the major environmental features in the southern Benguela in the 1990s. The biomass of adult anchovy appears to be driven largely by the strength of the early recruitment, corresponding to fish spawned in the first half of the summer spawning season. The biomass of adult sardine, however, is better explained on the basis of the biomass of 2-year-old and older fish in the previous year's survey. Anchovy tend to move east with age, whereas sardine appear to move both north, along the south African west coast, and east with increasing age.

Anchovy *Engraulis capensis* and sardine *Sardinops sagax*, are the main pelagic resources on the South African continental shelf, constituting more than 80% of the total national pelagic purse-seine catch. In the period 1970–1997, anchovy catches have fluctuated between 41 000 and 596 000 tons (average 254 000 tons), whereas sardine landings have ranged between 16 000 and 176 000 tons (average 66 000 tons), including the bycatch associated with the anchovy fishery. Most of these catches are landed along South Africa's west coast between 32°S and Cape Agulhas (Fig. 1).

In the early 1980s, Total Allowable Catch (*TAC*) limits were based on VPA analyses (Armstrong *et al*. 1983), which relied on catch per unit effort (*cpue*) as indices of abundance. However, subsequent research has shown that the pelagic fishery heavily undersampled older fish of both species and that the *cpue* was not proportional to abundance. A fishery-independent programme of acoustic surveys to estimate pelagic fish abundance directly was initiated in 1983 (Hampton 1987). Since 1995, results of those surveys have been used as the basis for the recommendation of *TAC*s. Between 1984 and 1993, concomitant daily egg production estimates of anchovy spawner stock have been conducted during the acoustic surveys (Armstrong *et al*. 1988, Hampton *et al*. 1990). The accuracy, reliability and usefulness of those surveys for the estimation of anchovy biomass have recently been examined by Hampton (1996).

The rationale and objectives of the acoustic programme and the initial survey results for anchovy for the period 1983–1986 are presented in Hampton (1987). The role of the surveys in the management of South Africa's pelagic resources for the period up to 1990 was discussed by Hampton (1992). Acoustic survey data post-1990 have been used extensively for management purposes, but the results have not been published. During that period, the southern Benguela has experienced several environmental perturbations, including *El Niño* – Southern Oscillation (ENSO) events during the periods 1991–1993 (Agenbag 1996) and 1997–1998.

The objective of this paper is to update the time-series of acoustic survey results on anchovy and sardine distribution and abundance presented in Hampton (1987, 1992), and to describe the dynamics of the two populations in the 1990s in terms of biomass trends, size frequencies and spatial distributions. Following on from Hampton's studies, the present contribution outlines the results and insights gained from one of the longest time-series of catch-independent estimates of pelagic fish abundance worldwide.

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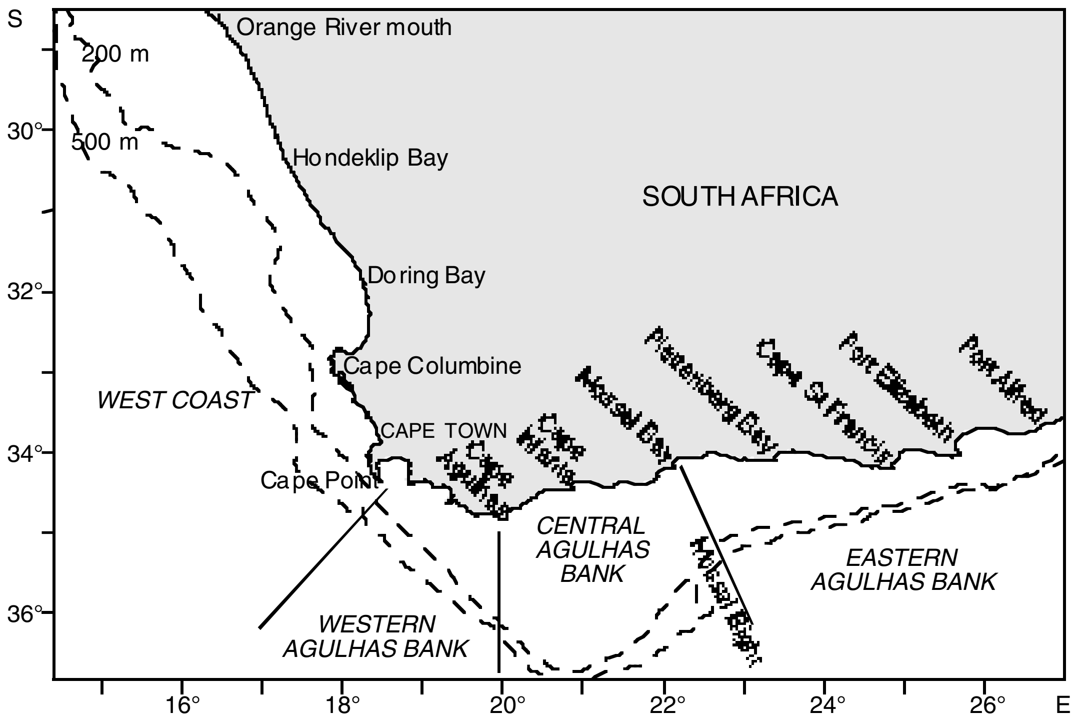


Fig. 1: Map of the study area showing the main geographical features and other places mentioned in the text

MATERIAL AND METHODS

Survey design

Adult anchovy and sardine spawn predominantly over the Agulhas Bank, a shallow area south of the African continent (Fig. 1). Anchovy spawn mainly between October and February (Shelton 1986, Hutchings *et al*. 1998), whereas sardine have a protracted spawning season, peaking between August and March (Shelton 1986). The larvae and juveniles of both species are transported northwards along the South African west coast, via a jet current that develops west and south of Cape Point (Fig. 1, Nelson and Hutchings 1983, Fowler and Boyd 1998). Larvae then move inshore to the productive West Coast environment in autumn (Hutchings 1992), and thereafter begin a southerly return migration to the major fishing grounds south of Doring Bay (Fig. 1). Purse-seiners target recruiting anchovy (<1 year old) for the production of fishmeal. During these operations, juvenile sardine are regularly caught as by-catch. Sardine are generally targeted for canning after their first year of age.

Two acoustic surveys are conducted annually to estimate the biomass and length composition of anchovy and sardine (Table I). In November each year, the shelf between Hondeklip Bay and Port Alfred (Fig. 1) is surveyed to determine the total adult biomass of both species. In May, a narrower strip along the West Coast is surveyed from the Orange River in the north to Cape Infanta on the East Coast (Fig. 1), primarily to estimate the number of recruits of anchovy and sardine. In recent years, the surveys have been extended farther east to confirm that recruitment is negligible east of Cape Infanta, an assumption made in the current modelling and management procedures.

Three estimates of recruitment are used in the assessment of South Africa's pelagic resources: survey estimates of recruitment, back-calculated recruitment, and recruitment estimated in the assessment model. For the purpose of this paper, recruitment generally refers to the survey estimates, except for the multiple regressions, which use back-calculated recruitment (see Discussion). This recruitment is a simple correction

Table I: Summary of the recruitment and spawner biomass cruises, 1990 –1997

Year	Recruitment cruises		Spawner biomass cruises	
	Month	Survey area	Cruise dates	Survey area
1990	5–15 May	30°S–Cape Agulhas	6–30 Nov.	Hondeklip Bay–Port Alfred
1991	7–24 May	Orange River–Cape Infanta	7 Nov.–3 Dec.	Hondeklip Bay–24°E
1992	12–28 May	Orange River–Cape Infanta	5 Nov.–2 Dec.	Hondeklip Bay– Port Elizabeth
1993	18 May–3 June	Orange River–Cape Infanta	9 Nov.–3 Dec.	Cape Columbine– Port Alfred
1994	3– 27 May	Orange River– Port Alfred	11 Nov.– 7 Dec.	Cape Columbine– Port Elizabeth
1995	6–28 June	Orange River–Port Alfred	22 Oct.– 4 Dec.	Hondeklip Bay–Port Alfred
1996	3– 25 June	Orange River– Wilderness	17 Oct.–18 Nov.	Hondeklip Bay–Port Alfred
1997	15–31 May	Orange River–Cape Infanta	28 Oct.–8 Dec.	Hondeklip Bay–Port Alfred

of the survey estimate to account for fishing mortality and the expected natural mortality that may have occurred between 1 January and the time of the survey. The model estimates of recruitment, which are not used in this paper, take into account all available data on fish abundance and age structure from surveys and commercial catches and are recalculated every year according to a log-likelihood function (see Appendix 1 in Butterworth *et al*. 1993).

Surveys consist of a series of pre-stratified, randomly spaced, parallel transects, designed to obtain unbiased estimates of stock size and sampling variance (Jolly and Hampton 1990). The strata are predefined according to expected distribution patterns, based on early surveys. Typically, the area is divided into five strata for the spawner surveys: Hondeklip Bay to Cape Columbine, Cape Columbine to Cape Point, Cape Point to Cape Agulhas, Cape Agulhas to Mossel Bay, and Mossel Bay to Port Alfred (Fig. 1). For the recruitment surveys, there are typically four strata on the West Coast, between the Orange River and Cape Point, and at least two on the South Coast.

Sampling methods

Estimates of acoustic back-scattering strength from November 1990 to 1996 were made using a 38-kHz Simrad EK400 scientific echo-sounder, calibrated by the standard sphere method, and interfaced to custom-built echo-integrators, as described in Hampton (1987, 1992) and Barange and Hampton (1997). Prior to November 1990, a Simrad EKS-38 echo-sounder was used. In 1997, the system was upgraded to the Simrad EK500 echo-sounder and the signal was integrated using Simrad EP500 and/or SonarData Echoview© software. An inter-calibration study of the EK400 and 500 systems (Barange 1998) showed that their performance was similar, except for volume back-scattering strengths in excess of –29.9dB, which were underestimated in the EK400 system as a result of receiver saturation. In order to compare the 1997 stock estimates with those of previous assessments, the recorded EK500 back-scattering strengths above the EK400 saturation limit were set at –29.9 dB and the data for the survey were re-integrated, thereby simulating the performance of the EK400 system.

During the surveys, the echo-sounder was run continuously along and between transects, except for *ad hoc* midwater trawling to identify scatterers and to occupy stations that are typically between 5 and 10 miles apart. Routine work at each station included *inter alia* the deployment of a CalVET or vertical Bongo net to collect pelagic fish eggs and zooplankton and to provide a temperature profile. A CTD cast was also taken on selected lines for the collection of various environmental parameters.

