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MODELLING ENVIRONMENTAL EFFECTS ON THE EARLY LIFE HISTORY OF THE SOUTH AFRICAN ANCHOVY AND SARDINE: A COMPARATIVE APPROACH

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By means of modelling, the South African anchovy *Engraulis capensis* and sardine *Sardinops sagax* are compared in terms of spawning, transport and survival of young stages. As there is variability in the areas across which adult anchovy and sardine spawn, two contrasting egg distritutions were modelled for each species. Dissimilarities found between the two species can be attributable to (i) differences in egg distributions, and hence in the paths along which eggs and larvae are transported passively by currents, (ii) differences in survival rates of eggs and larvae, (iii) differences in duration of stages until swimming age and (iv) differences in the duration of the spawning season. In the absence of advective losses, more anchovy reached swimming age than did sardine. However, anchovy spawned in regions that are more susceptible to advective losses. Adult biomass levels were low in the years when anchovy and sardine spawning was restricted to the South Coast. Also, advective losses of both species were greater when spawning distributions were contracted. Higher proportions of young reached the West Coast when spawning extended over the South and up the West coasts. Sardine accumulated farther west than anchovy. Anchovy eggs and larvae were lost to advection mainly on the South Coast between Cape Agulhas and Mossel Bay, whereas advective losses of sardine were restricted to areas west of the Cape Peninsula.

In upwelling regions in which anchovy *Engraulis* spp. and sardine *Sardinops sagax* co-occur, shifts in the dominant species have been observed on a decadal scale (e.g. Lluch-Belda *et al*. 1992). Spatial variation of anchovy and sardine is associated with these changes in abundance. Both species expand and contract the area they inhabit as stocks increase or decrease in size. Sardine often show shifts in a longshore direction, whereas anchovy tend to expand or contract their range about a geographic centre (Lluch-Belda *et al.* 1989). Sardine are generally more migratory than anchovy, often expanding their spawning areas upstream during times of increased abundance, for example in the Humboldt system (Lluch-Belda *et al.* 1992), off Japan (Kobayashi and Kuroda 1991) and in the southern Benguela system (Crawford 1981a). This may have the advantage of enhancing the transport of their eggs and larvae to additional nursery areas, which may be beneficial to the stock as it increases in size (Kobayashi and Kuroda 1991).

Sardine in the waters off central Japan can be divided into two groups, each having different migratory characteristics (Hiramoto 1991). Those in the open ocean are slow to mature, migrate over long distances and increase in abundance approximately every ten years. In contrast, sardine in coastal regions and in bays mature quickly, have limited migratory ranges and maintain a stable, low abundance (Hiramoto 1991). Sardine are often less migratory at low abundance, tending to adopt a similar strategy to anchovy during such periods. Lluch-Belda *et al.* (1989) suggest that this behaviour may be a result of the limited migratory capacity of the sardine stock when it consists mostly of young fish, as a result of high mortality rates. Those authors propose that intensive fishing may cause sardine to shift prematurely from a phase of high to one of low abundance, by reducing their lifespan and consequently their migration range.

Fish catches in the South-East Atlantic showed long-term meridional shifts (Crawford and Shannon 1988). Catches were displaced southwards during the late 1950s and 1960s and northwards in the mid 1970s, with similar displacements in predators (Crawford and Shannon 1988). According to those authors, trends in the distribution of fish catches in the southern Benguela correspond to the cumulative Southern Oscillation Index (SOI). This is at least partly explained by changes in leakages of Agulhas Current water around Cape Point and changes in the Antarctic Circumpolar Current, both of which depend on the macroscale wind field. The latter theory is supported by the model of Tyson (1986), which showed that westerly winds contract polewards and become stronger in the south during the high (wet) phase of

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the SOI, but weaken and expand northwards during the low phase (Crawford and Shannon 1988).

During periods of negative sea surface temperature anomalies off Namibia, spawning in sardine and anchovy shifted northwards, whereas spawning occurred both to the north and farther south during periods of positive sea surface temperature anomalies (Le Clus 1990). Fish catches matched these trends in egg abundances (Crawford and Shannon 1988). However, anchovy in the northern Benguela are often slower to respond to environmental change than sardine (Le Clus 1990). They respond differently when there is a transition from negative sea surface temperature anomaly to zero or positive anomalies (Le Clus 1990). Anchovy tend to avoid unfavourable spawning conditions by spawning early in the season. However, spawning by sardine in the north early in the season may expand southwards as conditions improve. Le Clus (1990) stressed that changes in locality of spawning do not necessarily result from changes in age structure or biomass of the stock, or from genetic differentiation. However, should altered environmental conditions result in changes in transport of eggs and larvae, changes in biomass may ultimately occur (Le Clus 1990).

Enrichment, concentration and retention are the three elements of Bakun's (1996) "fundamental triad" of factors which play vital roles in determining suitable habitats for reproduction by marine organisms. The present study considers the retention processes. It has been proposed that surface drift of eggs and larvae is a dominant environmental factor influencing recruitment of pelagic fish in the California system (Parrish *et al.* 1981). Many fish rely on transport of eggs and larvae from spawning grounds to nursery areas by currents (Norcross and Shaw 1984, Cushing 1986). Using a three-dimensional circulation model driven by tides, wind stress and inflow from the Scotian Shelf, Werner *et al.* (1993) examined the distribution and retention of cod and haddock larvae at different depths on the Georges Bank. Bernsten *et al.* (1994) used a three-dimensional model of transport of particles to represent the transport of larvae of sandeel *Ammodytes* sp. in the North Sea. Both those studies found that retention of larvae was extremely important in producing good year-classes. A numerical model of advection and diffusion of eggs and larvae of Japanese sardine *Sardinops melanostictus* indicated that their survival is significantly affected by onshore drift in the region, induced by the winter monsoon (Kasai *et al.* 1992). Norwegian capelin *Mallotus villosus* and North Sea herring *Clupea harengus* stocks are sustained by fish transported by currents from Iceland to the Norwegian coast (Bjørke and Sætre 1994). By means of a three-dimensional advection model of North Sea herring, Bartsch *et al.* (1989) showed that environmental modelling can improve the understanding of interannual variability in fish recruitment. Variability in mechanisms transporting fish larvae can often explain differences in distributions between years. For example, an advective model of larval drift of walleye pollock *Theragra chalcogramma* off Alaska highlighted interannual differences in the transport and distribution of larvae, linking these to differences in the mean large-scale atmospheric pressure systems prevailing during the same periods in different years (Hermann *et al.* 1996).

