

## Environmental change, regimes and middle-sized pelagic fish in the South-east Atlantic Ocean\*

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**SUMMARY:** There have been marked shifts, influenced by the environment, in the distribution and abundance of middle-sized, and smaller, pelagic fish in the South-east Atlantic Ocean. The changes have often been sustained over several years, giving rise to regimes in the structure of ecosystems. Global environmental change may initiate and sustain such regimes through a steady modification of habitat, or through episodic events that cause large changes in populations. Preliminary simulation studies indicate that altered advective processes off South Africa have little influence on mean year-class strengths of fish that spawn above the thermocline, as advective losses account for only a small fraction of the overall mortality of young stages. However, changed flow may alter the geographic distribution of young of the year.

**Key words:** Pelagic fish, environment, distribution, abundance, long-term regimes, advection.

**RESUMEN:** CAMBIOS AMBIENTALES, REGIMENES Y PECES PELÁGICOS MEDIANOS EN EL OCEANO ATLANTICO SUDESTE. – Han sido detectados cambios muy claros en la distribución y abundancia de los peces pelágicos medianos y los pelágicos pequeños en el Atlántico Sudoriental, influenciados por cambios ambientales. Los cambios a menudo perduran durante varios años dando lugar a cambios en la estructura de los ecosistemas. Los cambios ambientales de carácter global pueden iniciar y sostener tales cambios a través de una estable modificación del hábitat, o mediante eventos puntuales que causan fuertes cambios en las poblaciones. Estudios preliminares de simulación indican que la alteración de procesos advectivos en Sudáfrica tienen escasa influencia sobre la potencia media de la clase anual de peces que frezan sobre la termoclina, ya que las pérdidas advectivas son tan solo responsables de una pequeña fracción de la mortalidad total en la fase juvenil. Sin embargo los cambios de flujo pueden alterar la distribución geográfica de los juveniles del año.

**Palabras clave:** Peces pelágicos, ambiente, distribución, abundancia, cambios de largo período, advección.

### INTRODUCTION

Pelagic fish range in size from small planktivorous species, feeding at the lower end of the trophic chain, to large apex predators, amongst which are some of the most prized gamefish. Between the two extremes are 'middle-sized' pelagic fish, typical examples of which include mackerels *Scomber* spp. and horse (jack) mackerels *Trachurus* spp. This paper considers the influence of the environment on middle-sized pelagic fish in the South-east Atlantic Ocean.

The size of a pelagic fish has implications for its biology. Larger species generally eat larger organisms. Thus, chub mackerel *S. japonicus* is sometimes piscivorous (e.g. BAIRD 1978), whereas anchovies *Engraulis* spp. are entirely planktivorous (JAMES 1988). Also, larger species often undertake more extensive migrations than smaller forms, and are able to cross environmental barriers. Snoek *Thysites atun* and chub mackerel range widely in the South-east Atlantic Ocean (CRAWFORD and DE VILLIERS 1984, 1985). Conversely, stocks of anchovy *E. japonicus* north and south of Lüderitz are relatively discrete, and generally mix to a significant extent only when upwelling at Lüderitz dim-

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inishes (CRAWFORD *et al.* 1987). In such respects, middle-sized and small pelagic fish differ from each other.

However, when they are young, middle-sized pelagic fish are in many respects similar to smaller species. For example, young horse mackerel *T. trachurus* frequently swim in mixed shoals with young sardine *Sardinops sagax* (CRAWFORD 1980). At this stage, there is often extensive dietary overlap between these two and some other species (CRAWFORD 1987). The environment may be expected to influence the young forms of middle-sized and small pelagic fish similarly. On account of this, the paper also considers environmental influences on smaller pelagic species, such as sardines and anchovies, which have been intensively researched in the South-east Atlantic Ocean.

The paper is not a review of all the work that has been undertaken in the region. Rather it presents selected examples of the influence of the environment on the distribution and abundance of some plentiful species. The paper shows that there have been regimes in the abundance or availability to fisheries of horse mackerel in the South-east Atlantic Ocean. Ways in which global environmental change can initiate and sustain regimes of pelagic species are considered. Finally, some possible implications of long-term environmental change on pelagic populations off South Africa are explored through mode-

ling the impact of altered advective processes.