Echo returns exceeding a preset threshold were integrated between stations. The threshold was intended to eliminate plankton echoes. Typical survey speed was 10 knots. Back-scattering strengths were apportioned between the different pelagic species (generally anchovy, sardine and round herring *Etrumeus whiteheadi*, but also Cape horse mackerel *Trachurus trachurus capensis* and chub mackerel *Scomber japonicus*), on the basis of trawl samples. Transformation to fish density was done using a single expression for the back-scattering cross-section per kilogramme as a function of length, described by Hampton (1987, 1992). In the absence of an appropriate target strength expression for any of the above-mentioned species when the time-series was started, Halldørsson and Reynisson's (1983) 38-kHz target strengths expression for North Atlantic herring *Clupea harengus* was used. Although more realistic *in situ* target strength have now been obtained for most of these species (Barange *et al.* 1996), the old expression is still used for continuity of the time-series. However, it should be noted that use of a single expression for all the species assumes that anchovy and sardine of the same length have the same

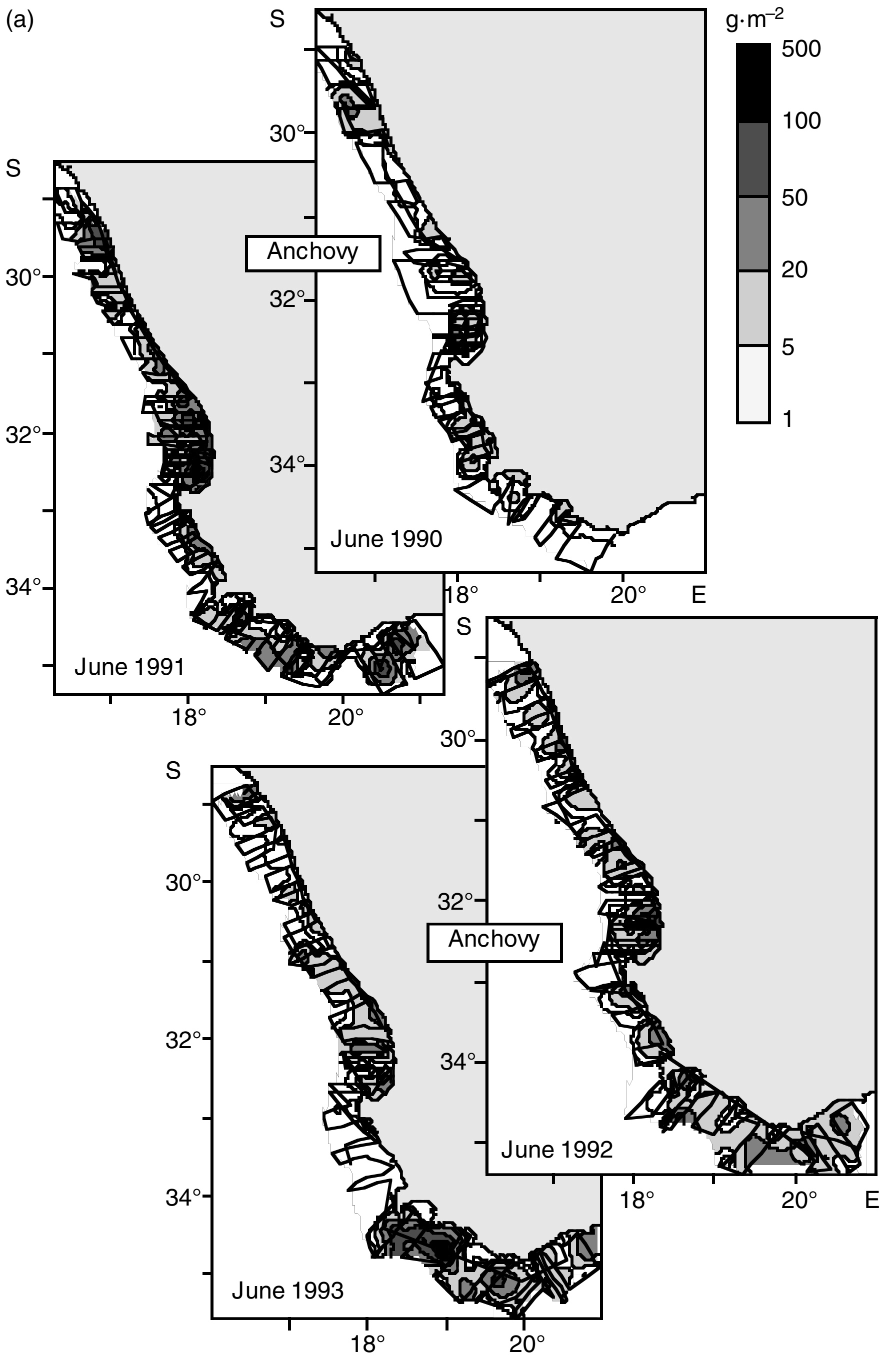


Fig. 2: Distribution of anchovy recruits and adults deduced from acoustic surveys, (a) 1990–1993, (b) 1994–1997, using interpolation by kriging. The survey tracks are shown

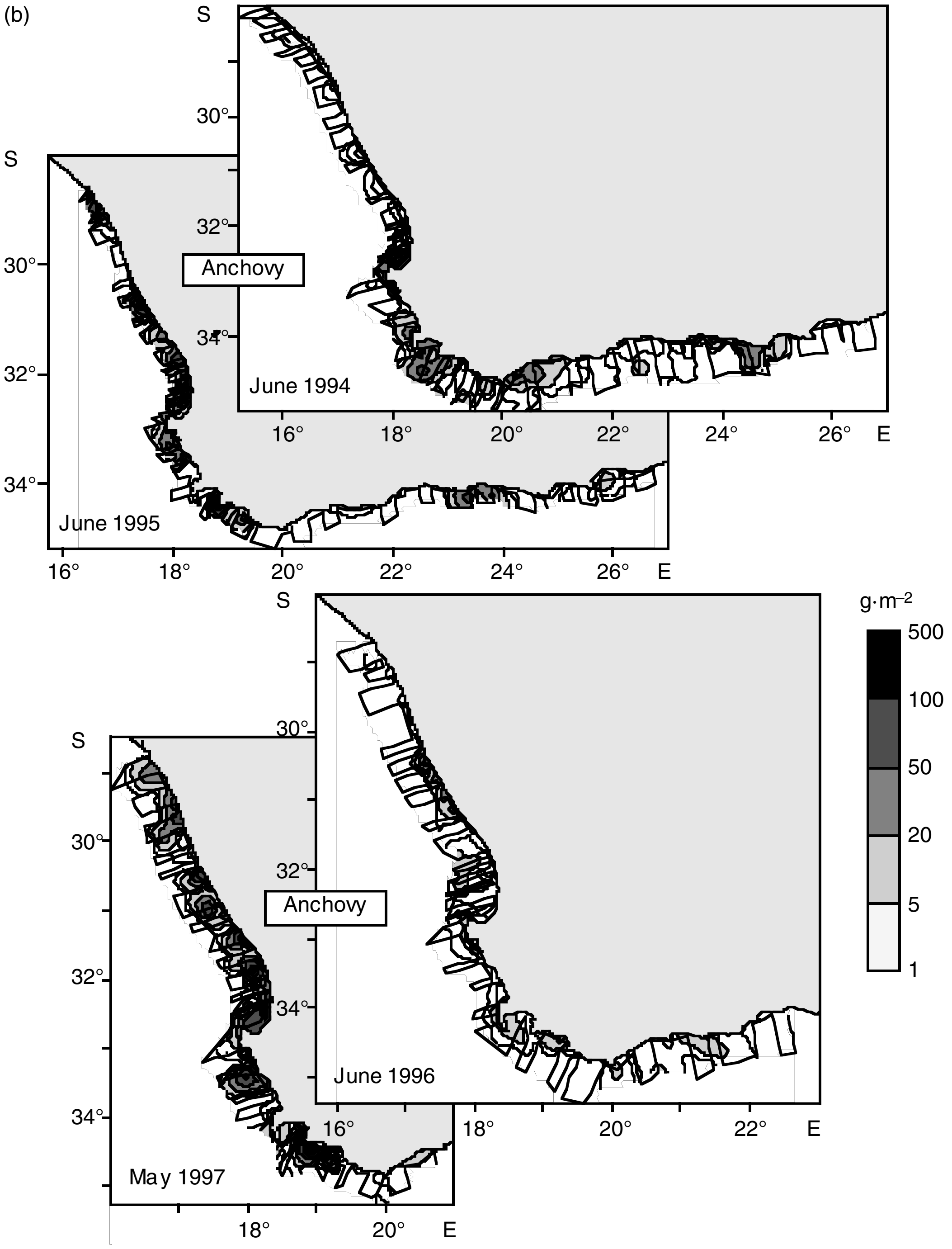


Fig. 2: *(continued)*

Table II: Summary of the anchovy survey results for the recruitment cruises, 1990–1997, including the percentage of total biomass of recruits per subarea surveyed

Parameters	1990	1991	1992	1993	1994	1995	1996	1997
Total biomass on survey (tons)	130 366	601 905	518 816	572 836	431.747	499 046	100 427	371 793
Total biomass on RG (tons)	130 366	601 905	518 816	572 836	420.186	399 172	80 484	371 793
Biomass of recruits on RG (tons)	129 790	377 019	388 461	162 614	109.879	397 727	68 112	369 404
Biomass of recruits on RG (%)	99.5	62.6	74.9	28.4	26.1	99.6	84.6	99.3
Mean mass of recruits (g)	3.3	5.3	4.6	1.9	4.3	3.5	3.0	4.3
Number of recruits on RG (billions)	38.9	70.6	86.3	84.3	25.7	114.6	22.9	86.7
CV(%) of recruit estimate	25	13	17	19	18	17	23	15
Subarea	*Percentage of total biomass*							
North of Doring Bay	43.4	21.5	25.4	13.7	5.2	29.2	30.5	45.8
Doring Bay–Cape Columbine	21.1	36.1	11.8	13.3	17.2	25.1	14.2	36.7
Cape Columbine–Cape Point	24.8	5.0	7.4	0.0	5.9	12.0	7.1	7.5
Cape Point–Cape Infanta	10.6	37.3	55.3	71.0	44.7	13.6	48.3	9.8
East of Cape Infanta	–	–	–	–	26.9	20.0	–	–

RG = Recruitment grounds

back-scattering cross-section per unit mass, an assumption that has been shown to be incorrect (Barange *et al*. 1996). For this reason, the stock estimates should be considered to be relative rather than absolute.

Trawl samples were pooled to obtain size compositions of the entire populations surveyed. Individual trawl length distributions were weighted according to the acoustically estimated biomass in the vicinity of the trawl. Weighted size frequencies were computed for all strata and summed to produce a size frequency for the survey. Composite size frequencies were also used to separate recruit and adult fish (according to length) in the recruitment cruises. The division was determined on the basis of the survey size frequency and approximated 10.5 cm caudal length (*CL*) for anchovy and 15.5 cm *CL* for sardine. Weighted size frequencies are only available from 1989 (anchovy) and 1990 (sardine).

Fish distribution maps were derived from data interpolation using standard Kriging routines (Barange and Hampton 1997). For the summer surveys, the surface areas covered by densities $>1 g \cdot m^{-2}$ were computed for both species to investigate relationships between stock size and spatial dispersion.

RESULTS

Recruitment surveys

ANCHOVY

Distribution patterns of anchovy in winter between 1990 and 1997 are presented in Figure 2. During that period recruits generally concentrated on the West Coast (Orange River to Cape Point), particularly in the St Helena Bay region, substantiating current opinions on anchovy migration patterns (Hampton *et al*. 1990, Hampton 1987, 1992). However, there were appreciable concentrations of recruits north of St Helena Bay in years of strong recruitment (Fig. 2). In some years, dense fish concentrations were also found on the South Coast (east of Cape Point), but these were mainly adult fish, which contribute little to the recruitment. Because adult fish are expected to occur farther east than the standard survey limits (the reason for extending the surveys during 1994–1996), no estimate of the total stock was provided by these surveys. Apart from 1993 and 1994, when the biomass of recruits was less than one-third the total biomass, recruits constituted more than 60% of the biomass in the recruitment grounds (Orange River – Cape Infanta, Table II).

Weighted size frequencies of anchovy are presented in Figure 3. The size of a typical recruit (6–7 months old) is 6–9 cm *CL* (7–11 cm total length). There was a high proportion of small recruits in 1990, 1992, 1993 (particularly so) and 1996 (Table II, Fig. 3), which was likely a result of such factors as increased mortality of early spawning products, a delay in peak spawning, slow larval growth during those years, or a combination of those factors. By counting daily-deposited otolith rings, Hutchings *et al*. (1998) concluded that the majority of the 1993 recruits were spawned in December and January, indicative of a delay in peak spawning.

