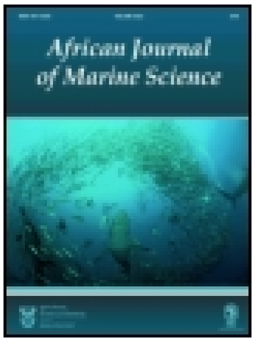

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"PREDATION" OF ANCHOVY BY AN AGULHAS RING: A POSSIBLE CONTRIBUTORY CAUSE OF THE VERY POOR YEAR-CLASS OF 1989

C. M. DUNCOMBE RAE, A. J. BOYD* and R. J. M. CRAWFORD**

There was a marked decrease in abundance of anchovy *Engraulis capensis* off South Africa between November 1988 and November 1990 caused by formation of poor year-classes in 1989 and 1990. The percentage of anchovy in the diet of Cape gannets *Morus capensis* indicated that the most marked decrease in anchovy biomass was between June and July 1989. A filament from the Benguela upwelling front was in the process of being entrained by a passing ring of Agulhas Current water at that time. The ring extracted a large volume of frontal water over a period of 2–3 months, prevented its return to the shelf region and possibly removed anchovy larvae and pre-recruits from the Benguela system. It may have played a role in depressing the 1989 anchovy year-class, and hence the 1989 recruit biomass.

Daar was 'n opmerklike afname in die talrykheid van die ansjovis *Engraulis capensis* teenoor Suid-Afrika tussen November 1988 en November 1990, wat veroorsaak is deur die vorming van swak jaarklasse in 1989 en 1990. Die persentasievoorkoms van ansjovis in die dieet van die Kaapse malgas *Morus capensis* het daarop gedui dat die duidelikste afname in die ansjovisbiomassa tussen Junie en Julie 1989 was. 'n Filament van die Benguela-opwelfront was toe besig om meegesleur te word deur 'n verbybewegende ring Agulhasstroomwater. Die ring het 'n groot volume frontwater oor 'n tydperk van 2–3 maande onttrek, sy terugkeer tot die vastelandsplatstreek verhinder en moontlik ansjovislarwes en -voorrekrute uit die Benguelastelsel verwyder. Dit het moontlik 'n rol gespeel in die verswakking van die ansjovisjaarklas van 1989 en so van die rekruutbiomassa van 1989.

Acoustic estimates of the spawner biomass of the Cape anchovy *Engraulis capensis* decreased from 1,1 to 0,3 million tons between November 1988 and November 1990. Estimates of the abundance of 0-year-old fish at the time of their recruitment to the fishery in June were of the order of 130 000 tons in both 1989 and 1990, compared with a mean of about 460 000 tons in the period 1985–1988 (I. Hampton, Sea Fisheries Research Institute, pers. comm.). In a report prepared by the Sea Fisheries Research Institute (Anon. 1991), exact causes for the decreased abundance of anchovy could not be pinpointed. Of the factors that could have caused the decline in anchovy abundance, i.e. fishing, predation or environmental conditions, all but environmental factors were considered of minor influence during the 1988/89 season. However, at the time of the decline in anchovy, an Agulhas ring, identified on two cruises and in satellite imagery, was found to be entraining a filament from the Benguela upwelling front.

The Agulhas Current flows down the east coast of Africa, guided by the shelf-edge topography. On the south-eastern edge of the Agulhas Bank, it leaves the shelf-edge and continues southwards or south-westwards and then turns eastwards again in a great loop called the Agulhas retroflection. Periodically, the retroflection pinches off rings, approximately 250–350 km in diameter, which move north-westwards into the South Atlantic Ocean. (For reviews of the Agulhas retroflection system, see Duncombe Rae 1991 and Peterson and Stramma 1991.) In their passage across the South Atlantic Ocean, these rings may come into contact with the Benguela system (Duncombe Rae *et al.* 1989, 1992, Lutjeharms *et al.* 1991).

Elsewhere in the world, in the Gulf Stream and in the Kuroshio and East Australian current systems, rings and eddies shed from the currents can and do affect the continental shelf margins (Smith 1983). However, in those systems, the shelf zone and the current producing the eddies are within the same ocean basin. It is only off the south-west coast of Africa that eddies from a western boundary current, the Agulhas, can influence directly an eastern boundary current upwelling region, the Benguela.