## Distribution

Snoek is a major predator in the Benguela ecosystem (WICKENS *et al.* 1992), where it is sought by fishermen using handlines. When handline catches are high off South Africa, those off Namibia tend to be low, and vice versa (Fig. 1). Application of Box-Jenkins techniques to remove systematic time-series effects (BOX and JENKINS 1976), and subsequent correlation of the pre-whitened residuals, showed the two catch series to be significantly negatively correlated (CRAWFORD *et al.* 1990b). The likely explanation for this is that snoek in some years are displaced to the north and in others to the south, leading to changes in the availability of snoek to handline fishermen in the two countries (CRAWFORD *et al.* 1990b). Handline catches off Namibia were notably poor from 1984-1989. In 1984 there was an intrusion of warm water onto the Namibian shelf from the north, a so-called Benguela Niño (SHANNON *et al.* 1986). This led to greatly decreased catches off Namibia of anchovy, an important food of snoek (BOYD *et al.* 1985). It is probable that snoek moved farther south to feed, and that in doing so they became less available to handline fishermen off Namibia. Thus environmental events may influence the distribution of middle-

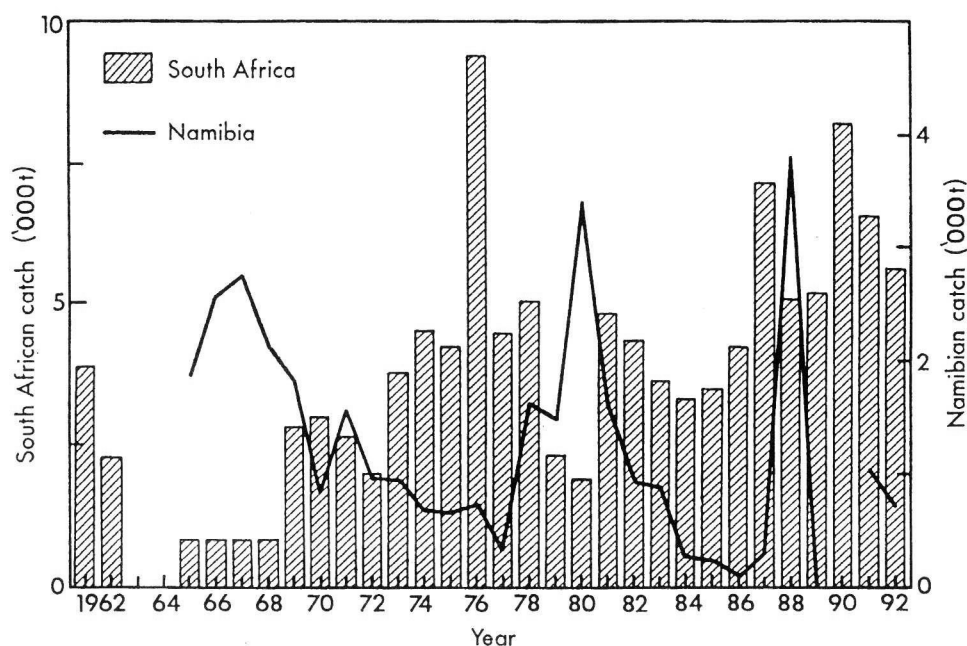


FIG. 1. — Catches of snoek made by handline off Namibia and South Africa, 1961-1992 updated from CRAWFORD *et al.* (1990b). Prewhitened residuals for the two catch series are negatively correlated ( $n = 26$ ,  $r = -0.374$ ,  $P < 0.05$ )

sized pelagic fish by influencing the distribution of their prey.