Recruitment estimates of anchovy and sardine and associated information for the 1990–1997 surveys are presented in Tables II and III, and for comparative purposes, the entire recruitment time-series is shown in Figure 4. Anchovy recruitment after 1990 was more variable than the previous five-year period, with low estimates in 1990, 1994 and 1996, followed by average

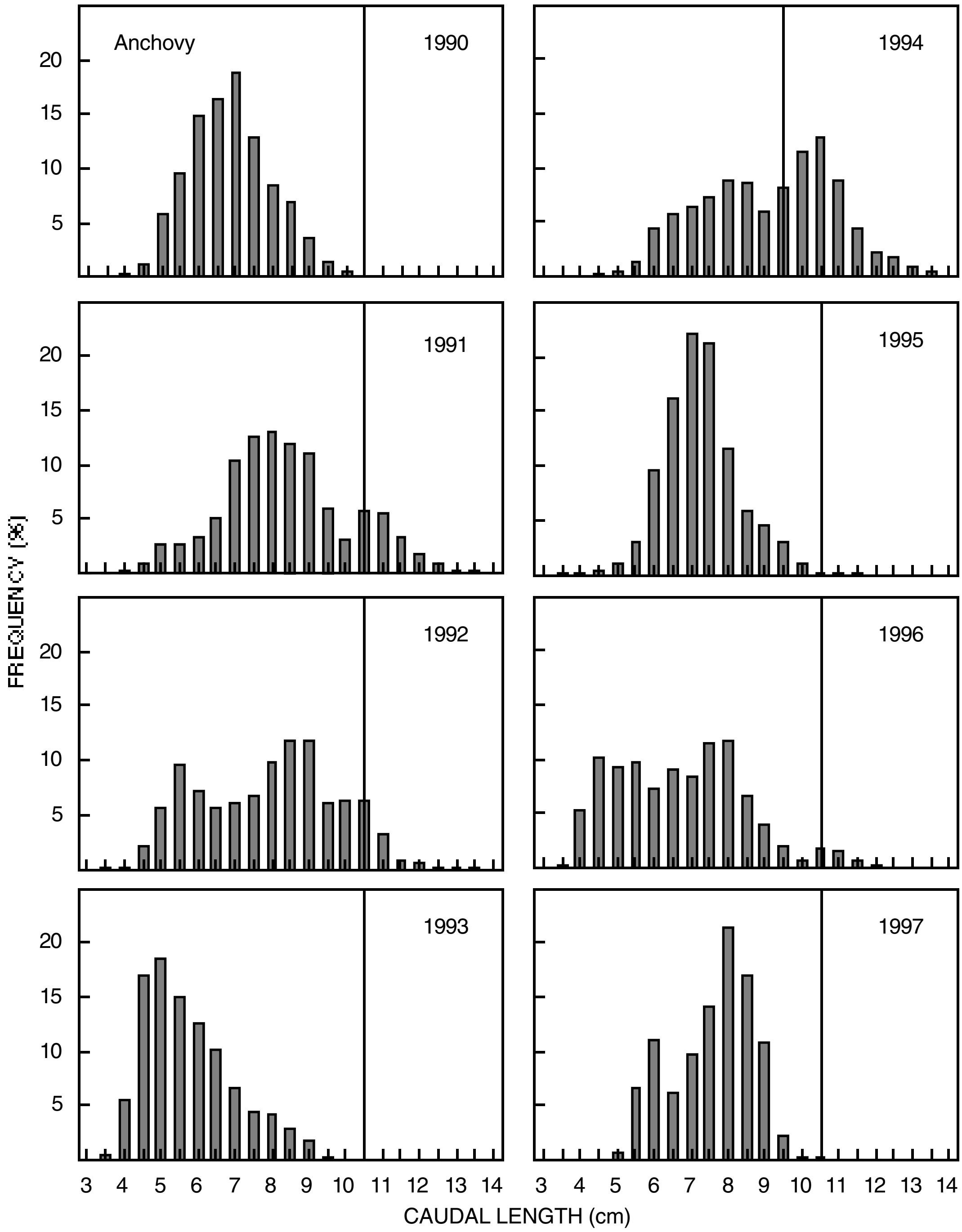


Fig. 3: Acoustically weighted size frequencies of anchovy, obtained from recruitment survey catches, 1990–1997. The length division between recruits and adults is shown

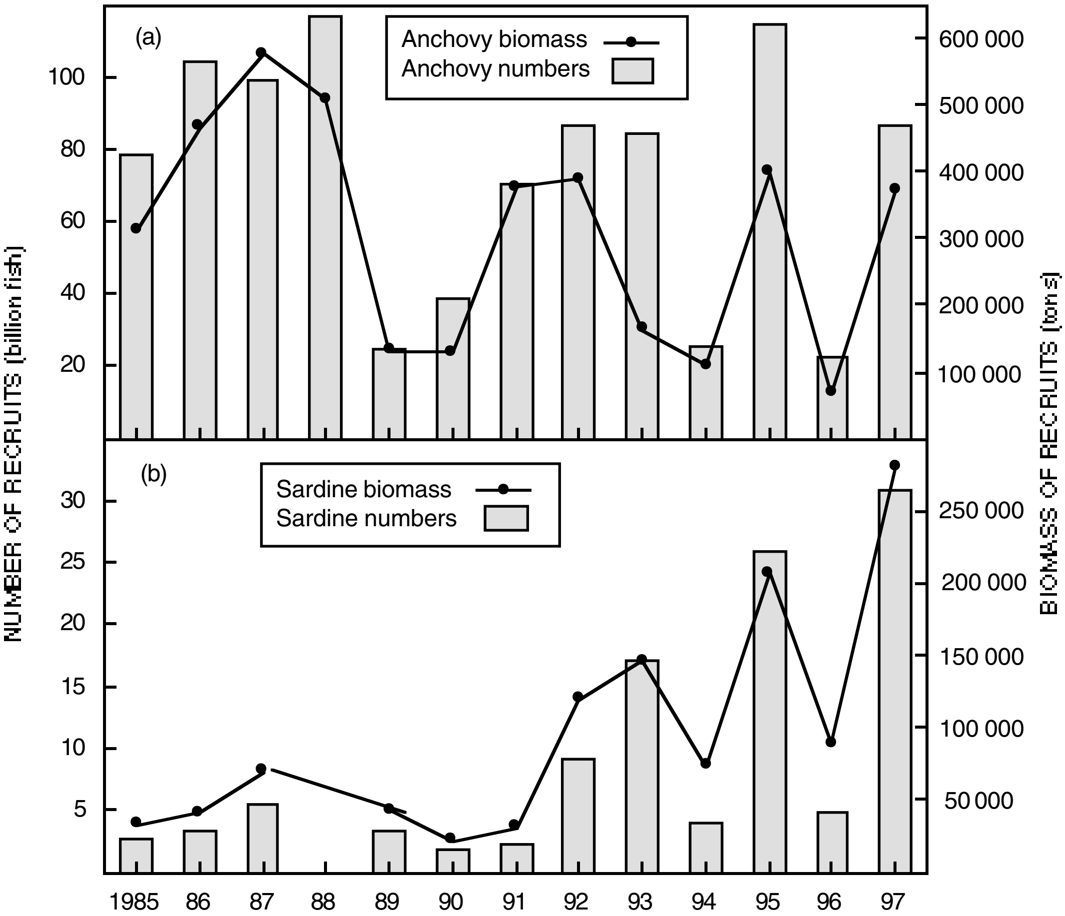


Fig. 4: Time-series of acoustic estimates of (a) anchovy and (b) sardine recruits in numbers of fish and fish biomass

or above-average recruitment in 1993, 1995 and 1997. Note that recruitment in 1993 was high by number but average by mass, because of the small mass of individual fish (Table II). Interestingly, these fluctuations in recruitment occurred during an apparent decline in the adult stock between 1991 and 1997 (Table IV). For example, despite poor recruitment and low spawner biomass in 1994, the highest recruitment was recorded for 1995. Also, recruitment was estimated to be high in 1997, although the spawner biomass was at its lowest level the previous spawning season (Table IV).

Variability in the recruit versus adult stock size in winter may be assessed from the two years (1994 and 1995) when a large proportion of their distribution was covered. In 1994, only 26% of the fish (by mass) were recruits, whereas in 1995 almost all of the fish were younger than one year. This indicates that, in years of good recruitment, juvenile fish dominate the anchovy stock in winter. This observation is consistent with the perception that adult anchovy are subject to a high rate of natural mortality.

SARDINE

Sardine distributions and weighted size frequencies during the recruitment surveys are presented in Figures 5 and 6. Contrary to anchovy, of which only a few adults were found in the recruitment surveys, several sardine age-classes contributed to the biomass estimated during the recruitment surveys. The interpretation of the results is therefore more complex. Figure 4 shows that sardine recruitment in

Table III: Summary of the sardine survey results for the recruitment cruises, 1990–1997, including the percentage of total biomass of recruits per subarea surveyed

Parameter	1990	1991	1992	1993	1994	1995	1996	1997
Total biomass on survey (tons)	57 359	288 098	171 570	169 599	514 303	300 858	372 456	561 849
Total biomass on RG (tons)	57 359	288 098	171 570	169 599	309 384	250 099	230 176	561 849
Biomass of recruits on RG (tons)	na	31 094	119 030	146 504	73 370	206 803	89 026	279 820
Biomass of recruits on RG (%)		10.8	69.4	86.4	23.7	82.7	38.7	49.8
Mean mass of recruits (g)	na	13.3	12.9	8.6	18.2	8.0	18.0	9.0
Number of recruits on RG (billions)	na	2.3	9.2	17.0	4.0	26.0	4.9	30.9
CV(%) of recruit estimate		37	28	26	15	18	31	13
Subarea	*Percentage of total biomass*							
North of Doring Bay	0.1	0.9	42.0	4.5	1.6	16.6	1.1	17.3
Doring Bay–Cape Columbine	5.2	6.3	4.6	68.9	4.7	34.0	5.3	17.0
Cape Columbine–Cape Point	51.8	0.4	0.0	7.2	0.0	2.7	8.2	37.5
Cape Point–Cape Infanta	42.7	92.4	53.3	19.2	53.7	29.8	85.3	28.3
East of Cape Infanta	–	–	–	–	39.8	16.9	–	–

RG = Recruitment grounds
na = Not available

1993, 1995 and 1997 was considerably higher than in other years, similar to the pattern for anchovy recruitment. In those surveys, a substantial portion of the sardine stock (Table III) was concentrated in St Helena Bay. When there were few fish there, the overall recruitment levels were generally low. Weighted size frequencies for years of high abundance show that fish 6–10 cm *CL* (c. 6–8 months old) were concentrated on the recruitment grounds (Fig. 6). This suggests that, despite the protracted nature of sardine spawning, spawning success during a relatively narrow spawning window the previous summer is crucial in determining recruitment success.