The dynamics of rings are such that they tend to move westwards and equatorwards (Cushman-Roisin *et al.* 1990). In the current systems other than that off South Africa mentioned above, this motion moves the rings towards the shelves they affect. There the rings are rapidly damped by being forced into contact with the continental slope (Kamenkovitch *et al.* 1986). In one such instance from the Gulf Stream, the total energy

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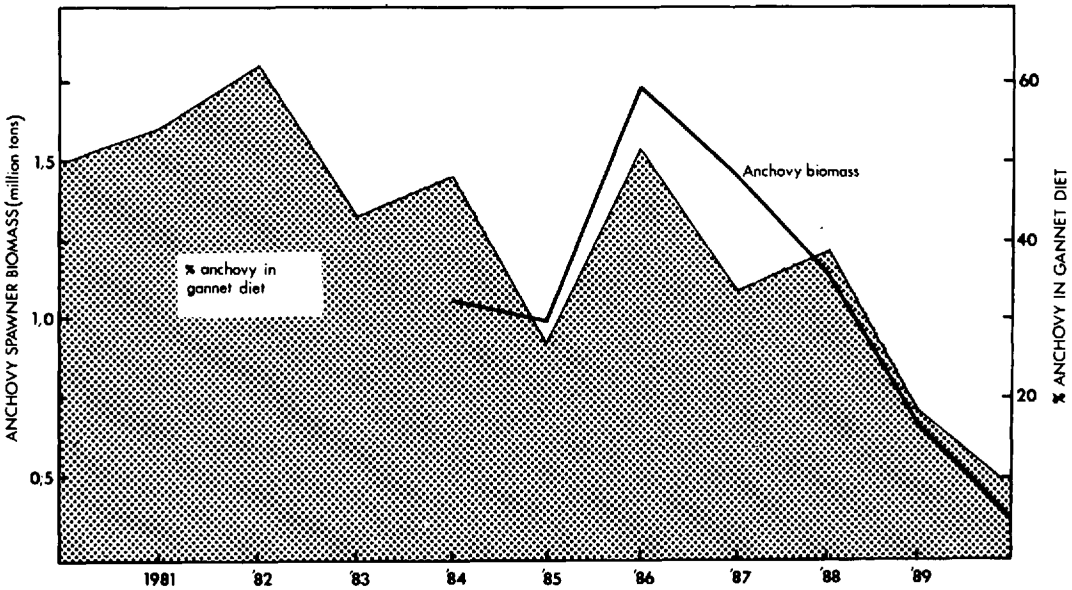

Fig. 1: Proportion by mass of anchovy in the diet of Cape gannets off western South Africa contrasted with acoustic estimates of anchovy spawner biomass, 1980–1990

content of the ring was reduced by nearly 60 per cent (Fornshell and Criess 1979). As a source of warm water, by generating shelf waves and by inducing mixing as they decay, the rings indirectly affect the fishing industries of the shelf regions. In the Agulhas/Benguela system, the rings tend to move away from the shelf. The shelf-edge topography then acts as a wave-guide, with minimal damping effect. If the ring has any effect on the shelf, it acts as a sink rather than as a source of water.

Eddies have been suggested as mechanisms for the loss of eggs and larvae from shelf regions elsewhere (Colton and Temple 1961, Butman *et al.* 1982). Further, Joyce *et al.* (1992) observed the transport of heat, salt and particulate matter from the continental shelf of the U.S.A. to the Gulf Stream by means of a warm-core Gulf Stream ring. Eddies as transport and retention mechanisms for plankton and phytoplankton have also been indicated in shelf, island and open-ocean environments (Boyar *et al.* 1973, Lobel and Robinson 1986, Perissinotto and Duncombe Rae 1990).

Eddies have previously been associated with the shelf-edge front of the Benguela system (Kaz'min and Sutyrin 1990, Shillington *et al.* 1990). However, those eddies were horizontally and vertically of too small an extent to have originated in the Agulhas Current (Duncombe Rae 1991), and they were probably generated by Rossby-type waves along the shelf-edge, in association with filaments from the upwelling front.

In this contribution it is suggested that, in addition to other environmental factors outlined by the SFRI report (Anon. 1991), interaction between an Agulhas ring and the Benguela upwelling front was a contributing factor to the decline of the anchovy stock. It is hypothesized that the ring drew off prerecruit juveniles and some late-stage larvae from the frontal jet in the vicinity of the nursery regions off the Orange River mouth, thereby removing them from the system and preventing their recruitment to the fishery and the spawner stock.