Up until the mid 1970s, most of the catch of chub mackerel in the Benguela ecosystem was taken in the south (CRAWFORD and SHANNON 1988). Then for a period of more than 10 years the bulk of the catch came from the north (Fig. 2). These trends reflect an altered fishing pattern. Off South Africa, substantial catches were made by purse-seiners in the late 1960s and early 1970s (CRAWFORD *et al.* 1987), based especially on good year-classes of 1966 and 1967 (NEWMAN and CRAWFORD 1980). Later, long-distance mid-water and bottom trawlers effected large catches off Namibia, where a powerful 1977 year-class contributed much of the catch between 1977 and 1981 (CRAWFORD and DE VILLIERS 1984). However, chub mackerel is sought after by South African purse-seiners (CRAWFORD 1989), and the relatively low contribution of the 1977 year-class to catches by this fleet indicates that it was less available to the purse-seiners than the year-classes of 1966 and 1967. Availability of chub mackerel to South African purse-seiners is significantly related to cool sea surface temperatures and north-westerly winds off north-western South Africa (VILLACASTIN-HERRERO *et al.* 1992).

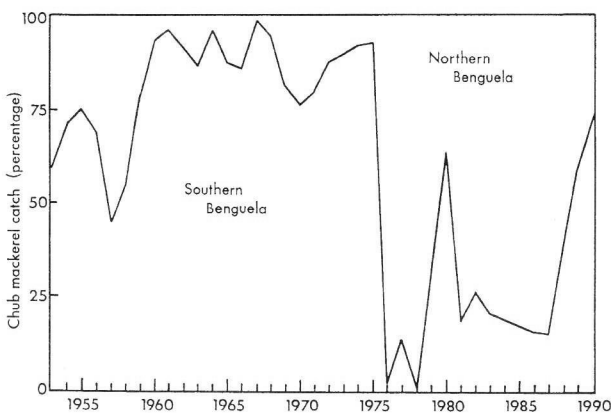


FIG. 2. – Proportional contribution by the northern and southern Benguela system to overall catches of chub mackerel in the South-east Atlantic, 1953-1990

## Abundance

In the South-east Atlantic, powerful year-classes of chub mackerel were formed in 1966, 1967 and 1977 (NEWMAN and CRAWFORD 1980, CRAWFORD and DE VILLIERS 1984). They gave rise to increased catches of this species (Fig. 3). Although environ-

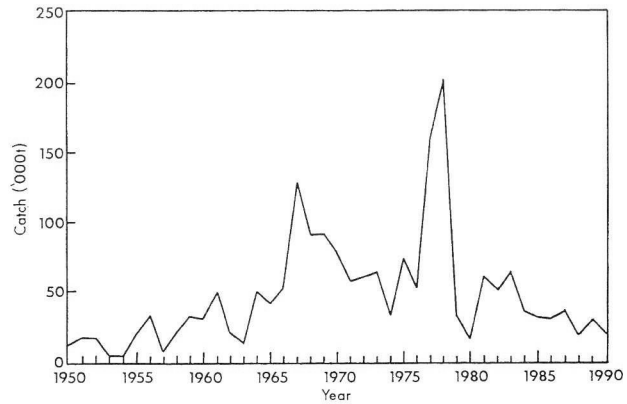


FIG. 3. Recorded catches of chub mackerel in the South-east Atlantic, 1950-1990

mental mechanisms influencing the formation of these strong year-classes are unknown, all three were formed after a period of reduced upwelling in the southern Benguela ecosystem (CRAWFORD and DE VILLIERS 1984).

There have been large variations in the strengths of year-classes of horse mackerel off South Africa. Powerful cohorts were formed in 1947, 1948 (GELDENHUYS 1973), 1974, 1977 and 1978 (KINLOCH *et al.* 1986).

In recent years there have been large variations in the strengths of anchovy year-classes in the southern Benguela ecosystem, as measured acoustically (HAMPTON 1987, 1992). Of particular interest were poor year-classes in 1989 and 1990, which caused a decrease in spawner biomass of anchovy from 1.106 million tons in 1988 to 0.469 million tons in 1990, followed by a greatly reduced catch and closure of two fish processing plants (Saldanha Bay Canning Company and Sandy Point Canning Company) in the early 1990s. Closure of the Saldanha Bay plant resulted in the loss of 297 jobs. Unfavourable offshore advection of larvae by an Agulhas ring (DUNCOMBE RAE *et al.* 1992) and insufficient food to sustain spawning (HUTCHINGS and BOYD 1992) are among factors that may have resulted in the poor year-classes of 1989 and 1990. Food may also influence production of eggs by anchovy off Namibia (SHANNON *et al.* 1992).