Spawner surveys

ANCHOVY

For most years between 1990 and 1997, the anchovy population was distributed over the Agulhas Bank, mainly between Cape Point and Plettenberg Bay

Table IV: Percentage of the total spawner biomass of anchovy and sardine in the areas surveyed on the West and South coasts, and the corresponding *CV*(%) of the survey, 1985–1997. Values >30% are highlighted

Area	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997
Anchovy													
West Coast	0	7.1	**37.8**	16.8	11.9	0	15.7	6.3	0	10.6	0	9.6	2.9
Western Agulhas	**73.1**	**66.8**	**50.9**	**61.3**	**57.8**	**49.8**	**39.3**	**44.5**	**45.6**	**39.8**	**79.1**	11.5	26.3
Central Agulhas	20.7	23.1	7.0	17.8	25.2	**50.1**	**45.0**	**36.1**	**40.9**	**47.4**	20.9	**50.4**	**32.9**
Eastern Agulhas	6.2	3.0	4.3	4.1	5.1	0.1	–	13.1	13.5	2.2	0	29.9	**37.8**
Total (thousand tons)	975	1 747	1 456	1 104	536	469	1 682	1 501	800	476	432	143	841
CV(%)	16	15	12	20	13	21	12	13	16	13	17	33	24
Sardine													
West Coast	na	na	**70.8**	**35.0**	25.1	2.5	13.7	4.0	15.4	**32.4**	9.2	6.8	18.1
Western Agulhas	na	na	11.5	**52.4**	**51.2**	**80.6**	**65.2**	**50.5**	**57.7**	**40.8**	**45.0**	**47.2**	**63.4**
Central Agulhas	na	na	17.7	12.6	6.4	12.1	21.1	10.1	19.8	1.2	9.5	12.9	18.1
Eastern Agulhas	na	na	0	0	17.3	4.7	–	**35.4**	7.0	25.6	**36.3**	**33.2**	0.3
Total (thousand tons)	54	160	129	113	286	263	441	327	464	597	620	505	769
CV(%)	39	41	32	55	21	27	26	36	28	25	36	21	22

na = Not available

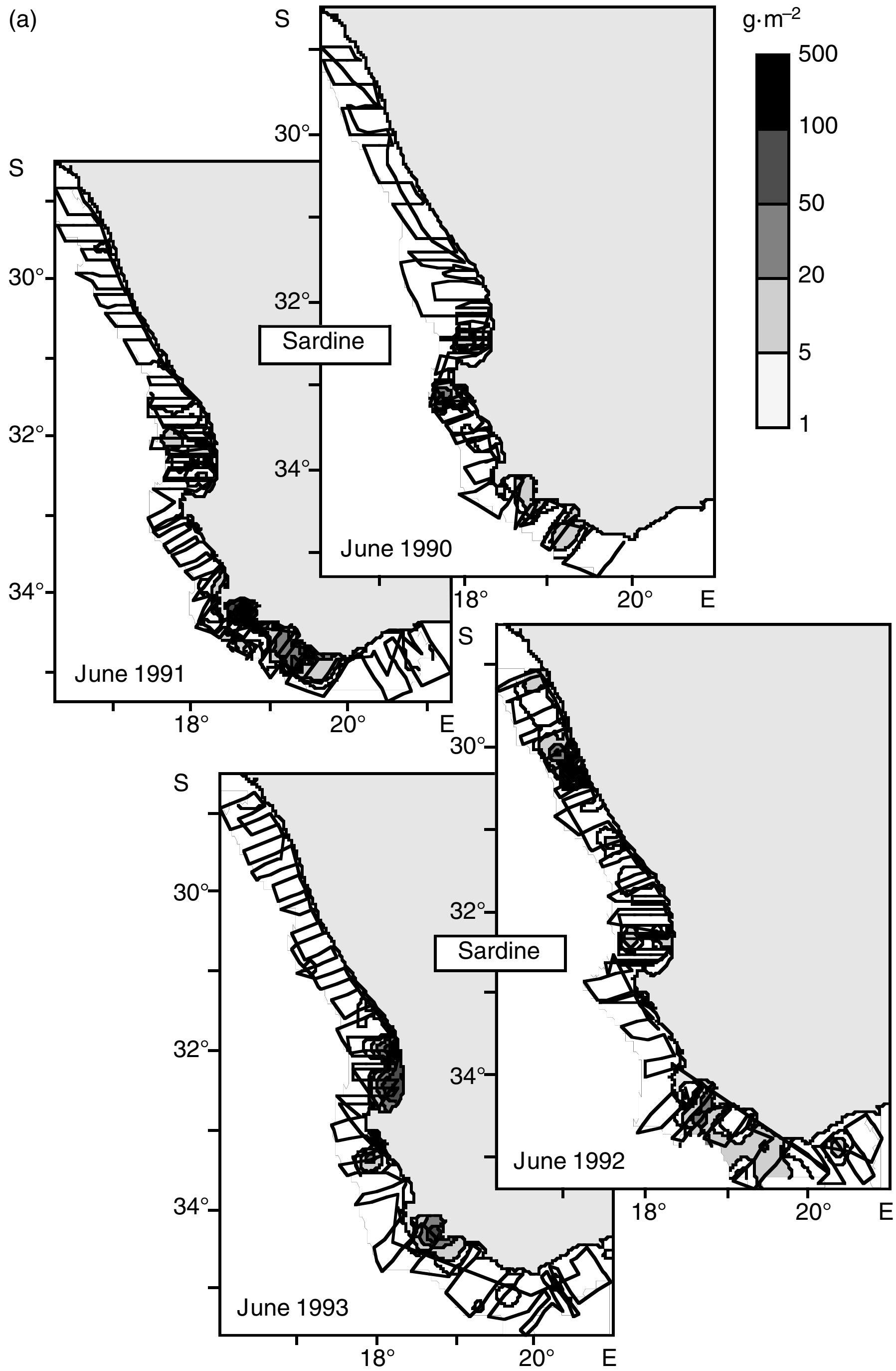


Fig. 5: Distribution of sardine recruits and adults deduced from acoustic surveys, (a) 1990–1993, (b) 1994–1997, using interpolation by kriging. The survey tracks are shown

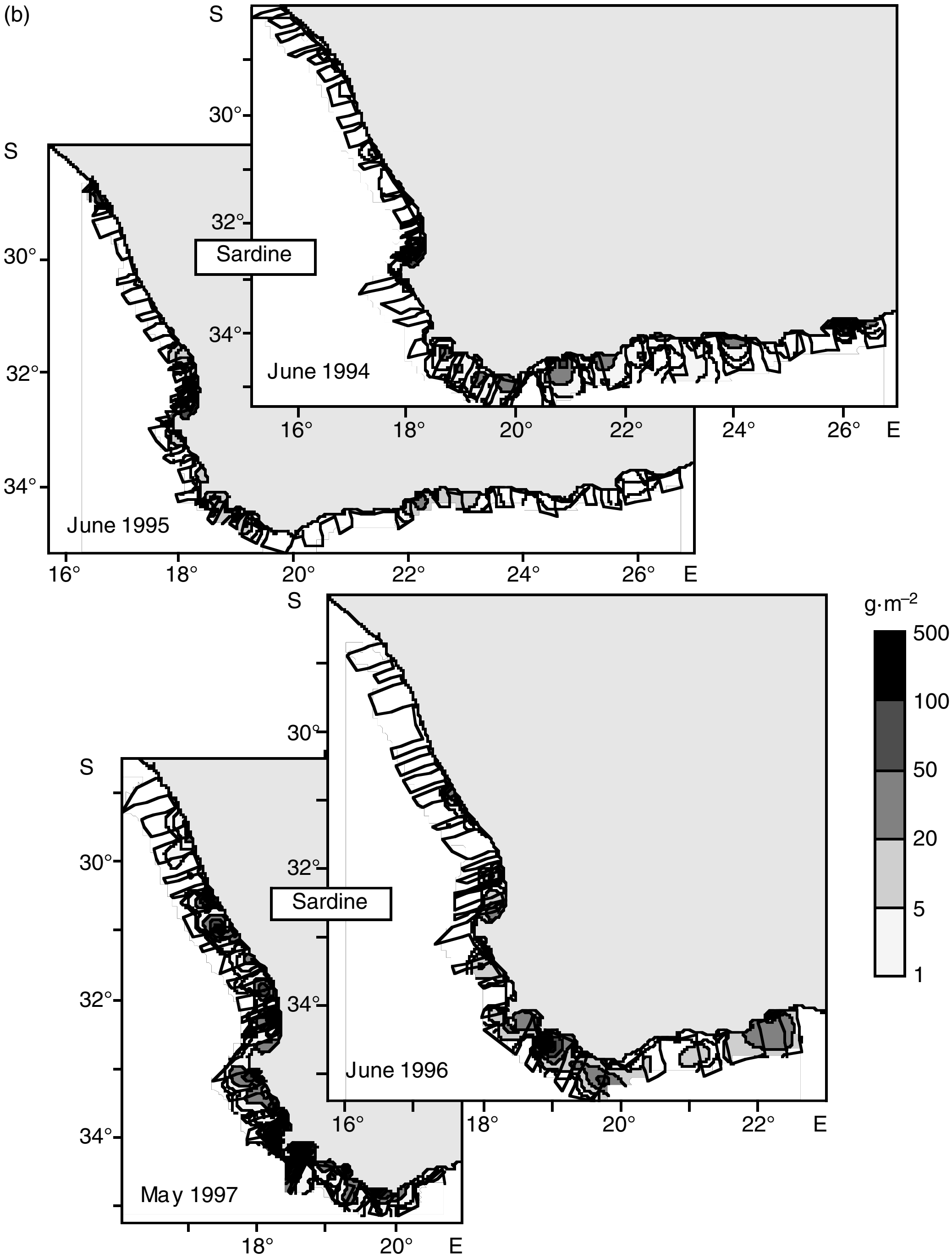


Fig. 5: *(continued)*

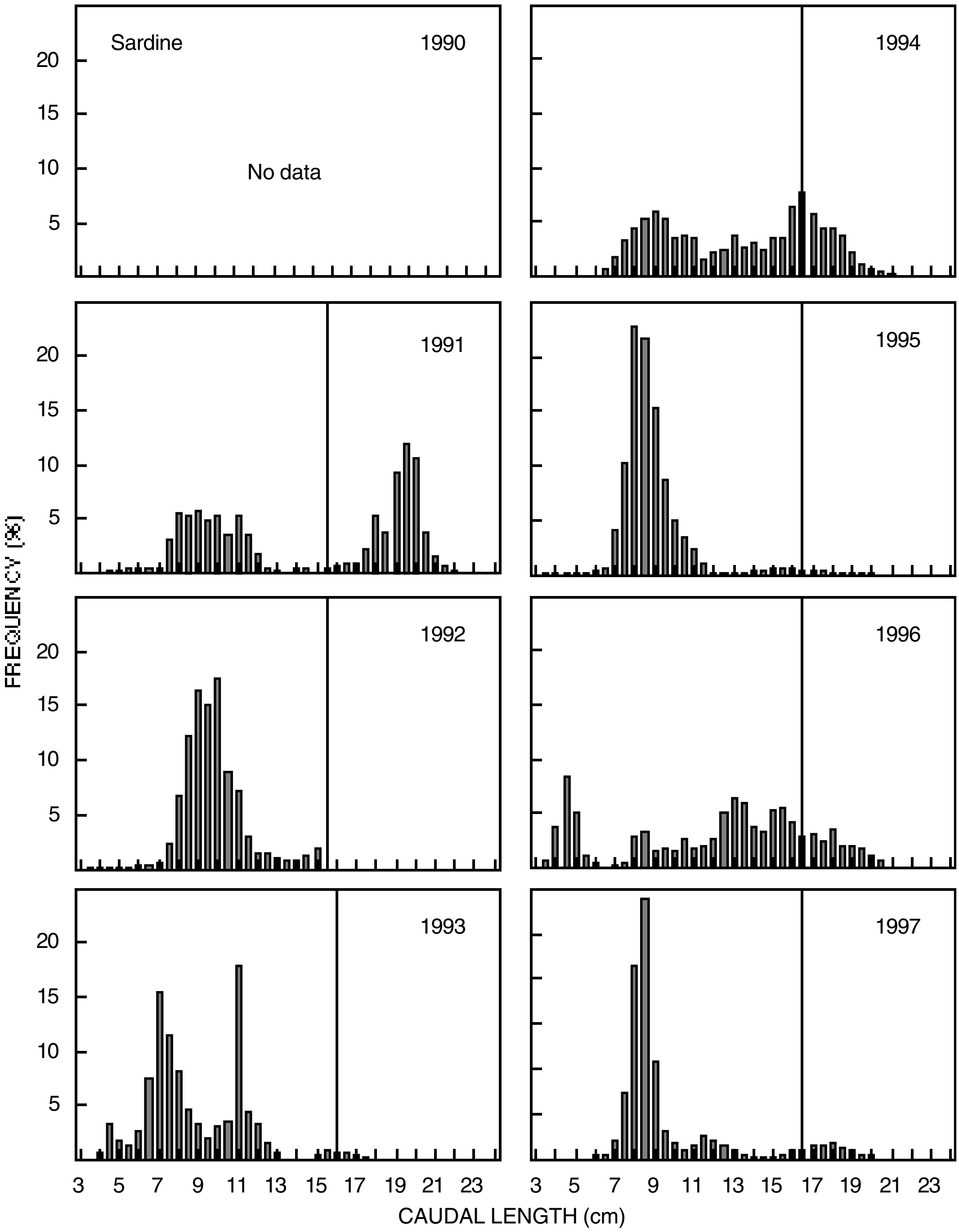


Fig. 6: Acoustically weighted size frequencies of sardine obtained from recruitment survey catches, 1990–1997. The length division between recruits and adults is shown