Off South Africa, anchovy *Engraulis capensis* spawn on the South Coast and their eggs and larvae are transported northwards in the shelf-edge jet current to nursery grounds along the West Coast (Shelton and Hutchings 1982). Modelling studies by Shannon (1995) and Shannon *et al.* (1996) of anchovy transport and advective processes off South Africa showed that the position of spawning in the flowfield, as well as perturbations of the flowfield, could account for a substantial proportion of the observed interannual variability in year-class strength. This paper expands on those studies by addressing the differences and similarities between South African anchovy and sardine, based on the influence of advection of eggs and larvae from different spawning areas. The study attempts to compare the role of passive transport in the survival of young stages of anchovy and sardine.

COMPARISON OF SARDINE AND ANCHOVY LIFE HISTORIES

South African anchovy and sardine show many similarities in their life histories, but differ in some respects. It is presumably in these differences, and therefore in the manner in which the two species react to certain environmental events or changes, that the secret to shifting species dominance lies.

Most anchovy are sexually mature in their first year of life and most sardine are mature after one or two years (M. Kerstan, Sea Fisheries [SF], pers. comm.). Therefore, large numbers of sardine older than one year are able to take advantage of the highly productive waters of the West Coast by delaying their southward migration to spawning grounds (Crawford 1981a). Anchovy and sardine may live to more than four years, the oldest age of anchovy and sardine currently recorded locally being five and 10 years respectively (M. Kerstan, pers. comm.).

Spawning area

Anchovy spawn mainly east of Cape Point (Crawford 1980) over the Agulhas Bank, particularly the western Bank. In most years spawning extends to the outer edge of the central Agulhas Bank (Hampton 1992). The fish tend to occupy a narrow band to the east of the Bank, coincident with the narrowing of the shelf in that region (Hampton 1992). Of interest is the expansion of spawners onto the West Coast during 1986, 1987 and 1988, and the subsequent contraction of the distribution of spawners back to the South Coast in 1989 and 1990 (Hampton 1992). There may be a relationship between spawner distribution and stock size, spawning anchovy expanding or contracting their range as the stock increases or decreases (Hampton 1992).

Off South Africa, sardine spawn over much the same area as anchovy, but their spawning distribution tends to extend farther east on the South Coast (Anders 1975, Hampton 1992) and, in some years, farther up the West Coast (Crawford 1981a, A. S. Anders, formerly SF, unpublished data). At small stock sizes of sardine, the distribution of their eggs is very patchy (SF, unpublished data). Like anchovy, sardine spawning extends over a wider area when abundance is high. Early surveys carried out during the years 1950–1958 between Lambert's Bay and Saldanha Bay showed that eggs were abundant up to 50 miles offshore (A. S. Anders, SF, unpublished data). When surveys were extended south during the years 1961–1964, two distinct spawning cells were found; one off Cape Columbine on the West Coast and the other farther south between Cape Hangklip and Danger Point (Crawford 1981a). However, during the years 1965–1967, spawning on the West Coast was restricted and eggs were more concentrated in the southern cell (Crawford 1981a). This contraction of the spawning area coincided with a decrease in sardine landings and a gradual increase in anchovy catches during that period.

Spawning season

Anchovy spawn mainly between October and January/February (Crawford 1980, Crawford 1981b), although spawning can start at a low level in September and extend to the end of March (Melo 1992). Sardine generally spawn between August/ September and February/March (Crawford 1981a, Armstrong *et al.* 1989, Akkers *et al.* 1996, Fowler *et al.* 1996). However, there is some indication that, at low abundance, sardine spawning has less seasonality and is year round, with peaks in late winter and early summer (Shelton 1986).

Preferred temperatures for spawning and egg development

Anchovy are capable of spawning at temperatures between 9.5 and 22°C, but the lowest temperature for successful development of eggs is 14°C (King *et al.* 1978). The optimum range for spawning is between 16 and 19°C.

Sardine occur mainly in 15–18°C water and are scarce in temperatures <12 and >22°C (A. S. Anders, unpublished data). Sardine eggs collected in the northern Benguela were reared in the laboratory at between 13 and 22°C, to the stage at which larvae could successfully begin feeding. The optimal range for spawning is between 16 and 21°C (King 1977). Off South Africa, sardine spawn in cooler waters of the West Coast rather than on the South Coast (A. S. Anders, unpublished data).

Anchovy may, therefore, be more severely affected than sardine, should there be an influx of cold water during the spawning season (King *et al.* 1978).

Natural mortality and duration of stages of eggs and larvae

EGGS

Given that anchovy and sardine occupy similar ecological niches for part of their lives, it has been suggested that physiological and behavioural differences may reduce competition (King *et al.* 1978). Incubation periods of *E. capensis* from blastodermal cap stage to hatching averages between 66 and 34 h at 15 and 20°C respectively (King *et al.* 1978). Using the algorithm developed by King *et al.* (1978), and estimating the period from fertilization to blastodermal cap stage from Lo (1985) for northern anchovy *E. mordax*, the incubation period from fertilization to hatching for *E. capensis* is equivalent to 58 h at 17°C. This is similar to the period of 2.5 days reported by Armstrong and Thomas (1989) for this species. A representative temperature for the upper mixed layer in the spawning area over the Agulhas Bank is 17°C (Anders 1965, Armstrong *et al.* 1988, Shelton 1979).