## Regimes

In the South-east Atlantic, as in other marine ecosystems (e.g. LLUCH-BELDA *et al.* 1989, 1992c), there have been regimes of high and low abundance or availability of some pelagic species, including horse mackerel. Off western South Africa, substan-

tial catches of horse mackerel were made by purse-seine boats in the 1950s and early 1960s. However, catches subsequently have been much smaller (Fig. 4). The purse-seine fishery has contributed most of the catch made off western South Africa (Division 1.6 of the former International Commission for the Southeast Atlantic Fisheries - ICSEAF). By contrast, trawl fisheries have accounted for most of the catch in the south (former ICSEAF Division 2). Whereas the catch in the west decreased during the 1950s and 1960s, concomitant with the decrease in purse-seine catches, the catch in the south increased through the 1960s and early 1970s, since when it has been relatively stable.

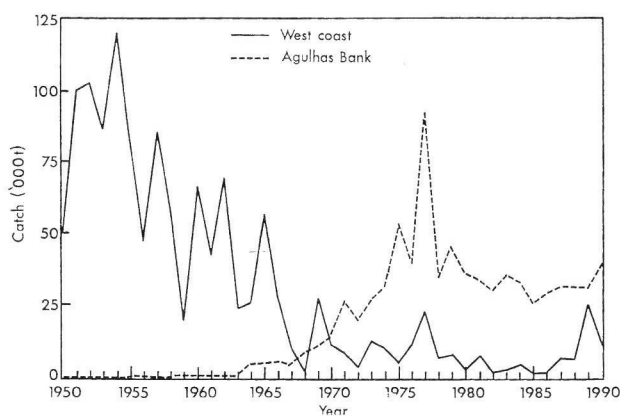


FIG. 4. – Catches of horse mackerel on the Agulhas Bank and off South Africa's west coast, 1950-1990

These trends may have been influenced by the fisheries. In the mid 1960s, the South African purse-seine fishery reduced the size of net meshes in order to exploit anchovy. Consequently horse mackerel became susceptible to capture at a much smaller size and a younger age (CRAWFORD 1981). There was little trawling in the south prior to the 1960s, and the increase in catches there in the late 1960s and early 1970s reflects the increased effort directed at horse mackerel. The status of the resource in the south in the 1950s remains uncertain. However, in the mid 1950s, well before the introduction of the smaller-mesh purse-seine net, there was a large decrease in research catches of juvenile horse mackerel made inshore in Division 1.6 with fine-meshed blanket nets (Fig. 5, CRAWFORD *et al.* 1990a). Over the period 1955-1967, blanket-net catches of round herring *Etrumeus whiteheadi* showed an opposite trend, suggesting environmental influence (CRAWFORD *et al.* 1990a).

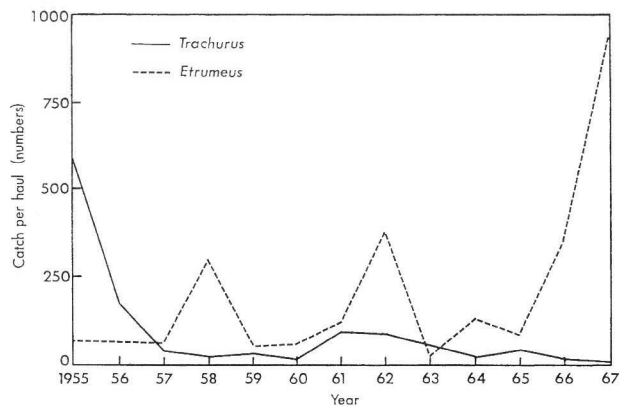


FIG. 5. – Trends in catch rates of horse mackerel and round herring off western South Africa during a research programme using fine-mesh "blanket" nets, 1955-1967 (from CRAWFORD *et al.* 1990a)

In the Humboldt ecosystem, there has been a steady increase in abundance of horse mackerel *T. symmetricus* since the early 1970s (SERRA 1991). The species has expanded its range and colonised oceanic areas as its biomass has increased (SERRA 1991).