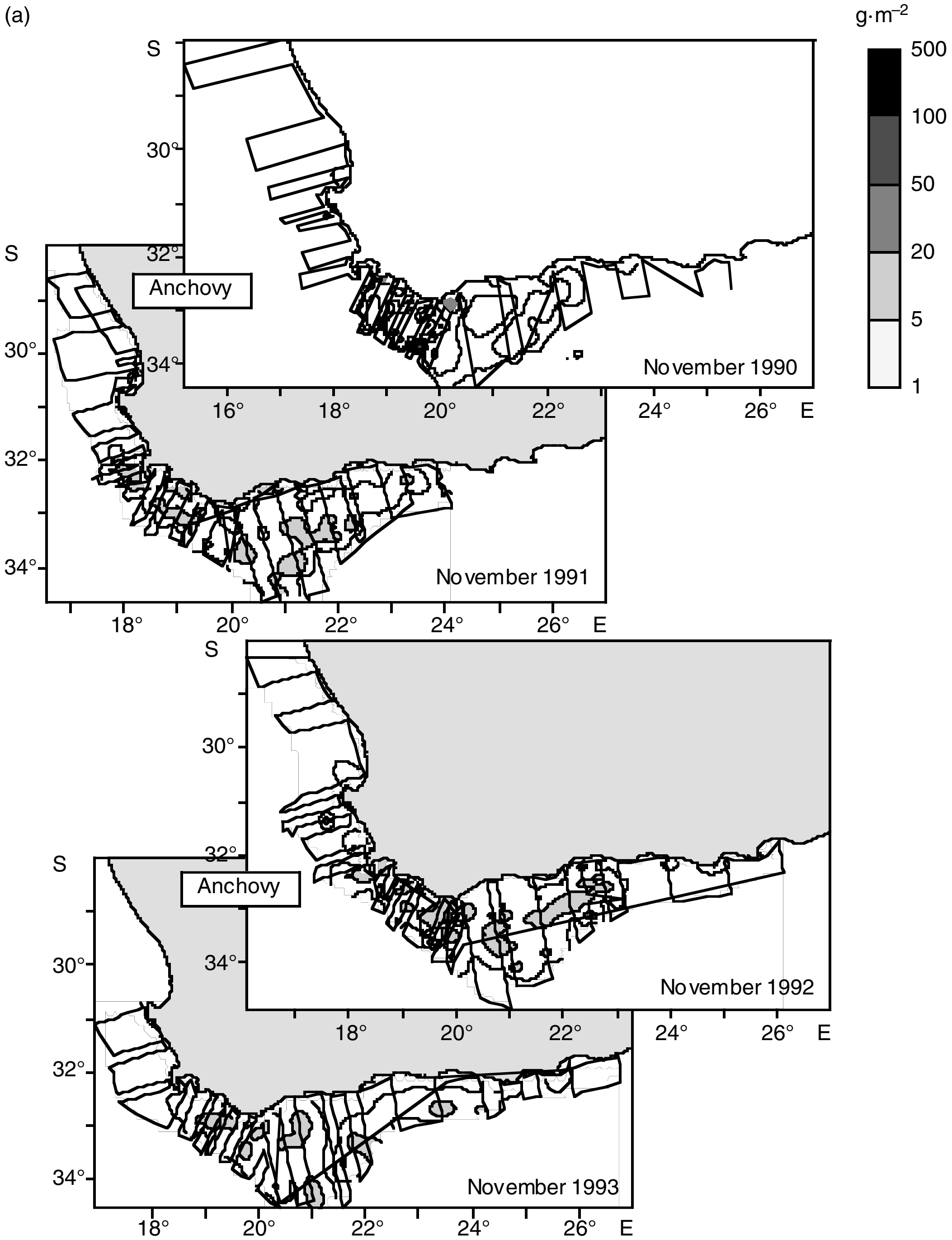


Fig. 7: Distribution of anchovy spawner biomass deduced from acoustic surveys, 1990–1993, (b) 1994–1997, using interpolation by kriging. The survey tracks are shown

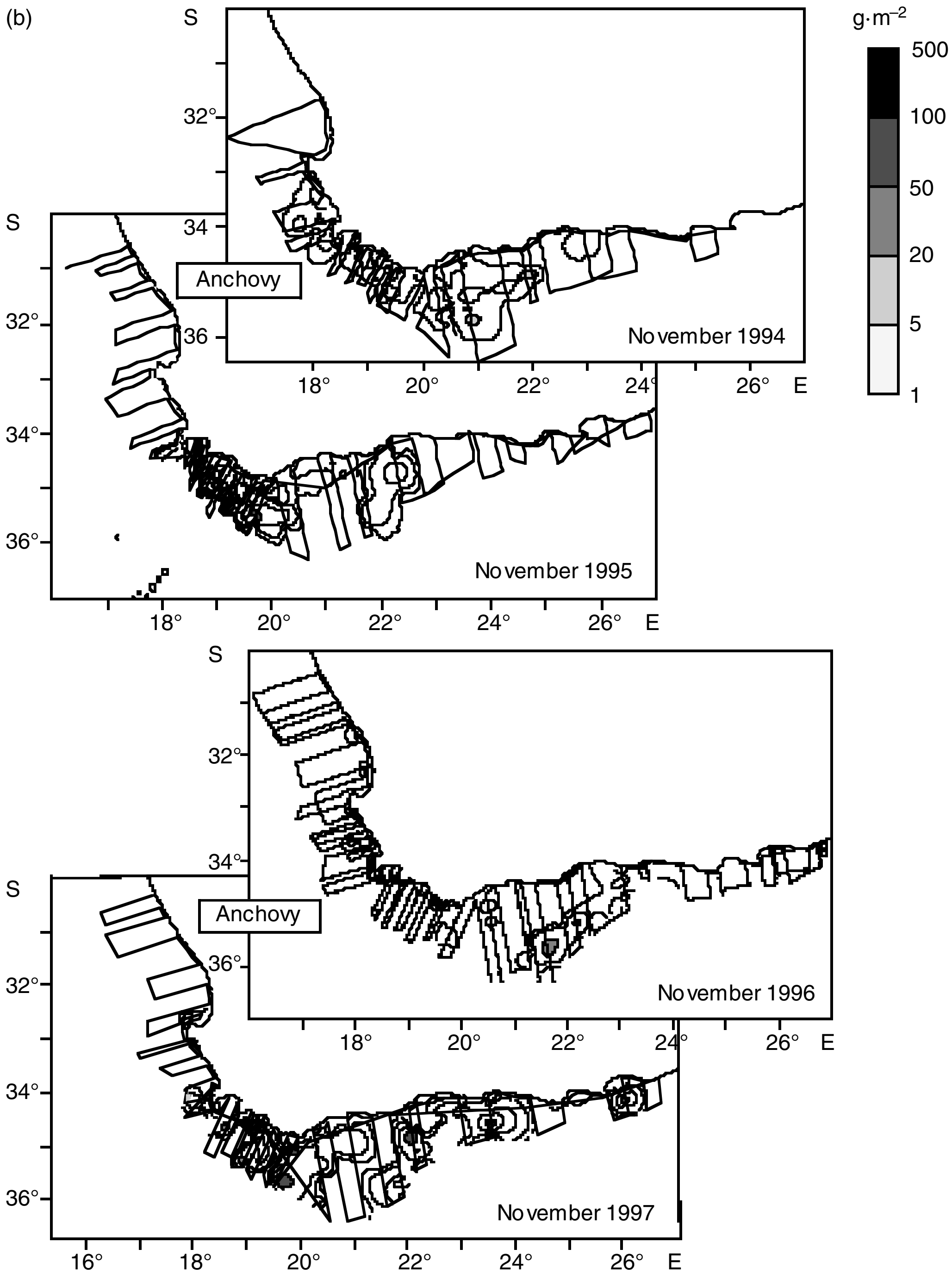


Fig. 7: *(continued)*

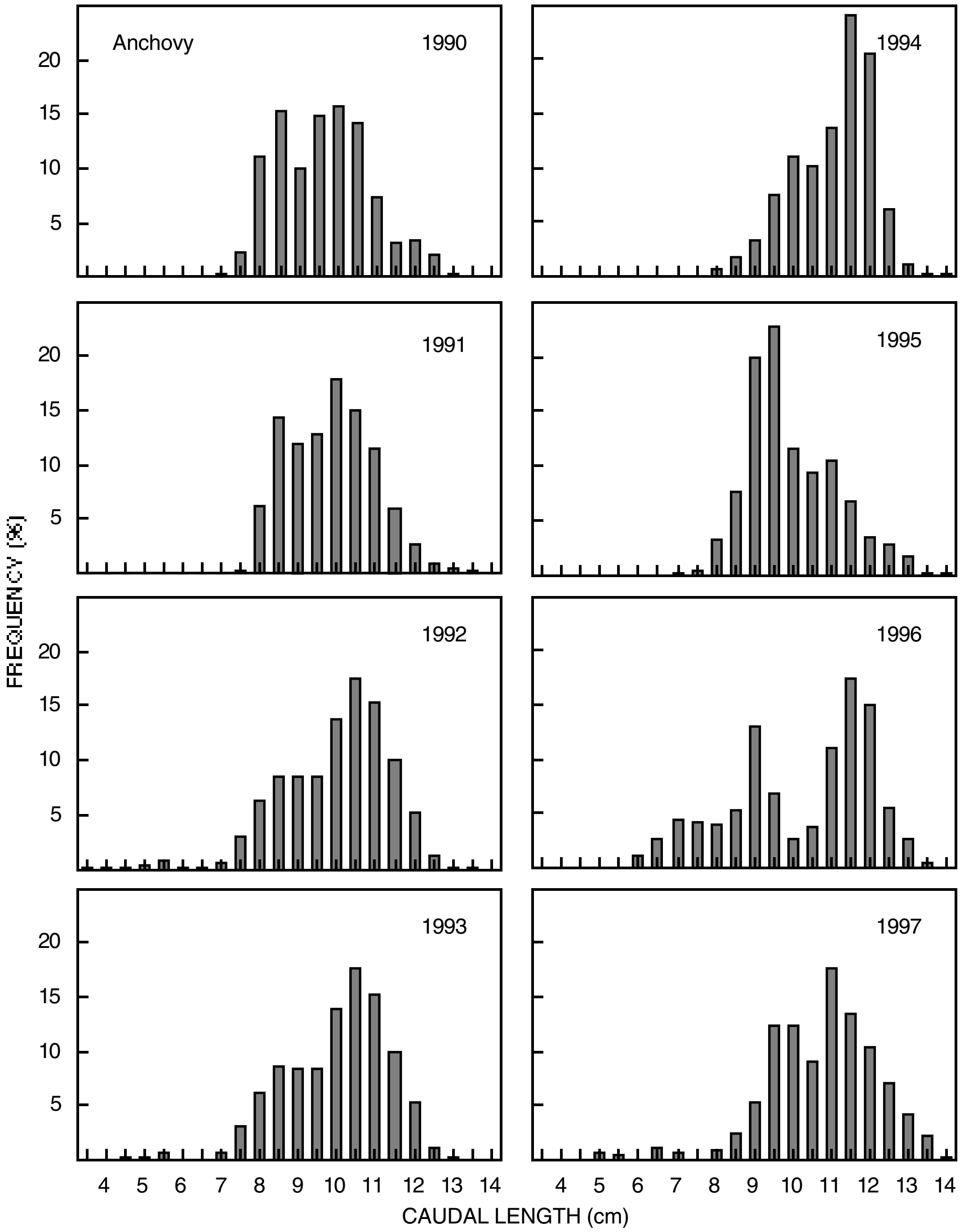


Fig. 8: Acoustically weighted size frequencies of anchovy obtained from the spawner biomass survey catches, 1990–1997