Incubation times for sardine from blastodermal cap stage to hatching ranges between 66 and 23 h (King 1977). Using the algorithm developed by that author, the period from fertilization to hatching at a temperature of 17°C is 51 h in the southern Benguela.

Table I: Mortality rates and duration of stages used in the models

Stage of development	Anchovy		Sardine	
	Instantaneous mortality rate ($\cdot$hour^{-1})	Duration of stage (hours)	Instantaneous mortality rate ($\cdot$hour^{-1})	Duration of stage (hours)
Fertilization until hatching	0.01[1]	58[3]	0.03 (instantaneous daily mortality of 0.72)[2]	51[4]
Hatching until age at swimming	0.00301 (mean rates for *E. mordax*)[2]	2 880 (120 days)	0.00535 (mean rates for *S. sagax*)[2]	2 400 (100 days)

[1] Valdés *et al*. (1987)
[2] Butler *et al*. (1993)
[3] King *et al*. (1978) and Lo (1985)
[4] King (1977)

Le Clus and Malan (1995) showed that the incubation period from fertilization to hatching was 50 h at 17°C in the northern Benguela. The incubation period is typically 70 h for northern anchovy, longer than the 60-h estimate for Pacific sardine *S. sagax* (Butler *et al.* 1993).

Eggs of both anchovy and sardine are tolerant of wide ranges of dissolved oxygen, and their egg development is unaffected by salinity (King 1977, King *et al.* 1978).

Daily instantaneous egg mortality for *E. capensis* was 0.25 and 0.24 for spawning during the period 1985–1986 (Armstrong *et al.* 1988) and 1986–1988 (Valdés *et al.* 1987, Valdés Szeinfeld 1991) respectively. These values are similar to the estimates of 0.25 and 0.231 for northern anchovy (Piquelle and Hewitt 1983, Butler *et al*. 1993). Daily instantaneous egg mortality of *S. sagax* in the Benguela system has not been estimated; off California, estimates for this species vary between 0.31 (Smith 1973) and 2.21 (Smith *et al*. 1989), with a best estimate of 0.72 (Butler *et al.* 1993).

LARVAE

Relatively little is known about the rates of development of sardine and anchovy larvae off South Africa. In the northern Benguela, Thomas (1986) found that growth rates of sardine larvae were more variable than those of anchovy. He observed differences in growth rates between different months, and sometimes in cross-shelf and longshore directions. Brownell (1983) noted that, under similar laboratory conditions, mortality rates of anchovy eggs and larvae (82 days after hatching) were higher than for sardine. This agrees with reports on the early juvenile stage of northern anchovy and Pacific sardine, although sardine mortality is higher than anchovy mortality during the egg, yolk-sac larval and late larval stages (Butler *et al.* 1993). Brownell (1983) found average mortality of anchovy larvae to be 6.1% per day over a period of 30 days after hatching. This value corresponds to an instantaneous daily mortality rate of 6.3%, which is comparable to the 5% estimated by Smith (1985) for late larvae of the northern anchovy and the 7% best estimate compiled by Butler *et al.* (1993). However, the instantaneous daily mortality of early larvae of that species was found to be between 16 and 29% (Hewitt and Methot 1982, Butler *et al.* 1993). Instantaneous daily mortality of larvae of the South African sardine was estimated in the laboratory to be 1.2% (Brownell 1983). Elsewhere, the daily instantaneous mortality of larvae of northern anchovy and Japanese sardine have been estimated to be an order of magnitude higher, at 22 and 10% respectively (Nakai and Hattori 1962, Zweifel and Smith 1981).

MATERIAL AND METHODS

A comparison of the spawning, transport and survival of young stages between anchovy and sardine was attempted using the "anchovy transport model" developed by L. J. Shannon and G. Nelson (SF), detailed in Shannon (1995). The model is based on a rectangular grid, consisting of quarter-degree (latitude and longitude) blocks extending from 29° to 36°45′S and from 15° to 28°00′E. Currents above the thermocline (vertically-averaged 30 and 50 m currents) were averaged for each grid block. The model was based on ADCP data collected during cruises on F.R.S. *Africana* between September and March, 1989–1993. An error in the settings of the ADCP in November 1990 necessitated correction of the data by −3° (Boyd *et al*. 1998). To these measured mean currents, hourly random small-scale perturbations were added to impart more realism to the transport process (Shannon 1995).

Transport of fish eggs and larvae was modelled for the period from hatching until larvae are considered able to swim against currents. Off South Africa, the largest sardine and anchovy caught in a Methot net are between 3 and 4 cm long, and are considered to be passively transported by currents (J. D. Hewitson, formerly SF, pers. comm.). Anchovy and sardine of this length are between 90–120 and 50–100 days old respectively (S. Bloomer, formerly Benguela Ecology Programme, pers. comm.). In this study, the age at which anchovy and sardine are considered to be capable of swimming against currents is 120 and 100 days respectively (Table I).

For each block in which eggs were found, eggs spawned on any day were considered to be transported as a unit through the flowfield until age of swimming. For modelling purposes, the spawning season of anchovy extended over five months, from October to February, and for sardine over six months, from September to February. These are the periods when anchovy and sardine stocks are most abundant (Crawford 1981a). Transport of eggs and larvae was modelled on an hourly time-scale, based on interpolation of currents in surrounding blocks. Numbers of eggs and larvae were reduced hourly to account for natural mortality. Mortality rates of young anchovy and sardine were based on rates from yolk-sac stage to early juvenile stage, according to Butler *et al.* (1993) from work done off California. The algorithm for each stage is calculated as follows:

$$A_{t_1} = A_{t_0}\, e^{-m(t_1 - t_0)} \qquad ,$$

A_{t_0} where is the number of fish at the end of time t_1 of a stage, A_{t_0} is the number of fish at the start of time t_0 of a stage, *m* is the instantaneous hourly mortality rate of the stage being considered and $t_1 - t_0$ is the duration in hours of a life history stage.