### Global environmental change and regimes

Regimes of high or low abundance of pelagic fish have attracted considerable interest, especially the frequently observed alternation between sardines and anchovies (e.g. DAAN 1980, SKUD 1982, SILVERT and CRAWFORD 1988, LLUCH-BELDA *et al.* 1989, 1992c, KORRUBEL 1992, SHELTON 1992). Various hypotheses regarding the initiation and maintenance of regimes of high or low abundance have been proposed. Two that are concerned with global environmental change are briefly considered here.

In the first, KAWASAKI (1983, 1991) postulated that the abundance of sardines in three well separated regions of the Pacific Ocean - off Japan, in the California system and in the Humboldt system - was being influenced by global climate. This was based on the observation that catches of sardine in all three regions have risen, been sustained and fallen more or less in synchrony. KAWASAKI and OMORI (1988) suggested that variations in solar radiation lead to variations in primary production. Sardines are able to utilize phytoplankton to a greater extent than competitors, and populations increase when phytoplankton stocks increase. This leads to less food available for anchovy, whose stock then decreases (KAWASAKI 1993). Off Japan, catches of sardine and anchovy are inversely related. Catches of chub mackerel increased coincidentally with those of sardine until 1978, but then declined. KAWASAKI (1993)



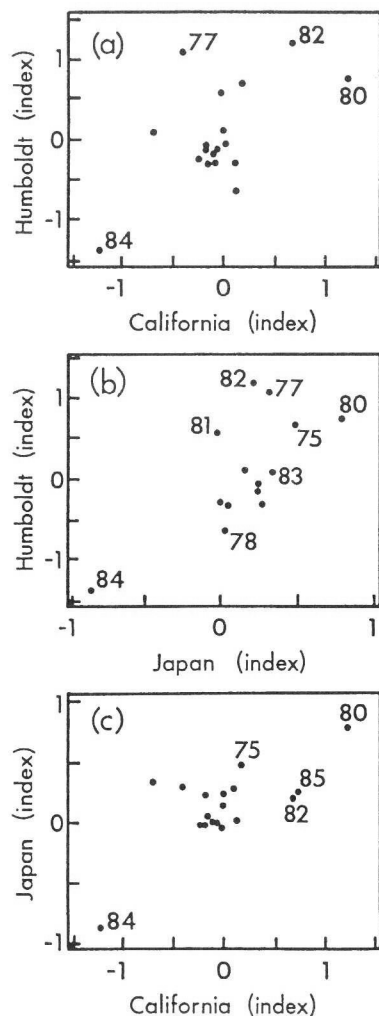


FIG. 6. – Relationships between prewhitened residuals of catches of sardine in the Japan, California and Humboldt systems (modified from CRAWFORD *et al.* 1991). In each instance, dates have been adjusted to account for the differing ages at which sardine recruit to the fisheries. In all instances residuals were low in 1984, but high in 1980 and 1982.

attributed this to chub mackerel feeding exclusively on zooplankton, whereas the major food of sardine is phytoplankton. However, there was regional replacement of chub mackerel by sardine (KAWASAKI 1993).

The second hypothesis is that of LLUCH-BELDA *et al.* (1991a), who proposed that, off the Californias, the sardine population retreated southwards in cold years, but expanded both its spawning and feeding range to the north during warm periods. This resulted in increased egg production in warm years (LLUCH-BELDA *et al.* 1992a). Off the Californias, sardines spawn over a wider temperature range (13–25°C) than anchovies (11.5–16.5°C), and thus are better able to take advantage of warm conditions (LLUCH-BELDA *et al.* 1991b). Sardine in the

Humboldt system also expand in warm periods (LLUCH-BELDA *et al.* 1992b).