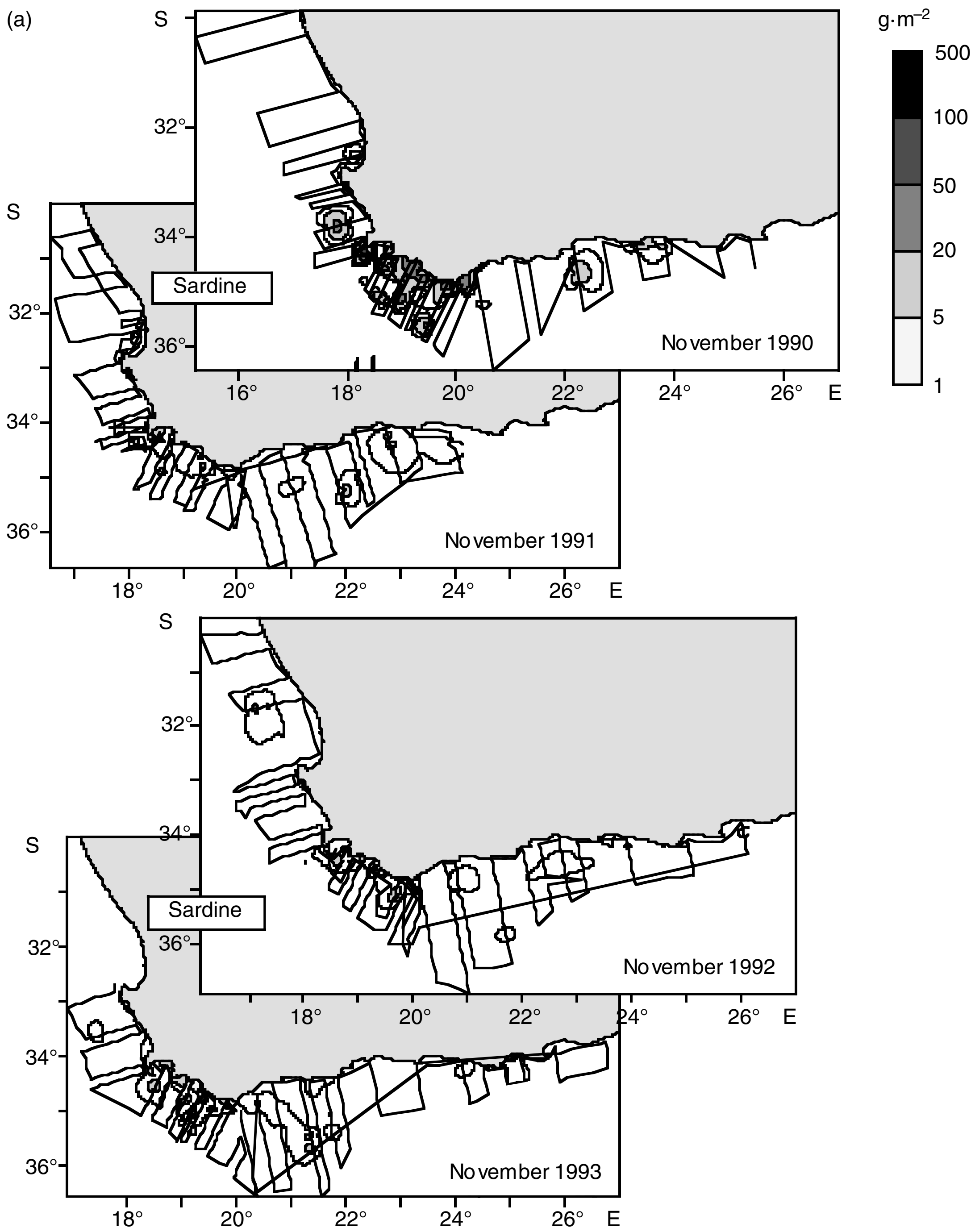
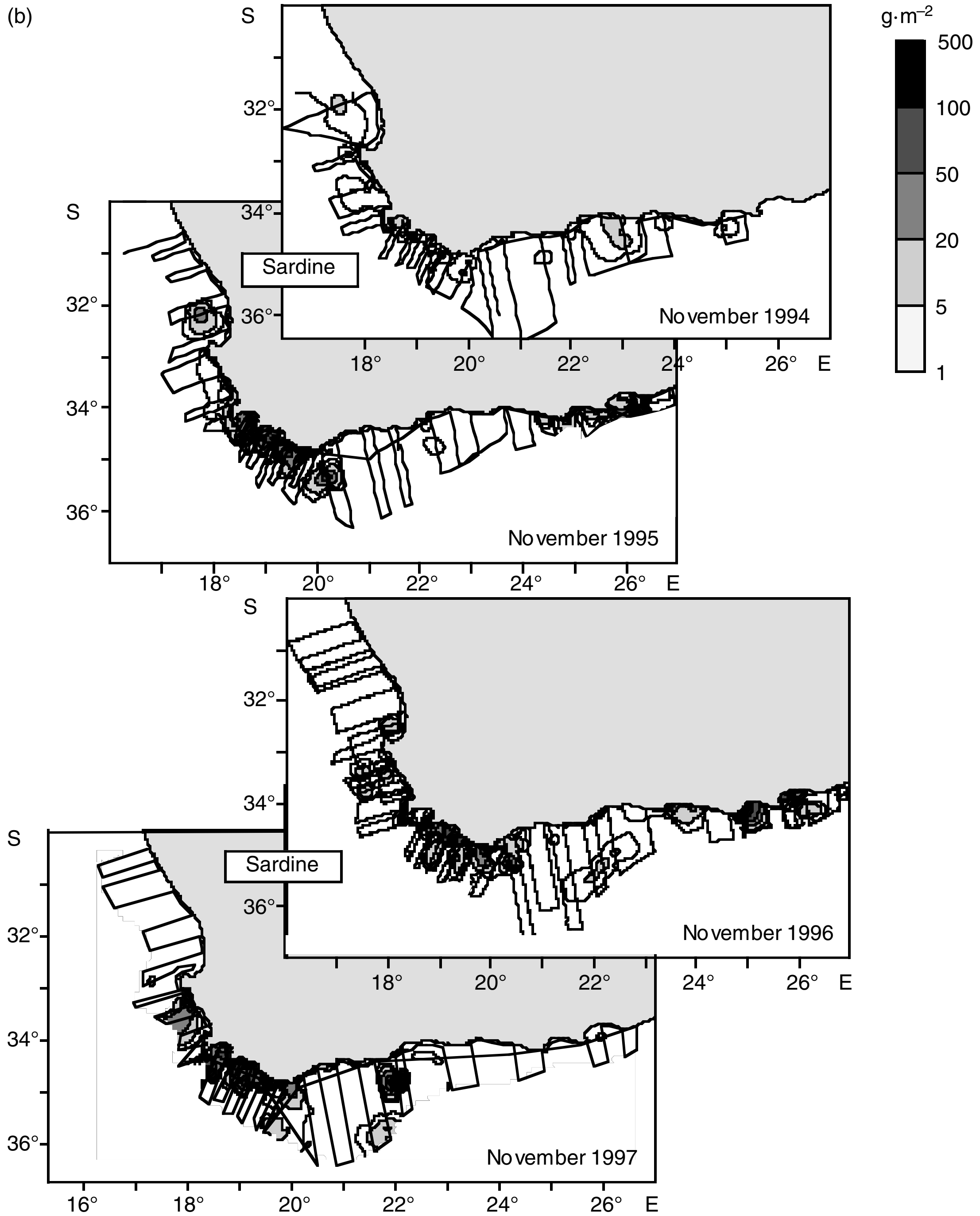


Fig. 9: Distribution of sardine spawner biomass deduced from acoustic surveys, 1990–1993, (b) 1994–1997, using interpolation by kriging. The survey tracks are also shown



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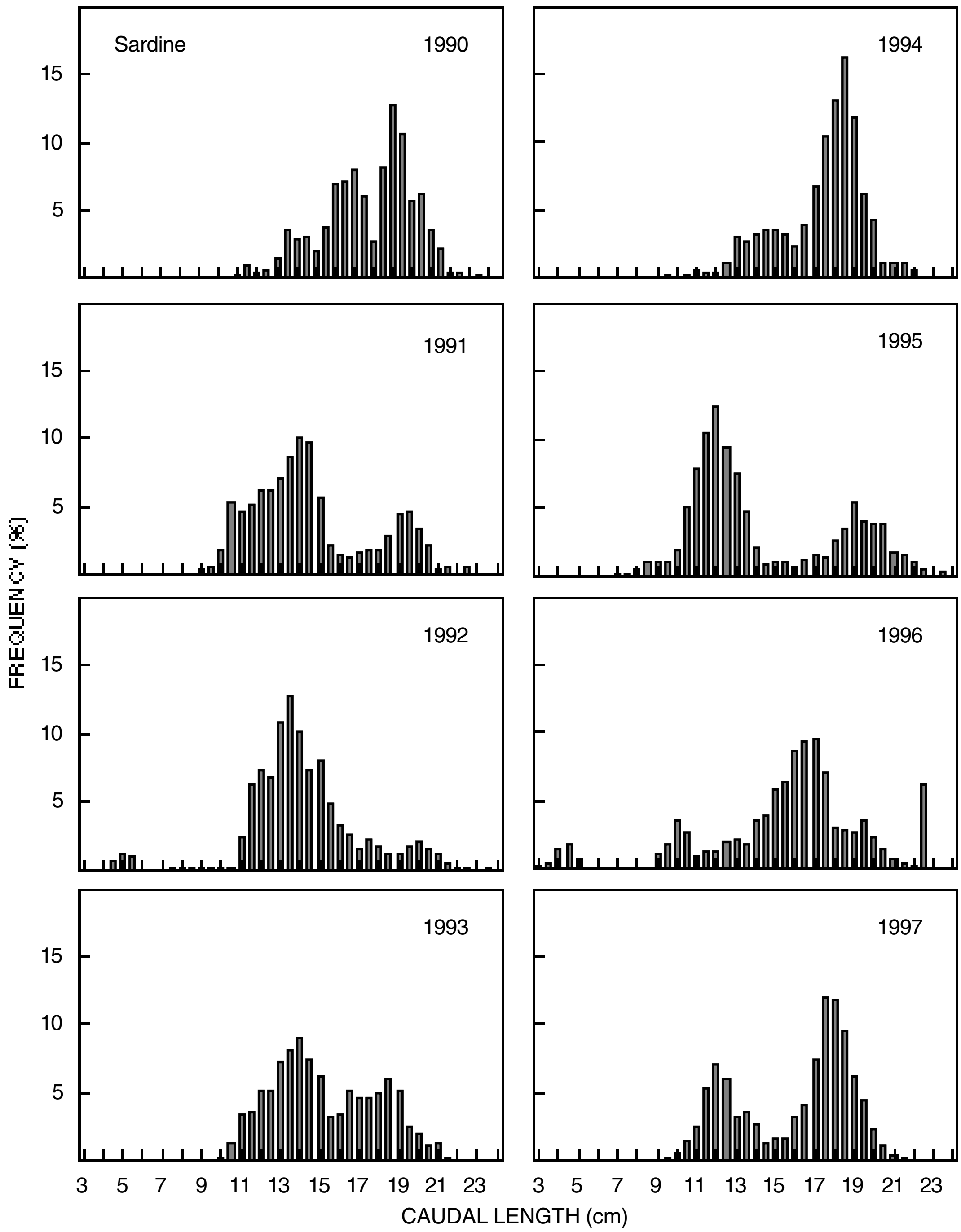