Batches of eggs and larvae advected across an offshore boundary and into oceanic water, where survival is considered unlikely, were lost to the model system. These batches were reduced further by natural mortality for the remaining days in the period modelled (100 or 120 days) in order to yield the number of larvae of swimming age that would have survived had they not been lost to unfavourable advection. In this way, the relative importance of advection in determining the survival of larvae was investigated.

In Shannon's (1995) model, the egg production of anchovy was calculated from the spawner biomass for each block. However, biological parameters needed to estimate egg production from a given spawner biomass are presently poorly understood for sardine. Consequently, the original anchovy model was altered to use egg distributions, rather than spawner distributions, to facilitate the comparison of the two species. Two contrasting egg distributions for each species were used and the number and the locality of surviving fish to age at first swimming were modelled. Differences between contrasting egg distributions and between species are expected to arise from:

(i) differences in egg distributions, and hence in the paths along which eggs and larvae are transported passively by currents, causing losses as a result of advection offshore;
(ii) differences in survival rates and durations of the egg and the larval stages; and
(iii) differences in the length of the spawning season.

In order to explore these possible differences, both within and between species, three modelling experiments were undertaken using the new transport model. Model results consisted of a) the numbers and spatial distribution of fish surviving to swimming age and b) the numbers lost and spatial distribution of losses as a result of advection across offshore boundaries. Numbers of swimmers were expressed as a proportion of total eggs spawned per season. Numbers of fish lost to advection were reduced by natural mortality to estimate the number of potential swimmers that were lost to advection. Losses were expressed as a proportion of the sum of fish surviving to swimming age and the potential swimmers lost to advection. The mean hour at which batches were lost offshore was weighted by the number of larvae in the batch at the time of loss (Shannon 1995). Losses and swimmers were spatially separated into five strata (Strata 1–5) and four strata (Strata 2-5) respectively (Fig. 1).

Experiment 1: differences between dispersed and contracted spawning distributions

Ia. Comparison of the two contrasting spatial distributions of eggs for a) anchovy and b) sardine.
IIb. Comparison of the above between species.

Experiment 2: differences in mortality rates and stage durations between species

IIa. Comparison of the numbers of fish surviving to swimming age when mortality rates, time to hatching and age of first swimming of a) anchovy

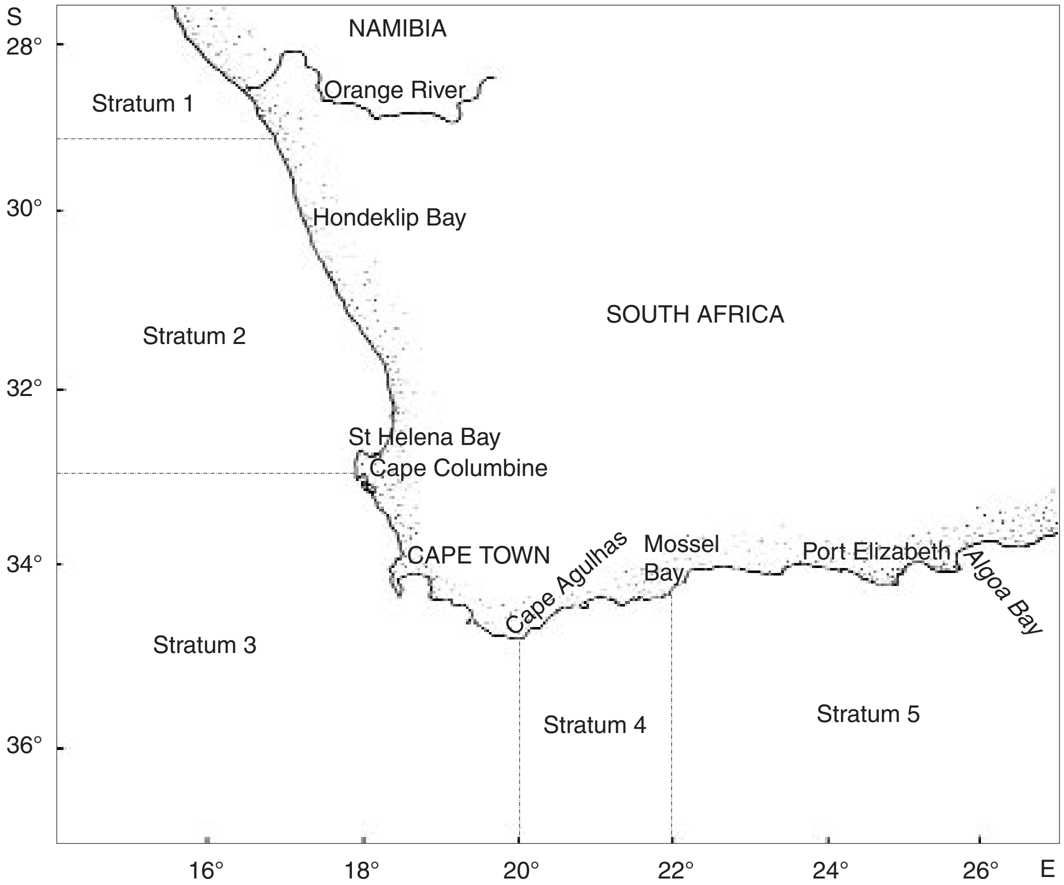

Fig. 1: Map of South Africa showing the five strata used in the model and the locations mentioned in the text, and a schematic flowfield of near-surface currents based on ADCP data collected between November 1989 and January 1992 (after Boyd *et al.* 1992

and b) sardine were modelled. This was investigated using the biological component of the transport model.

IIb. Comparison of results obtained when survival rates of a) anchovy and b) sardine were modelled for all four distributions of eggs (using the transport model).

Experiment 3: differences in length of spawning season

IIIa. Comparison of results when spawning extended over six months, with those when spawning occurred only over five months, for a) anchovy and b) sardine.