When Box-Jenkins (BOX and JENKINS 1976) techniques are applied to the catch series of sardine in the three regions of the Pacific Ocean, to remove systematic time-series effects, there is strong positive correlation between all three series at lags similar to ages at which sardines recruit to the various fisheries (CRAWFORD *et al.* 1991). This supports the hypothesis of global forcing. The significant correlations are driven by particular years (CRAWFORD *et al.* 1991). For example, 1980 appears to have been a favorable year in all three regions, and 1984 unfavorable (Fig. 6). An exceptionally strong year-class was formed off Japan in 1980, whereas in 1984 there was poor survival of larvae (KAWASAKI 1993).

Further evidence in support of global climate influencing marine ecosystems has been provided by the observation that oceanographic anomalies in different regions of the World occur at the same time (HARRIS *et al.* 1992, HARRIS and CRAWFORD in preparation).

Off Japan, in the period 1955–1985, anomalous southward intrusions of the Oyashio Current (ASIOs) along the east coast of Japan took place in 1963, 1974, 1981 and 1984 (SEKINE 1991). The average southward limit of Oyashio water in the boreal spring is approximately 39°–39°30'N, but in anomalous years it intrudes to about 36°N (SEKINE 1991). Off Tasmania, periods of low zonal westerly winds (LZWWs) cause a form of Tasmanian “El Niño”, during which sea surface temperature rises, nutrients become scarce in surface waters, and productivity decreases. There were LZWWs over Tasmania during 1949–50, 1960–63, 1973–74 and 1984–85 (HARRIS *et al.* 1992). In the southeast Atlantic, Benguela Niños (BNs) advect warm, more saline water from the north onto the Namibian shelf. This water may intrude about 600 km farther south than normal. Such events have been reported for 1934, 1949–50, 1963, 1974 and 1984 (SHANNON *et al.* 1986, 1988).

There is clear correspondence between the four periods of LZWWs off Tasmania and the four most recent BNs off Namibia. Information on ASIOs off Japan is only available since 1955, but ASIOs occurred in each subsequent period of LZWWs off Tasmania and BNs off Namibia. Of particular interest is 1984, when oceanographic anomalies were recorded off Japan, Tasmania and Namibia, and when the environment was apparently unfavorable for sardines in the Japan, California and Humboldt systems.

To summarize, two categories emerge of mechanisms whereby environment operating at a global scale may influence abundance of pelagic species. There may be steady modification of habitat, e.g. a trend to warming that enables an expansion in spawning range and enhanced egg production (LLUCH-BELDA *et al.* 1992a). Alternatively, there may be episodic environmental events that trigger changes in populations and ecosystems in well separated areas. Formation of powerful year-classes could cause a population to quickly expand and, for short-lived species, a few poor year-classes could result in a rapid population decrease. Empirical evidence exists for both these forms of global environmental influence. At this stage, the mechanisms by which steady modification of habitat may influence populations are better understood. Further insights into global linkages, and the influences of episodic events, are likely to result from improved modeling of global processes.

### Long-term environmental change and South African pelagic stocks

To investigate the influence of long-term environmental change on pelagic stocks off South Africa, Monte Carlo simulation models are being developed. An initial study has investigated the influence of altered advective processes on the strengths of anchovy year-classes off South Africa. Anchovy spawn over the Agulhas Bank and off western South Africa (CRAWFORD 1980). Some ichthyoplankton is transported westwards and northwards (SHELTON and HUTCHINGS 1982). Young-of-the-year anchovy later recruit to a purse-seine fishery off South Africa's west coast, before migrating south to join the spawning shoals in the austral spring and summer (CRAWFORD 1980).