Fig. 10: Acoustically weighted size frequencies of sardine obtained from the spawner biomass survey catches, 1991–1997

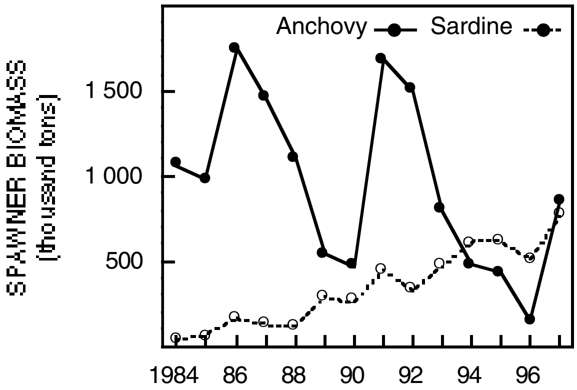

Fig. 11: Time-series of acoustic estimates of anchovy and sardine spawner biomass, 1984–1997

(Fig. 7). The distribution was centred over the mid-shelf. In 1995, 1996 and 1997 (and possibly in 1990), there was a degree of separation between the eastern and western Agulhas Bank populations. The eastern portion of the population was often found close to the Mossel Bight (Fig. 1). This region is characterized by intrusion of Agulhas Current water onto the shelf and the formation of counter-currents (Boyd and Shillington 1994), which is caused partially by the narrowing of the Bank to the east (Fig. 1). The phenomenon was particularly evident in 1996, when most of the fish were associated with a region of reversed (eastward) flow (Boyd and Barange in prep.). Fish from the eastern population were larger and older than those from the western population. The separation between the populations on either side of the Bank tended to disappear when the stock size was at its maximum (e.g. in 1991 and 1992). An analysis of the biomass per stratum indicates that a low, but appreciable, proportion of the adult stock is found on the West Coast in years of large anchovy biomass (Table IV). On the other hand, the proportion of the stock on the central and eastern Agulhas Bank combined appears to have increased since 1990 (Table IV).

The mean size of anchovy was similar between 1990 and 1992 (Fig. 8), confirming the belief that most fish are 1-year olds at the time of the surveys (Hampton 1992). The increase in mean size between 1992 and 1994 was likely a result of poor recruitment levels and a concomitant larger proportion of older fish in the population during that period.

SARDINE

Peak densities of sardine spawners were inshore of

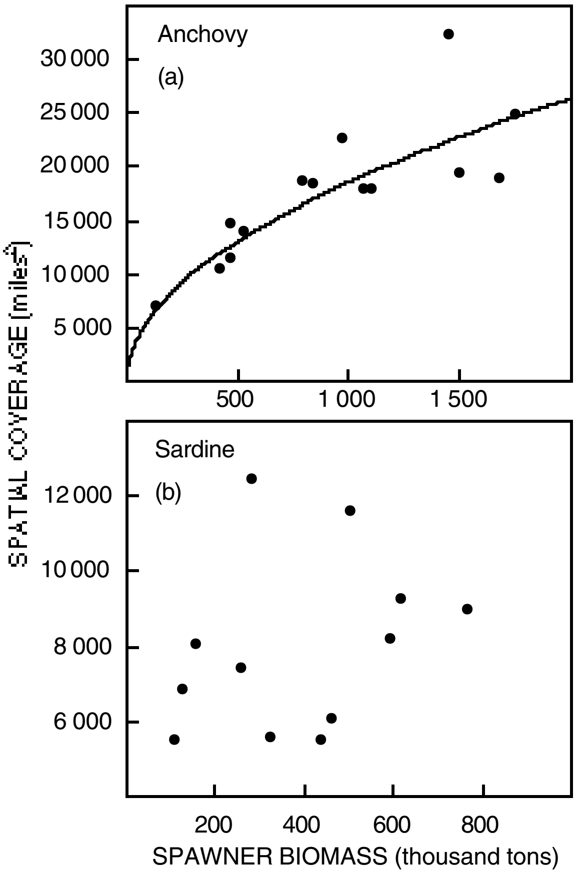

Fig. 12: Relationship between size and spatial coverage of (a) anchovy and (b) sardine stocks for the period 1984–1997

anchovy spawners, mostly on the western Agulhas Bank (Fig. 9). There were isolated populations on the West Coast during most surveys, but they were often concentrated farther offshore than the sardine on the western Bank. In recent years (particularly 1995 and 1996), appreciable proportions of the stock were found in the eastern part of the survey grid. These fish were mainly 1- and 3+-year olds in 1995 and 2-year olds (15–17 cm modal length) in 1996. In later years, when the anchovy stock was low, sardine were more offshore.

Sardine size frequencies (Fig. 10) tended to follow recruitment trends established during the recruitment surveys. In 1991, 1992, 1993, 1995 and 1997, there were large peaks of 12–15 cm fish, reflecting the large numbers of 8–10 cm recruits sampled six months

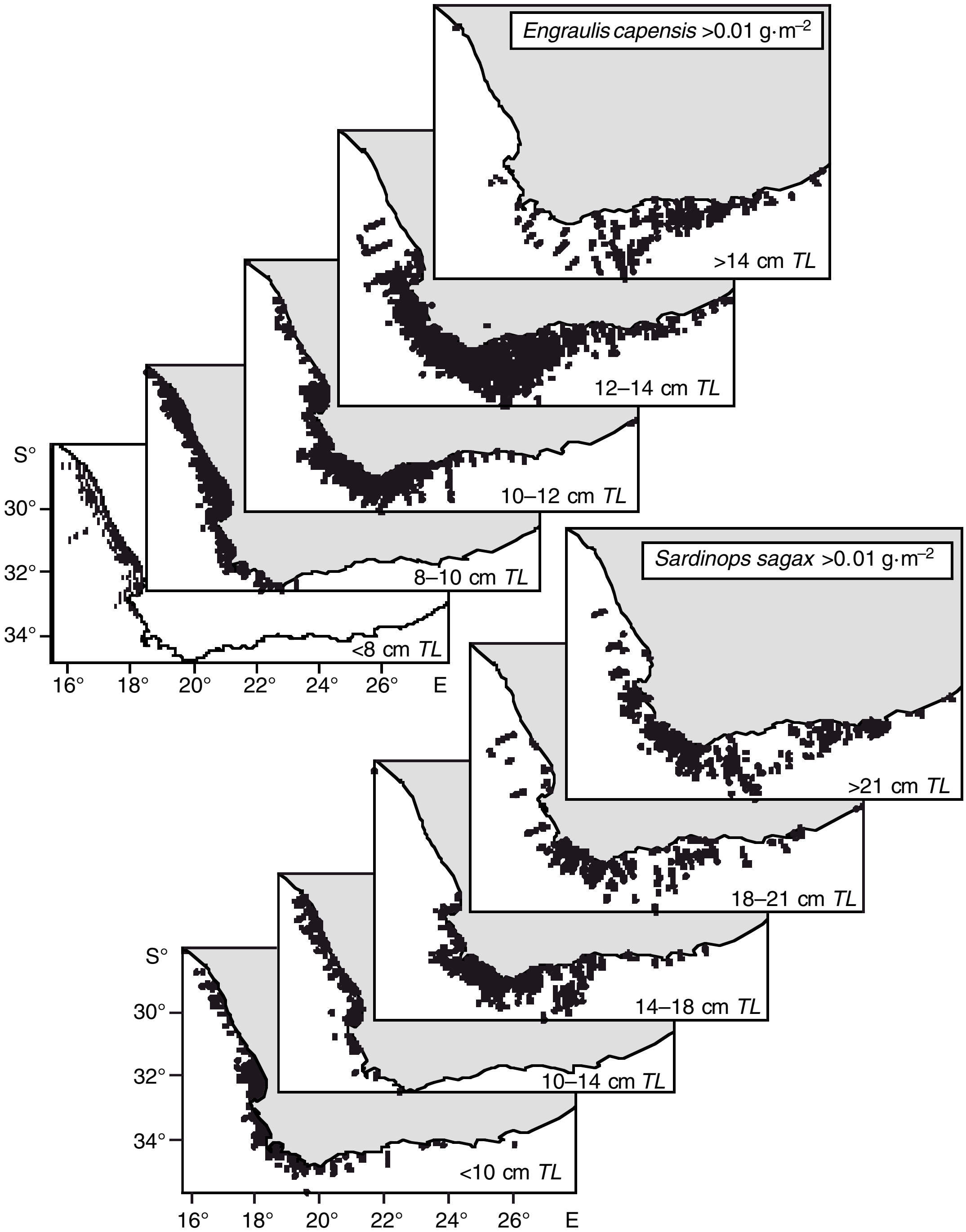

Fig. 13: Distribution of anchovy and sardine by size derived from all acoustic/midwater trawl surveys for the period 1984–1996

earlier (Fig. 6). The stock size of sardine has been increasing steadily during the past decade, with the possible exception of 1996 (but note the high *CV*s, Table IV), when, in addition to poor recruitment, the high biomass of 1year-old fish in 1995 was not reflected in the following year. This could be attributable to the high mortality of the adult stock in 1996.

Contrary to anchovy, for which large fluctuations in spawning biomass have been observed since the beginning of the time-series (Fig. 11), biomass of sardine have steadily recovered, particularly since 1990.

Spatial versus stock size

Anchovy seem to expand their spatial distribution in years when stock size is large and to contract it when the stock is small (Fig. 12). However, the relationship between spatial distribution and stock size is less clear for sardine, possibly because of the spatially less coverage and the smaller biomass levels observed during the surveys.

To investigate the migratory movements of anchovy and sardine along the South African seaboard, size-class data obtained from recruitment and spawner biomass surveys are presented (Fig. 13). Most young anchovy inhabit the West Coast, shifting southwards and eastwards with increasing size. Young sardine follow a similar trend, but older fish seem to spread both eastwards and northwards. Of note is the separation in the sardine population around Mossel Bay for fish >14 cm, particularly for the larger (>21 cm) fish.

Relationship between recruits and spawning

There was a positive, significant relationship ($p < 0.05$) between anchovy and sardine spawner biomass and the strength of their respective recruitment, estimated approximately five months earlier (Fig. 14a, b). Recruit values were derived from the survey estimates back-calculated to the beginning of the year, taking natural and fishing mortality into account (Butterworth *et al*. 1993). This relationship held for anchovy, except in 1995 when a good recruitment was followed by a small biomass of adults at the end of the year. A significant relationship is perhaps unexpected for sardine, because several age-classes contribute to the adult biomass and therefore the stock should not respond directly to good or bad recruitment. The regression appears to be driven by the large recruitment estimates for 1993, 1995 and 1997. Anchovy and sardine recruitment appears to be uncorrelated, partially as a result of the poor sardine recruitment and low adult biomass levels prior to 1990. However, recruitment levels of both species from 1990 to 1997 have followed a similar trend ($r = 0.74$, $p = 0.051$). However, this trend was not supported by the 1998 survey data (data not shown).

DISCUSSION

The ongoing acoustic survey programme of spawner and recruitment biomass of pelagic fish has formed the basis for management of the anchovy resource since 1985 (De Oliveira 1995) and sardine since 1987 (De Oliviera *et al*. 1998). It has therefore proven its worth in the management of a fishery whose landings amount to a wholesale value in excess of US$ 80 million per year (Cochrane *et al*. 1998). The stability in the programme has allowed for the development of a robust assessment procedure, ensuring that management decisions are based on the best scientific information available, which is critical to the implementation of responsible fisheries management (F.A.O. 1997).