BACKGROUND INFORMATION

Anchovy spawn on the Agulhas Bank during the period October–January (Crawford 1981). Surface currents result in the transport of eggs and larvae from the Agulhas Bank around Cape Point and northwards. A strong shelf-edge jet carries the larvae farther north along South Africa's west coast, from the Cape Peninsula to the nursery and larval retention areas between St Helena Bay and the mouth of the Orange River (Shelton and Hutchings 1982, Boyd *et al.* 1992). They

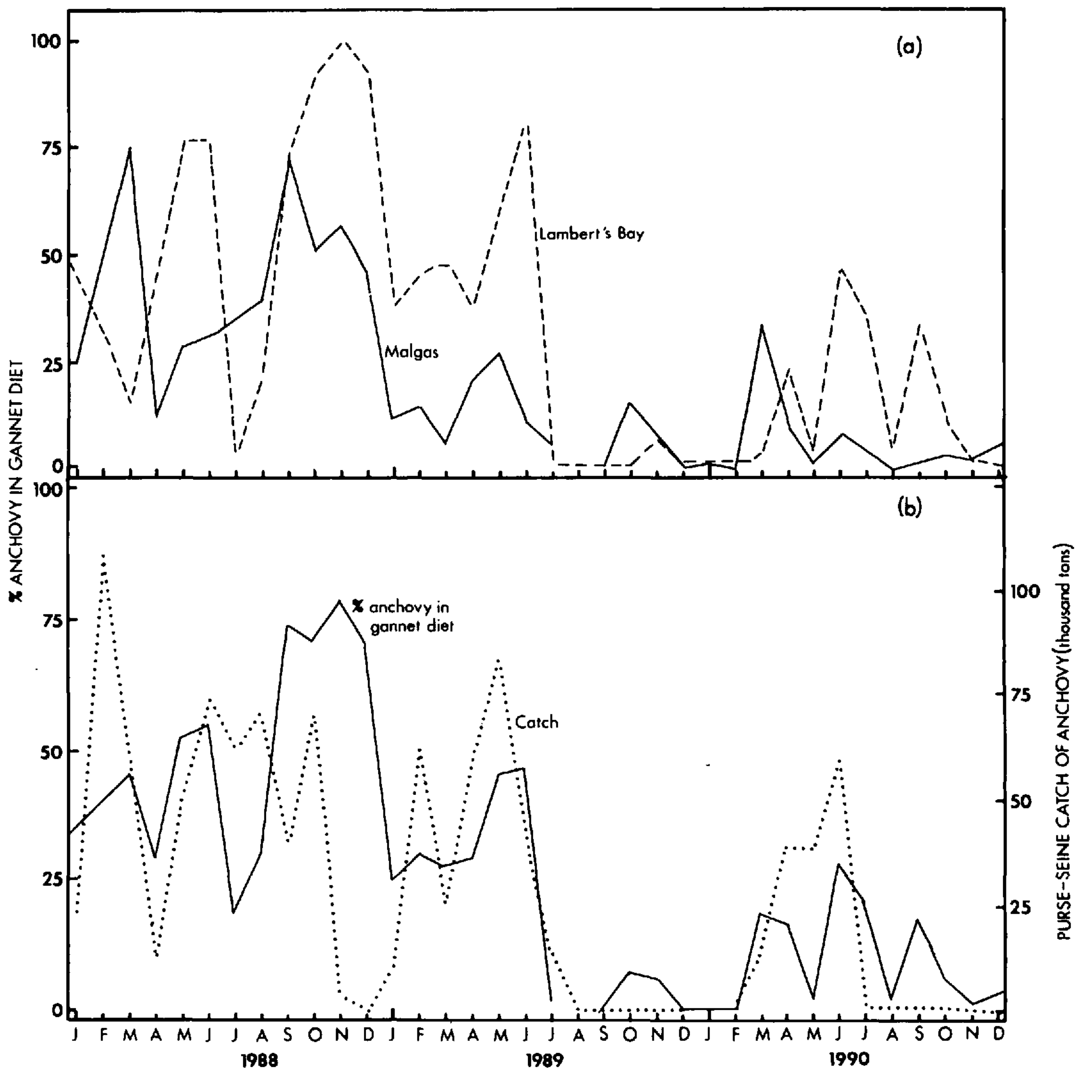

Fig. 2: (a) Percentage by mass of anchovy in the diet of Cape gannets at two sites off western South Africa, Lambert's Bay and Malgas Island, 1988–1990; (b) combined gannet diet data for the two sites contrasted with the purse-seine catch of anchovy, 1988–1990, showing the collapse of anchovy in mid 1989. At the end of July 1989 the fishery was closed

remain in those areas, recruiting to the purse-seine fishery off the west coast of South Africa. As adults, they return to the spawning grounds on the Agulhas Bank towards the end of their first year, swimming south close to the coast (Crawford 1980, Armstrong and Thomas 1989).