Because the egg distributions of anchovy in November 1987 and 1990 were very different, these distributions were chosen for comparison. In 1987, anchovy spawned along the West Coast as well as over the Agulhas Bank, whereas in 1990 spawning was mainly restricted to the South Coast (Fig. 2). Also, spawner biomass was much larger in 1987 than in 1990.

Modelling sardine is more problematic. Surveys to assess the spawner biomass of anchovy and sardine have been conducted in November, at the peak of the anchovy spawning season. However, sardine egg distributions from these surveys over the past decade have not been reliable indicators of their spawning distributions (M. Barange, SF, pers. comm.). This is attributable to the patchy nature of the eggs and spawner distribution for sardine, presumably a result

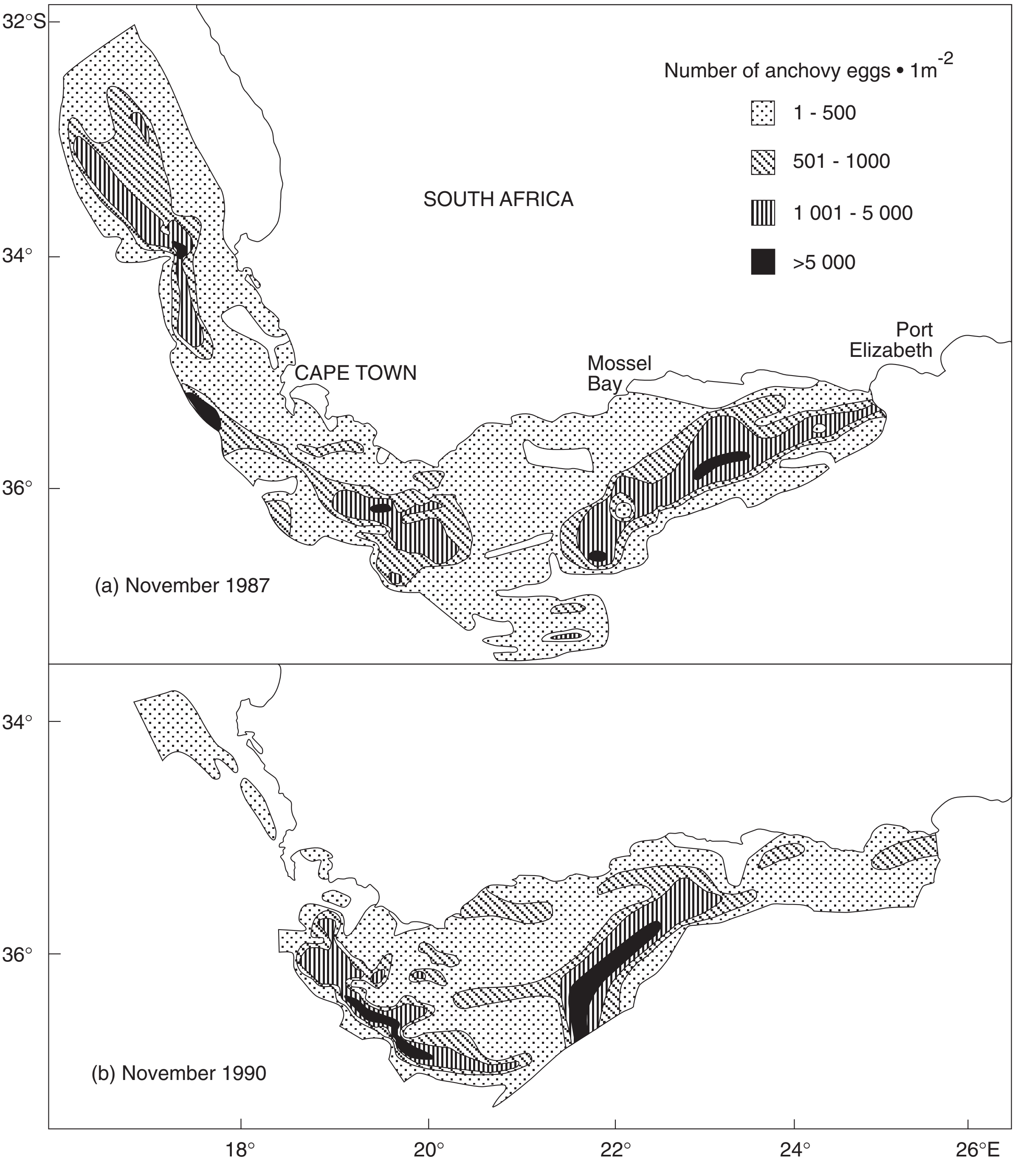

Fig. 2: Distribution of anchovy eggs in a) November 1987 and b) November 1990

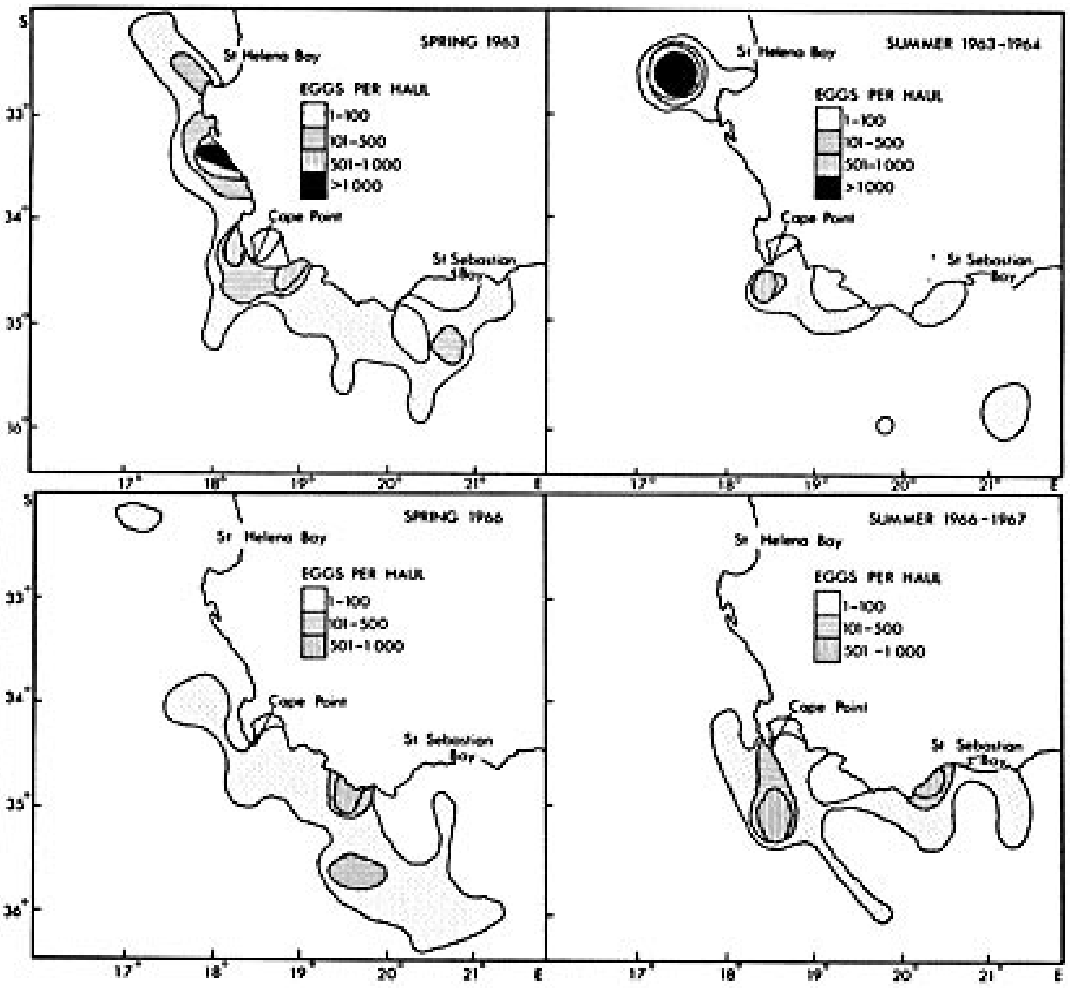

Fig. 3: Distribution of sardine eggs in a) spring and (b) summer 1963/1964 and (c) spring and (d) summer 1966/1967 (after Crawford 1981a, modified from A. S. Anders, unpublished data)

of the November surveys not coinciding with the peak period of sardine spawning. In order to alleviate this possible bias, historical distribution of eggs from monthly collections taken in the 1960s, when sardine were more abundant, were used in the model. For comparative purposes, distributions of high (spring 1963 and summer 1963–1964) and low egg abundance (spring 1966 and summer 1966–1967) were selected (Fig. 3).

It should be noted that the anchovy egg data were based on egg abundance under 1m^2 (0–100 m depth), whereas egg data for sardine were based on surface (0 – 5 m) tows. However, absolute numbers of eggs sampled were not used directly in the model. Instead, they were used to give an indication of the proportion of eggs in each block. Therefore, differences in data type are considered unlikely to influence the model objectives. Anchovy egg proportions were obtained from mean egg densities and mean positions of all samples taken in each block. Sardine egg proportions were taken from egg densities at individual station positions, because no more than one station was sampled per block.

For each of the four egg distributions modelled,

Table II: Mean eggs per haul and estimates of *PR* and *E* (see text) per months for anchovy and sardine