In the simulation model for anchovy, the oceanic area off South Africa is divided into 635 blocks of 15' by 15'. A spawning distribution is selected from seven patterns observed on acoustic surveys from October to December during each year between 1986 and 1992 (HAMPTON 1992). This distribution is assumed to remain constant for the duration of the spawning season. However, the spawner stock is decreased by mortality throughout the season, the hourly mortality rate being equivalent to an annual rate of 1.33 (VALDÉS-SZEINFELD and COCHRANE 1992). The egg production in each block, based on the spawner biomass in each block, is calculated using the

following algorithm:

$$E = B r S f/W$$

where

*E* is the total egg production per day,

*B* is the total spawner biomass in a particular block,

*W* is the mean weight of a female anchovy,

*r* is the proportion of the spawning biomass that is female (by mass),

*S* is the female spawning fraction per day, and

*f* is the batch fecundity (eggs/female/batch).

Thereafter, transportation of anchovy eggs, larvae and prerecruits from the location of spawning to their position at an age of 180 days is modelled using an hourly time step.

Eggs and larvae occur predominately above the thermocline (SHELTON and HUTCHINGS 1982) and prerecruits are also most abundant in this zone (J. HEWITSON, Sea Fisheries Research Institute, pers. comm.). The transport of eggs and larvae from one block to an adjacent block is computed from mean current vectors above the thermocline, obtained from Acoustic Doppler Current Profile (ADCP) data collected during survey cruises of the Sea Fisheries Research Institute.

The model simulates transient features such as eddies and filaments by adding random components (turbulence) to the ADCP vectors over 24 hours. Typical scales for such features are 12 to 24 hours, representing spatial scales of 10 to 20 km. In addition, smaller scale diffusion, applicable to objects as small as eggs and larvae, is added to the ADCP averages. For this the time scale is fixed at one hour and the spatial scale is in the order of meters.

Numbers of eggs and larvae are reduced by published rates (VALDÉS-SZEINFELD *et al.* 1987, BROWNELL 1983), and numbers of prerecruits by a rate chosen to ensure that the mean strength of year-classes is similar to that determined from surveys (HAMPTON 1992). The durations of the egg and larval stages are assumed to be constant, and equivalent to values experimentally determined for temperatures of 17°C.

Eggs and larvae transported offshore are assumed to be lost, but those that survive and remain on the shelf are summed to estimate year-class strength.

The model has two variables, the distribution of spawning and the transport processes. Information for both of these is based on empirical observations.

The model was run for scenarios in which advective processes were based on observed information, and in which the westward component of advection was increased and decreased by factors of 25% and 50%. Westward advection was altered over the entire area, as well as only between 33°S and 35°S, the region where the direction of a jet current that facilitates transport of ichthyoplankton from the Agulhas Bank to nursery grounds (SHELTON and HUTCHINGS 1982) is known to vary. In all instances the seven most recent spawning distributions were applied, and the mean and standard deviation of anchovy year-class strength and of individuals lost to advective processes were computed (Tables 1 and 2).

Single factor analysis of variance (ANOVA) tests were carried out to determine whether results obtained under the various scenarios of westward flow (normal flow conditions, 25% and 50% increased westward advection, and 25% and 50% reduced westward advection) showed significant differences. Although advection was changed over the entire area, as well as only between 33°S and 35°S, neither year-class strength nor advective losses were significantly different at the 5% level for the seven spawning

distributions considered. Despite this lack of significance some interesting trends emerged.

When westerly advection was increased or decreased by 25% and 50% over the entire area, there was little impact on mean year-class strength (Table 1). Advective losses of ichthyoplankton increased by as much as 32% when westward flow was 50% greater. Advective losses decreased when westward flow slackened, by 47% for a 25% decrease in flow (Table 1).

Similarly, when westerly advection was changed only in the latitudinal zone there was minimal change in year-class strength (Table 2). Again advective losses increased with strengthened westward flow and vice versa (Table 2).