Distribution patterns

Adult anchovy and sardine concentrate over the Agulhas Bank during summer, coinciding with their major spawning season in the southern Benguela (Crawford 1980, Crawford *et al*. 1980, Armstrong *et al*. 1985, 1987, 1988, 1991, Hampton 1987, 1992). Sardine occur closer inshore than anchovy (Hampton 1992, Barange and Hampton 1997), but this pattern may be seasonal (Hampton 1992). From trends in fish size, Armstrong *et al*. (1991) and Hampton (1992) suggested that, during their second year of life, anchovy move eastwards across the shelf. The present results substantiate this belief (Fig. 13), which shows eastward and offshore shift of fish with age. The suggestion by Roel *et al*. (1994) that anchovy stocks may remain off the West Coast during periods of particularly high biomass cannot be tested using the present data, because the anchovy resource has been generally declining in recent years.

The results show that sardine recruits reside mainly on the West Coast, and move to the Agulhas Bank as they get older. Thereafter they disperse both eastwards and northwards along the West Coast. The sardine recorded on the eastern Agulhas Bank during the period 1994–1996 (Fig. 13) may not be a result of this migratory trend, but rather as a consequence of an influx of adult fish returning from their winter excursion up the East Coast. Spawning by sardine has been observed in Eastern Cape waters and off KwaZulu-Natal (Beckley and Hewitson 1994, Connell 1996), but the low density of juvenile sardine found in that area

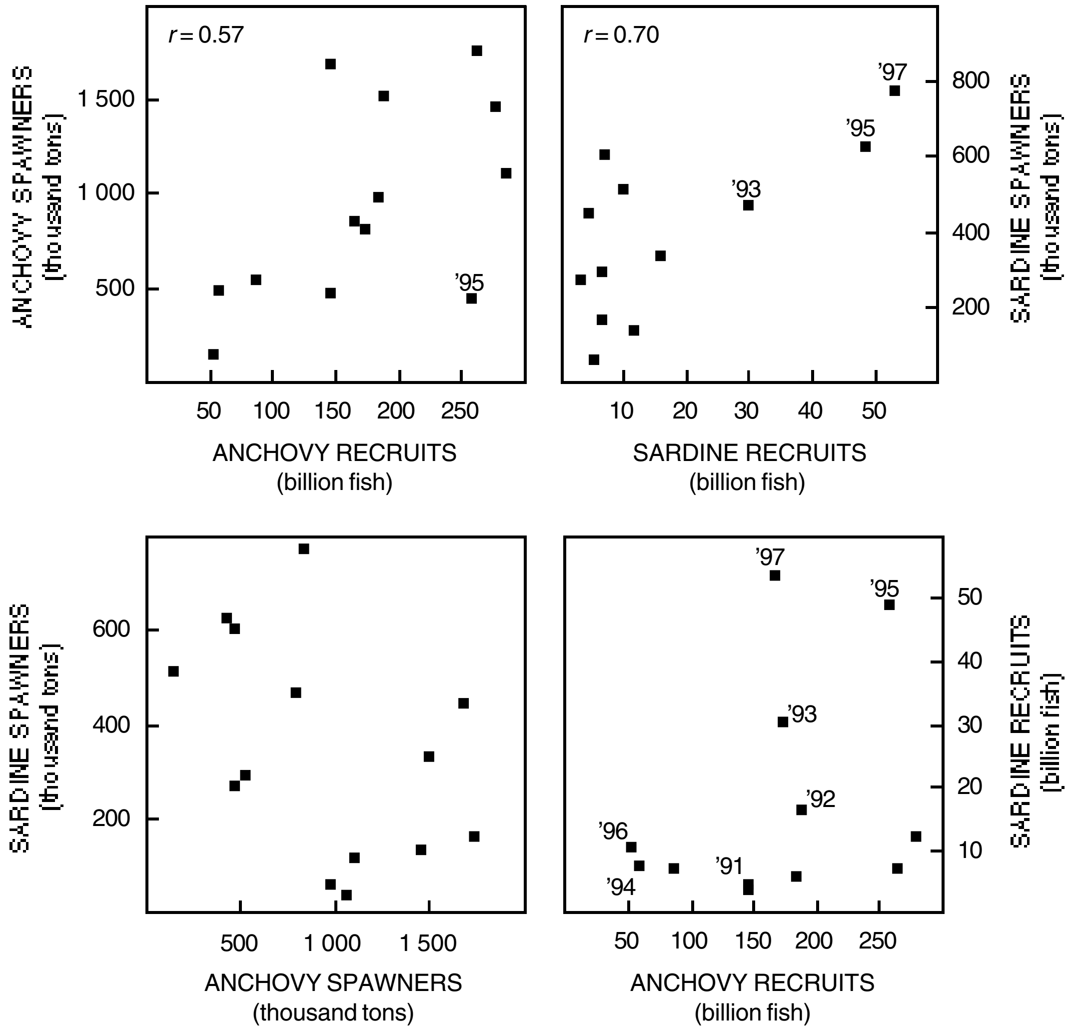

Fig. 14: Relationships between anchovy and sardine spawner and recruit biomass for the period 1984–1997. Significant correlation coefficients ($p < 0.1$) are shown

(Fig. 13) suggests that there is little recruitment there. It is suggested here that part of the adult sardine population moves towards the warmer edges of the southern Benguela system with age, whereas the core of the adult stock remains on the Agulhas Bank. The linkages between these different components of the sardine stock are still poorly understood, including the phenomenon of the annual "sardine run" that develops in KwaZulu-Natal and the Eastern Cape in winter. This phenomenon has generated some debate on the integrity of the sardine stock as well as the wisdom of limiting the spawner biomass survey to Port Alfred. In addressing this issue, Baird (1971) concluded that sardine populations off KwaZulu-Natal originate in the region of the Cape and may migrate eastwards with the help of inshore countercurrents. This theory is supported by the present data. However, Armstrong *et al.* (1991) reported that, whereas sardine densities on the East Coast are fairly high, the productive area is too small to contribute appreciably to the total adult stock.

Table V: Results of a multiple regression model of anchovy and sardine spawner biomass as a function of the recruitment-of-the-year and the biomass of adults in the previous year's survey. The regression is forced through the origin. Significantly values ($p < 0.05$) are highlighted

Parameter	Anchovy			Sardine		
	Mean biomass(tons)	Beta	p	Mean biomass(tons)	Beta	p
R^1_n	66 706	−0.26	0.47	69 908	−0.06	0.82
R^2_n	183 669	**0.835**	0.03	65 185	0.678	0.22
$S^1_{n\text{-}1}$	260 408	0.130	0.72	138 008	−0.25	0.54
$S^2_{n\text{-}1}$	504 035	0.323	0.48	321 562	**0.618**	0.08
N	8 (1990–1997)			7 (1991–1997)		
ANOVA (p)	0.012			0.013		
R^2	0.933			0.968		
Cut-off R^1/R^2	7 cm			10 cm		
Cut-off $S^1_{n\text{-}1}/S^2_{n\text{-}1}$	10 cm			15.5 cm		

R^1_n = Biomass of late recruits in year n
R^2_n = Biomass of early recruits in year n
$S^1_{n\text{-}1}$ = Biomass of young adults in year n-1
$S^2_{n\text{-}1}$ = Biomass of older adults in year n-1
R^2 = Proportion of the explained variability about the origin

Therefore, it is concluded that the current survey coverage is sufficient for management purposes.

Stock fluctuations

The biomass of adult anchovy has fluctuated over an order of magnitude during the period 1984–1997. Such fluctuations have been observed elsewhere. Sedimentary records of fish scales in the California Current have showed that large fluctuations in sardine and anchovy abundance were common in that region even before the advent of large-scale fishing (Baumgartner *et al*. 1992).

In order to understand the factors that control the strength of anchovy biomass, a model was fitted using survey estimates of recruit biomass and the biomass of adult fish in the previous year as independent variables. To account for differences in fish mortality with age, the variables were subdivided into early and late recruits and 1-year-olds and older fish, on the basis of fish length (Table V). The results show that the fluctuations in the end-of-year anchovy biomass are largely driven by the strength of the early recruitment (fish spawned between October and December), whereas late recruitment (January–March) may not contribute appreciably to the adult biomass. This emphasizes the need to separate early and late recruits before interpreting the results of recruitment surveys in the future.

Sardine abundance has been increasing over the survey period (1985–1997). This has been partially attributable to the careful management strategy to rebuild the stock (Cochrane *et al*. 1998). Given that several age-classes contribute to the adult stock of sardine, the relationship between adult and recruit biomass is not expected to be as strong as it is for anchovy. It is likely that the current high level of biomass of sardine is a result of the above-average recruitment observed in 1995 and 1997. Therefore, the mechanisms that resulted in the high mortality of anchovy recruits in the second half of 1995 did not have a similar effect on the sardine recruits. Using the same modelling exercise for sardine as described earlier for anchovy (Table V), it is evident that the sardine spawner stock size in any given year is best explained on the basis of the biomass of adult fish in the previous year. Therefore, the biomass of adult sardine is less dependent on the year's recruitment and displays smaller fluctuations in stock size than anchovy.

Given the different trends in the biomass of anchovy and sardine, the significant correlation found between recruit numbers of those species for the period 1991–1997 (but not 1998) indicates that spawning success and larval survival for both species may have been controlled by the same environmental and biological factors during that period. This does not seem to be the case for those factors influencing the survival of the recruits. For example, in 1995, it seems that transport processes between the recruitment and the spawning grounds may have determined anchovy mortality more so than that of sardine, possibly because a substantial proportion of the sardine population remains east of Cape Point throughout the year.

Studies in other upwelling areas (e.g. the Chile-Peru Current) suggest that anchovy prefer a relatively cold environment, whereas sardine favour warm conditions (Yañez *et al*. 1998). In the southern Benguela, Boyd *et al*. (1998) postulated that fluctuations in anchovy recruitment could be influenced strongly by advective losses during periods of strong South-East winds, coinciding with the global signal of the high phase of an ENSO event. If transport from the spawning to the recruitment grounds and potential advective losses are important factors in determining the success or failure of anchovy and sardine recruitment in the southern Benguela, then differences in the timing of their spawning peaks should be considered. Anchovy spawn primarily in summer (December–March), during the peak upwelling season (Richardson *et al*. 1998), whereas sardine have a protracted spawning period, peaking in September–October and February–March (Shelton 1986), on either side of the maximum upwelling period. Such differences in their spawning strategy and the lesser dependence of the sardine stock on a consistently successful recruitment to maintain a healthy adult biomass are some key considerations in explaining differences in the fluctuations in sardine and anchovy abundance in the southern Benguela.

Spatial versus stock size

The area occupied by adult anchovy appears to be related to the size of the stock (Fig. 12). This supports MacCall's (1990) hypothesis that populations expand their geographical range with increased abundance, as individuals begin to occupy poorer habitats. This suggests that fish density remains constant, at least until all suitable habitats are occupied (Swain and Sinclair 1994). This trend was not observed for sardine, although the range of stock sizes and spatial coverages were not as extensive as for anchovy. It may be speculated that increases in sardine stock size are directly reflected in the actual densities of the schools, without a necessary corresponding increase in spatial coverage. Work is currently under way to investigate this possibility. In this context, it is noteworthy that anchovy are particle-feeders in the southern Benguela, a strategy that requires that a minimum distance be maintained between individuals to ensure successful feeding (Van der Lingen 1994). However, sardine are filter-feeders and would not necessarily benefit energetically from maintaining a constant school density. This reasoning supports the contention that both species may have different strategies of occupying space, something that has implications for the design of surveys aimed at estimating the size of both stocks concurrently (Barange and Hampton 1997).

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