Month	Eggs per haul	*PR*	*E*
Anchovy			
October	318	0.1773	5.90858×10^{12}
November	247	0.1377	4.58937×10^{12}
December	1 035	0.5769	1.92307×10^{13}
January	147	0.0819	2.73132×10^{12}
February	47	0.0262	8.73281×10^{11}
Sardine			
September	225	0.1692	5.63909×10^{12}
October	128	0.0962	3.20802×10^{12}
November	89	0.0669	2.23057×10^{12}
December	173	0.1301	4.33583×10^{12}
January	451	0.3391	1.13032×10^{13}
February	264	0.1985	6.61654×10^{12}

egg production per day (*EP*) over the spawning season (six months for sardine and five months for anchovy) per block was calculated as

$$EP = F \times E \quad ,$$

where *F* is the proportion of total eggs present in a block in a particular season and *E* is the number of eggs produced on any given day. The value *E* was calculated as

$$E = PR \times 10^{15} / n \quad ,$$

where *PR* is the proportion of the mean number of eggs per haul per month of the sum of means over an entire season (Table II), and *n* is the number of days per month (30 in all cases). The value 10^{15} is considered to be the number of eggs produced per season by each species. The mean number of eggs per haul per month between 1951 and 1967 was used for sardine (A. S. Anders, unpublished data, Crawford 1981a). Data collected between 1965 and 1967 were used for anchovy (Crawford 1981b).

RESULTS

Experiment 1: differences between dispersed and contracted spawning distributions

ANCHOVY

A slightly larger proportion of anchovy survived to swimming age in 1987, when spawning extended over both the South and West coasts, than in 1990 when spawning was restricted to the South Coast (Table III). Losses to advection were greater for the contracted spawning distribution in 1990, as were the weighted average number of hours at which losses occurred (240 h), compared to 194 h for the dispersed distribution in 1987. There was little difference among years in the proportion of anchovy of swimming age reaching the area north of Cape Columbine (Stratum 2, Figs 4). The expanded distribution in 1987 led to a larger proportion of young accumulating on the easternmost stratum (Stratum 5), and there were losses to advection from all 5 strata, particularly in Stratum 4 (Fig. 5). From the contracted spawning distribution in 1990, losses offshore were restricted to the area between Cape Agulhas and Mossel Bay.