For all scenarios when advection was changed over the entire area and between 33°S and 35°S, there was no loss of ichthyoplankton across the eastern boundary for any of the seven spawning distributions. Flow off southern South Africa is predominantly westward (HUTCHINGS and BOYD 1992). Small advective losses (less than 0.2% of total advective losses) occurred across the western boundary for two spawning distributions when the west-

TABLE 1. – Mean and standard deviation for year-class strength and advective losses of anchovy obtained by simulation when westward advection was altered by the indicated proportion throughout the study area

Westward advection (proportion of measured)	Mean year-class strength ( $10^{11}$ )	Standard deviation of year-class strength ( $10^{10}$ )	Mean number lost by offshore advection ( $10^{14}$ )	Standard deviation of mean number lost by offshore advection ( $10^{14}$ )
1.00	4.433	2.451	1.118	1.371
1.25	4.409	2.097	1.168	1.461
1.50	4.255	2.936	1.476	1.592
0.75	4.480	2.807	0.594	0.798
0.50	4.267	3.883	0.993	1.001

TABLE 2. – Mean and standard deviation for year-class strength and advective losses of anchovy obtained by simulation when westward advection between 33° and 35°S was altered by the indicated proportion

Westward advection (proportion of measured)	Mean year-class strength ( $10^{11}$ )	Standard deviation of year-class strength ( $10^{10}$ )	Mean number lost by offshore advection ( $10^{14}$ )	Standard deviation of mean number lost by offshore advection ( $10^{14}$ )
1.00	4.433	2.451	1.118	1.371
1.25	4.426	2.349	1.167	1.443
1.50	4.353	2.782	1.265	1.505
0.75	4.478	2.404	0.706	0.773
0.50	4.407	2.500	0.755	0.757

ward advection was increased by 25% and 50%. That losses are small at this boundary results from northward transport of ichthyoplankton off western South Africa by a frontal jet (SHELTON and HUTCHINGS 1982).

Advection across the southern boundary (36°45'S) decreased from 36% of total advective losses when the flow field was unchanged, to 30% when westward advection in the latitudinal zone was augmented by 50%. When advection was reduced by 50% in the same zone, 72% of advective losses were due to advection across the southern boundary. Equivalent values when changes were made over the entire area were nil and 100% respectively. Therefore, stronger westward flow reduces loss to the south. For all scenarios, there was minimal loss across the northern boundary (29°S). However, losses at this boundary were greatest when westward advection was increased over the whole area.

The percentage of recruits that accumulated offshore, as opposed to coastal areas, was 57% under normal advective conditions. It increased to 80% when westward advection was increased by 50% over the entire area. As westward advection was weakened, smaller fractions of total recruitment occurred offshore - only 20% under the 50% reduced westward advection scenario. A possible explanation for this is that there is a greater chance of retention in inshore coastal areas along the south coast when westward advection is reduced. Therefore, advective processes will influence the distribution of young fish.

A matched pairs *t*-test showed that year-class strength obtained when westward advection was increased over the entire area by 25% and 50% was significantly different than when similar changes were made to advection only in the zone between 33°S and 35°S ( $0.2 < P < 0.5$ ). A lower mean year-class strength was computed when changes were made to the entire region (Tables 1 and 2).

Year-class strength did not differ significantly between scenarios when westward advection was reduced by 25% everywhere and only in the latitudinal band ( $P > 0.5$ ), but there was a significant difference when advection was reduced by 50% ( $0.1 < P < 0.2$ ). The mean strength of year-classes was lower when westward advection was reduced by 50% over the whole area than when reduced only within the latitudinal band. There were significant differences between advective losses sustained when advection was reduced by 25% and 50% everywhere and only in the specified area ( $0.2 < P < 0.5$ ).

To summarise, the geographic extent and magnitude of changes in water flow above the thermocline can influence the distribution of recruits and the extent of advective losses, although long-term changes in advective processes may not significantly alter the mean size of year-classes. This results from most of the mortality of early stages in the model arising from causes other than advective loss. If this is correct, it means that pelagic fish populations in the South-east Atlantic may be relatively robust to long-term changes in advective processes. However, it should be borne in mind that not the full spectrum of advective processes in the South-east Atlantic was modelled. For example, the influence of Agulhas rings (DUNCOMBE RAE *et al.* 1992) and variability in the frontal jet off western South Africa on year-class strength were not considered. It should also be noted that fractions of the ichthyoplankton lost to the south varied greatly from one spawning distribution to another. Therefore, spawner distribution seems to be of importance in determining the ultimate destination of new recruits.

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