The SFRI report (Anon. 1991) identified fishing, predation and environmental conditions as possible causes of the poor anchovy year-classes of 1989 and 1990. Each of these is discussed as a cause below.

Fishing

Fish catches in 1987 and 1988, immediately prior to the decline in the anchovy stock, were high. However, good recruitment was also measured in those years. The biomass of the parent stock was estimated to be above average in November 1988, in spite of the high catches during 1987 and 1988. For that reason, the high catch rates were not implicated in causing the poor year-class of 1989. Without some other factor, such as adverse environmental conditions or heavy predation, recruitment should have attained at least average levels. After young anchovy were found to be scarce in June 1989 (Anon. 1989), fishing was stopped (at the end of July). Therefore, fishing alone could have had no further influence on the anchovy stock that year.

Predation

The larger predators of anchovy (cetaceans, seabirds, South African fur seals *Arctocephalus pusillus pusillus*, predatory fish such as snoek *Thyrsites atun* and squid *Loligo vulgaris reynaudii*) feed predominantly on larger sizes and tend to adjust their diet to the abundance of their prey (Nepgen 1979, Berruti 1987, Crawford 1987). As an example, this is clearly seen in the percentage of anchovy in the diet of Cape gannets *Morus capensis* (Fig. 1). The proportion of anchovy in the diet of gannets closely follows the change in biomass of the prey species, as estimated by surveys. Predation by the larger predators was therefore probably not responsible for the poor anchovy year-class measured midway through 1989 (Anon. 1991). However, the proportion of anchovy in the diet of Cape gannets pinpoints the timing of the most severe failure of anchovy recruitment (Fig. 2).

Predation of the larvae and eggs of anchovy by planktivorous predators such as pilchard *Sardinops ocellatus* may have been higher in the 1988/89 spawning season than in previous years. However, there are no direct data to support this theory. Nevertheless, of other potential small predators, round herring and squid were abundant off western South Africa during 1989.

Environmental conditions

During the November 1988 acoustic survey of anchovy spawner biomass, it was found that, although spawner biomass was relatively high, the abundance of planktonic food for the spawning anchovy was very low on the western Agulhas Bank, a critical spawning region (Peterson *et al.* 1992). In fact, 16,9 per cent of the fish were re-absorbing eggs, a condition usually associated with sustained poor conditions for feeding

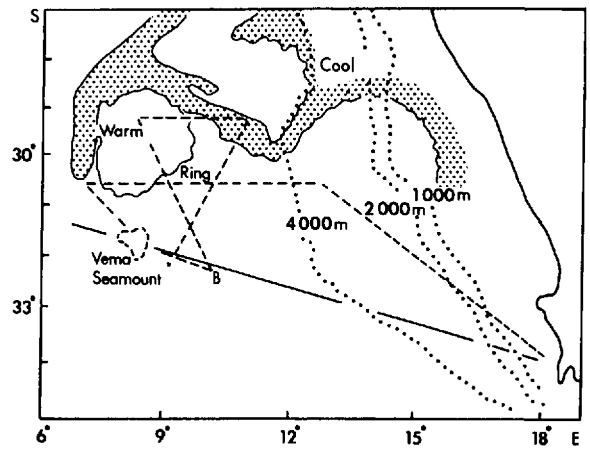

Fig. 3: Cruise tracks of F.R.S. *Africana* (solid line) in April 1989 and R.S. *Benguela* (dashed line) in May 1989. The approximate position and shape of the ring as seen in NOAA infra-red imagery in June 1989 is shown (after Duncombe Rae *et al.* 1989)

(Y. C. Melo, Sea Fisheries Research Institute, pers. comm.). During January 1989, warm water and low concentrations of chlorophyll *a* were encountered in the West Coast nursery areas, again indicating poor feeding conditions for anchovy larvae (Anon. 1991). Therefore, a series of adverse environmental conditions resulted in both poor food availability for spawning adult anchovy in the second half of the spawning season, and poor first-feeding conditions for larvae. However, no single major catastrophic event, such as the Benguela *Niño* of 1983/84, was identified (Anon. op. cit.). Anchovy in fact continued to contribute substantially to the diet of Cape gannets off western South Africa until May/June 1989 (Fig. 2).