SARDINE

The proportion of sardine swimmers lost to advection was less than for anchovy (Table III). Although losses were small when spawning was contracted in 1966, the

Table III: Survival and losses to advection of young stage anchovy and sardine, as predicted using the model

Run number	Species and sampling year of egg distribution modelled	Length of spawning season (months)	Survival rates and stage durations modelled	Proportion of eggs released surviving to swimming age (%)	Proportion of potential swimmers lost to advection(%)	Proportion of batches lost to advection (%)
1	Anchovy 1987	5	Anchovy	8.789×10^{-3}	8.668	9.984
2	Anchovy 1990	5	Anchovy	8.557×10^{-3}	11.076	4.651
3	Sardine 1963/4	6	Sardine	5.743×10^{-5}	0.006	4.651
4	Sardine 1966/7	6	Sardine	5.743×10^{-5}	0.013	2.381
5	Anchovy 1987	5	Sardine	5.246×10^{-5}	8.654	9.984
6	Anchovy 1990	5	Sardine	5.108×10^{-5}	11.076	4.651
7	Sardine 1963/4	6	Anchovy	9.622×10^{-3}	0.006	4.651
8	Sardine 1965/6	6	Anchovy	9.621×10^{-3}	0.013	2.381
9	Anchovy 1987	6	Anchovy	8.788×10^{-3}	8.671	10.017
10	Anchovy 1990	6	Anchovy	8.542×10^{-3}	11.227	4.651
11	Sardine 1963/4	5	Sardine	5.743×10^{-5}	0.006	12.240
12	Sardine 1965/6	5	Sardine	5.743×10^{-5}	0.013	6.120

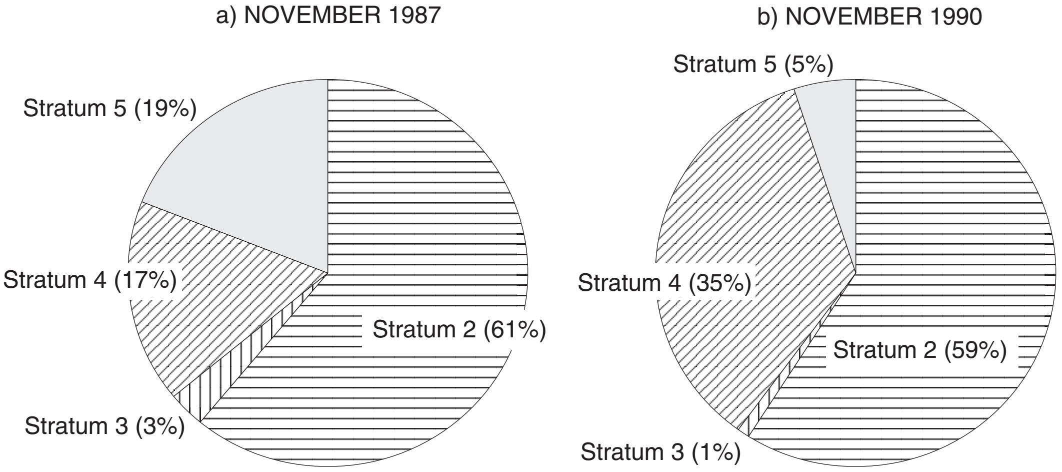

Fig. 4: Proportion of anchovy surviving to swimming age (120 days) accumulating in Strata 2–5, modelled using the egg distributions of (a) November 1987 and (b) November 1990

proportion of potential swimmers lost to advection was more than double that for the dispersed spawning distribution in 1963. Because advective losses were very small compared to the numbers of swimmers that survived, differences between the two spawning distributions in the proportion of sardine surviving to swimming age were minimal (Table III). The spawning distribution in 1963/64 resulted in >90% of surviving swimmers reaching the area north of Cape Columbine (Stratum 2, Fig. 6). When the contracted distribution of 1966 was modelled, more than one-third of the swimmers accumulated in the area between Cape Columbine and Cape Agulhas (Stratum 3, Fig. 6). For both spawning distributions, all losses to unfavourable advection resulted from adults spawning too far offshore from the Cape Peninsula.

Although the contracted distribution of both anchovy and sardine eggs led to greater losses of potential swimmers, the proportions of batches of eggs lost to advection were only about half those for the dispersed distributions (Table III).

Experiment 2: differences in mortality rates

Despite the older age at first swimming of 120 days used for anchovy, and therefore the longer time during which mortality could occur, the biological component of the model showed that fewer sardine reached swimming age. Of the 10^{15} eggs spawned per species, 5.75×10^8 sardine reached swimming age, compared to 9.63×10^{10} anchovy. The higher rates of mortality used for sardine are therefore not offset by their faster larval growth.

Modelling anchovy spawning distributions using sardine mortality rates and stage durations yielded

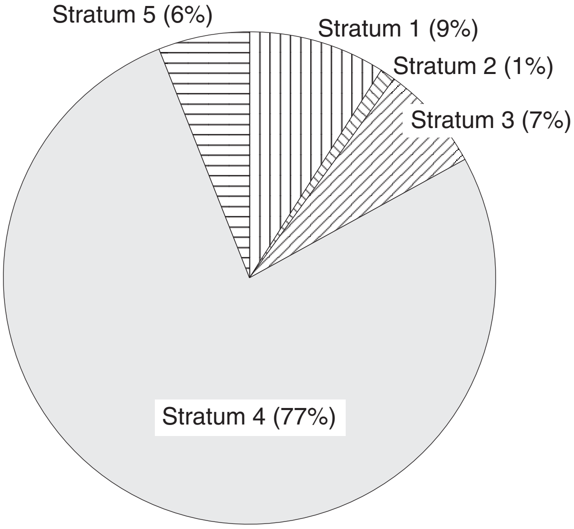

Fig. 5: Proportion of losses to advection of anchovy swimmers in Strata 2–5, modelled using the egg distribution of November 1987

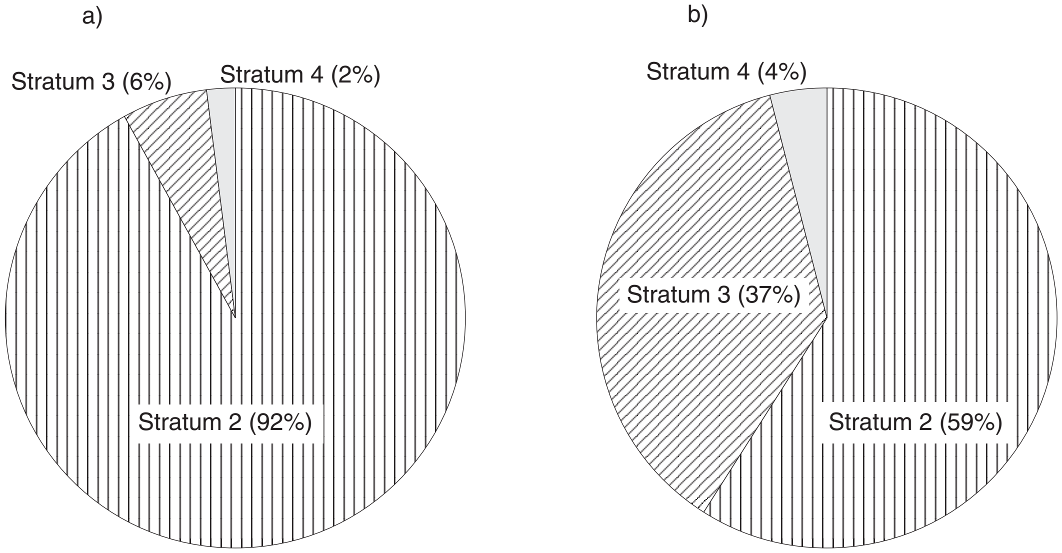

Fig. 6: Proportion of sardine surviving to swimming age (100 days) accumulating in Strata 2–5, modelled using the egg distributions of (a) spring/summer 1963/1964 and (b) spring/summer 1966/1967

smaller survival proportions than when sardine distributions were modelled using sardine parameters (Table III, Runs 5 and 6 v. Runs 3 and 4). Conversely, when sardine distributions were modelled using anchovy parameters, survival was higher than when anchovy distributions were modelled using those parameters (Table III, Runs 7 and 8 v. Runs 1 and 2).

Experiment 3: differences in length of spawning season

Survival of swimmers was slightly reduced and the proportion of potential swimmers lost to advection was moderately enhanced when the anchovy spawning season was extended from five to six months (Table III, Runs 9 and 10 v. Runs 1 and 2). The spatial distributions of swimmers and advective losses remained the same, regardless of length of spawning season.

When the sardine season was modelled at five months instead of six months, losses to advection were slightly greater. However, losses were small, with negligible impact on overall survival (Table III, Runs 11 and 12 v. Runs 3 and 4). Like anchovy, spatial distributions of swimmers and advective losses in sardine were unaffected by length of the spawning season.

DISCUSSION

In the absence of advective losses, a larger proportion of anchovy reached swimming age than did sardine. However, anchovy spawned in regions that were more susceptible to advective losses. In particular, anchovy spawned on the outer edge of the Agulhas Bank, where offshore losses are more likely. This was shown by means of the transport model, using literature-derived mortality rates and stage duration values for related species (Table I).

The percentage of batches lost to advection, when the dispersed spawning distributions of both species were modelled (1987 and 1963 for anchovy and sardine respectively), was double that when spawning was restricted to the southern region (1990 and 1966). Therefore, expanding the spawning area may enhance the chances of batches being lost offshore. Despite this, total losses to advection were less using dispersed spawning distributions, because spawning products in this study were more widely and sparsely distributed. Losses from dispersed egg distributions were often from areas where spawners were sparse. When spawning was dispersed, there was intense spawning farther up the West Coast, minimizing the losses to advection during the transport from the Agulhas Bank to nursery areas along that coast. Adult biomass levels were low in the years when anchovy and sardine spawning was restricted to the Agulhas Bank, compounding the detrimental effect of advection when spawning was contracted to the south in the model.

Applying MacCall's (1990) "basin hypothesis", spawning would be expected to be contracted to the most favourable habitats at low levels of abundance (when rates of density dependence are low). Considering advection, this study shows that anchovy and sardine spawn in areas less favourable to survival when they are at low levels of abundance. This indicates that other environmental factors may have restricted suitable areas available for spawning. For example, ambient water temperatures may have forced pelagic fish to spawn in areas more susceptible to advective losses, but where eggs could develop successfully or where feeding conditions were better.

When spawning extended over the Agulhas Bank and up the West Coast, larger proportions of young fish reached the nursery grounds of the West Coast. Generally, young sardine accumulated farther west than anchovy. Anchovy eggs and larvae were lost to offshore advection mainly between Cape Agulhas and Mossel Bay, whereas losses of sardine spawning products were restricted to between Cape Columbine and Cape Agulhas.

Modelling a five-month spawning season for anchovy and a six-month season for sardine gave greater survival to swimming age than a six- and five-month season for anchovy and sardine respectively. This suggests that fewer, larger batches decreased the chance of offshore advection of anchovy. The influence of length of season on survival of young stages of pelagic fish would be better understood if circulation patterns were better known on a monthly or seasonal basis. For example, convoluted flow may be more common later in the summer, and more efficient northward transport may be more prevalent in spring. The duration and timing of spawning are important factors in determining the fate of young pelagic fish.

This paper has highlighted some of the differences between South African sardine and anchovy spawning and subsequent transport of their eggs and larvae. Further analysis of ways in which other environmental parameters influence these two species is needed.

The limited research on survival and growth rates after hatching of South African anchovy and sardine necessitated using literature-derived mean values for related species for the current study. Although mean values and trends can be useful in the exploratory stage, specific modelling studies require detailed knowledge of the early life stages of pelagic fish in the South African region. Combining information on species in different regions may lead to very different results to those when parameters of the species in the region modelled are used. It is hoped that future research will provide modellers with the necessary, more detailed information.

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