In April 1989, an Agulhas ring was identified by means of expendable bathythermograph probes on a cruise of F.R.S. *Africana* between Cape Town and Vema Seamount (Fig. 3). In May 1989, a cruise of R.S. *Benguela* confirmed that the ring was of Agulhas origin. It was estimated that the ring was shed from the Agulhas retroflection south of Cape Town during late December 1988 (Duncombe Rae *et al.* 1992). Further, NOAA infra-red satellite imagery suggested that the ring was in the process of capturing a filament from the Benguela upwelling front (Duncombe Rae *et al.* 1989). The first sign of this interaction with the Benguela upwelling front was seen in an image from 30 April 1989, when the base of the filament was just north of the Orange River. In images obtained in mid June 1989, the filament is seen to extend in a loop, from between the Orange River and Lüderitz to nearly

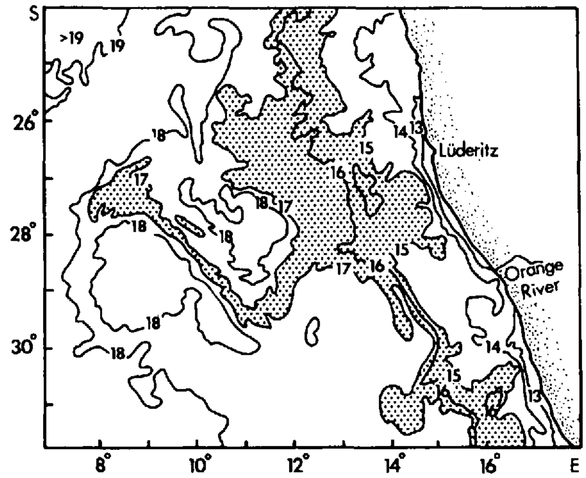

Fig. 4: An interpretation of the surface isotherms for 15 June 1989. The cool frontal water entrained by the ring is shown shaded. The flow of water within the front is south to north throughout (after Lutjeharms *et al.* 1991)

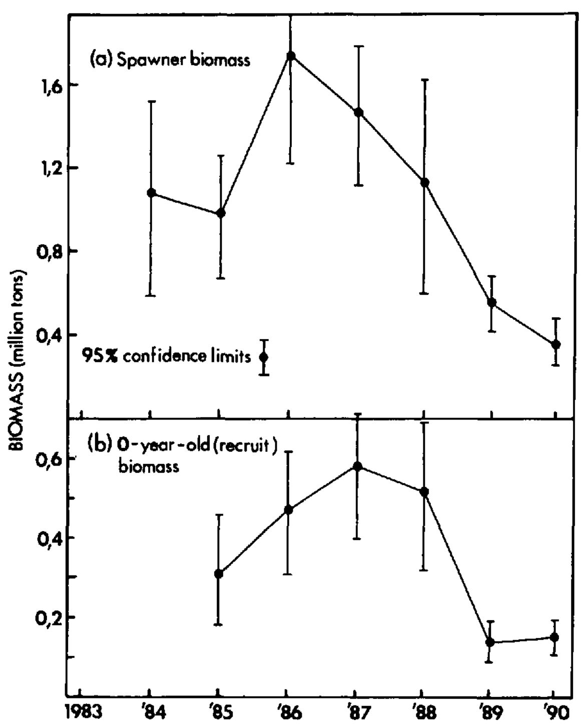

Fig. 5: Acoustic estimates of (a) spawner biomass of anchovy in November 1984–1990 and (b) abundance of 0-year-old anchovy in June 1985–1990 (after Anon. 1991)

800 km from the coast, revealing filament capture by the ring to be almost complete (Fig. 4). The *Benguela* survey in May 1989 confirmed the presence at the edge of the ring of frontal water from the coastal region of the Benguela system. The ring could have drawn off 5×10^{12} m^3 of upwelled surface water from the Benguela upwelling front over the period of the ring-filament interaction, representing a volume flux of $1{,}5 \times 10^6$ $m^3 \cdot s^{-1}$ (Lutjeharms *et al.* 1991, Duncombe Rae *et al.* 1992).

DISCUSSION

The sharpest downward trend in acoustically determined spawner biomass of anchovy was detected between November 1988 and November 1989 (from 1 200 000 to 600 000 tons, Fig. 5a), and in similarly deduced abundance of 0-year-olds between June 1988 and June 1989 (from 500 000 to 180 000 tons, Fig. 5b). The most marked decline in the contribution of anchovy to the diet of Cape gannets feeding off western South Africa was between June and July 1989 (Fig. 2), coinciding with the period of the ring/filament interaction.

Juvenile anchovy have been found several times in the vicinity of the Orange River (Crawford 1981, Schülein 1986, Cruickshank *et al.* 1990). Acoustic surveys have established that the density of shoals of juvenile anchovy there can approach that of shoals on the traditional fishing grounds farther south. Indeed, shoals near the Orange River contribute a significant proportion of the recruitment to the fishery farther south (Cruickshank *et al.* op. cit.). Offshore transport in the upwelling zone off Lüderitz, north of the Orange River, constitutes a barrier to interchange between the Namibian and South African stocks of anchovy, which are thought to be relatively discrete (Crawford *et al.* 1988). Moreover, the coast around the mouth of the Orange River is the most northerly nursery area for the South African stock of anchovy (Cruickshank *et al.* op. cit.). In February 1989, anchovy post-larvae and juveniles were concentrated near the mouth of the Orange River, just south of Port Nolloth (29°15'S, 16°55'E) and in the vicinity of the Olifants River mouth (31°42'S, 18°15'E) — O'Toole and Hampton (1989).

Even if the interaction of the ring with the filament is vastly overestimated, the northernmost nursery areas for the South African anchovy stock were well within the possible range of influence of the ring. The waters off the mouth of the Orange River were adjacent to the base of the affected filament at the time the interaction began. Maximum surface current speeds within the filament, estimated from feature-tracking in the satellite imagery, were of the order of 70 cm·s^{-1} (Duncombe Rae *et al.* 1992), far greater than the swimming speed of even adult anchovy (Nelson and Hutchings 1987). Any larvae or prerecruits still present in the frontal jet from the time of the first interaction of the ring with the front would have had great difficulty resisting entrapment by the ring. The base of the filament was 100 km wide and current speeds of up to 50 cm·s^{-1} were indicated there. Although the greatest speeds of the water entering the filament are in the frontal jet, some shelf water is also involved (J. J. Agenbag, Sea Fisheries Research Institute, pers. comm.). Therefore, it is suggested that, with the water drawn off from the upper layers of the Benguela system, the passing ring may have extracted a significant proportion of prerecruit anchovy, and possibly also larvae, from the coastal waters. This would have precluded their subsequent migration south to the Agulhas Bank and could have contributed to the very low abundance of 0-year-old anchovy measured acoustically in June 1989. Also, of course, it would then explain the simultaneous decline in availability of anchovy to the purse-seine fishery and Cape gannets (Fig. 2). The poor year-class would have reduced the spawner biomass of anchovy drastically in 1989, as indeed was subsequently measured (Fig. 5). This reduced spawner stock may in turn, and assuming at least some still-to-be-proved stock-recruit relationship, have been responsible for the poor year-class in the following year (1990).

It is estimated that nine rings are shed from the Agulhas retroflection region per year (Lutjeharms and Van Ballegooyen 1988), of which some may enter the Antarctic Circumpolar Current and return to the Indian Ocean. Gordon and Haxby (1990) used satellite altimeter data to estimate that five rings per year enter the South Atlantic. Of these, most move farther west than the ring detected in 1989. In addition, as the structure of Agulhas rings is dynamically coherent up to depths of 1 000 m (McCartney and Woodgate-Jones 1991) and evident throughout the water column (Gordon and Haxby op. cit.), the proximity of the rings to the coastline is limited by the shelf topography. Rings can be expected to interact only with very long filaments from the upwelling system, and such extreme filaments occur on average only 1,5 times per year (Lutjeharms *et al.* 1991). Therefore, the likelihood of ring-filament interaction coinciding with the presence of large quantities of juvenile anchovy near the base of the filament can fortunately be considered small.

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