$$pa_{t+1} = \frac{[paa_t + pAa_t/2]\,[U + (1-U)\,(1-Xm_t)]}{[pAA_t + pAa_t + paa_t]}$$

Where Xm_t is the mean sex ratio produced by mated females at time t

$$= \frac{pA_t XA + pa_t Xa}{pA_t + pa_t}$$

and U_t is the proportion of the total eggs laid in generation t that are produced by uninseminated females (see Appendix 1). The population sex ratio at $t + 1$ is then

$$Xp_{t+1} = \frac{pAA_{t+1} + pAa_{t+1} + paa_{t+1}}{pAA_{t+1} + pAa_{t+1} + paa_{t+1} + pA_{t+1} + pa_{t+1}}$$

and the frequency of the allele A is

$$fA_{t+1} = \frac{2pAA_{t+1} + pAa_{t+1} + pA_{t+1}}{2(pAA_{t+1} + pAa_{t+1} + paa_{t+1}) + pA_{t+1} + pa_{t+1}}$$

Appendix 3. *Analysis of male–female conflict over sex ratio control*

In terms of the resulting number of gene copies in the F_3 generation, the relative fitness of an A-male (RF_m) compared with an a-male is

$$RF_m = \frac{XA[0.5 + XA(1-U)]}{Xa[0.5 + Xa(1-U)]}$$

with no recombination (or if only the A gene is considered), or

$$RF_m = \frac{XA[0.5 + (XA(1-U) + Xp)/2]}{Xa[0.5 + (Xa(1-U) + Xp)/2]},$$

where $Xp = (1-U)\,(pA\,XA + pa\,Xa)$ if the entire genome is considered and recombination is taken into account. For $U = 0$, $XA = 1.0$ and $XB = 0.5$, the first yields $RF_m = 3$ for all $Xp > 0.5$, and the second $RF_m = 2.5$ for $Xp = 0.5$, decreasing to $RF_m = 2.4$ for $Xp = 1.0$. The A allele will therefore be strongly favoured at all frequencies. This analysis does not include limits to k, nor the effects of Xp on U, and therefore requires further attention. However, the fixation of A in all the simulations carried out suggests that the above conclusion will not be significantly altered by further analysis.

Similarly, the fitness of a female mated by an A-male (RF_f) compared with one mated by an a-male will be

$$RF_f = \frac{XA(1-U)(0.5+Xp) + Xp[U+(1-XA)(1-U)]/(1-Xp)}{Xa(1-U)(0.5+Xp) + Xp[U+(1-Xa)(1-U)]/(1-Xp)}$$

if no recombination of genes occurs (i.e. her genes and her mate's genes segregate completely during gamete production in her daughters). If random recombination of genes occurs, the relative fitness will be

$$RF_f = \frac{XA(1-U)[0.5+(Xp+XA(1-U))/2] + Xp[U+(1-XA)(1-U)]/(1-Xp)}{Xa(1-U)[0.5+(Xp+XA(1-U)))/2] + Xp[U+(1-Xa)(1-U)]/(1-Xp)}$$

With $U = 0$, $XA = 1.0$ and $Xa = 0.5$, the first equation yields $RF_f = 1$ for $Xp = 0.5$, and $RF_f < 1$ for all. $Xp > 0.5$, while the second yields $RF_f = 1.25$ for $Xp = 0.5$, $RF_f = 1$ for $Xp = 0.6085$ and $RF_f < 1$ for $Xp > 0.6085$. As the gene A spreads, females mated by A-males will therefore benefit until $Xp = 0.6085$, which with $U = 0$ occurs at $pA = 0.217$. The population sex ratio at which $RF_f = 1$ is reduced by increasing U. This analysis is at present being extended to include genes allowing females to evade male control.

Shedding of an eddy from the seaward front of the Agulhas Current

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The important role of mesoscale features in the circulation dynamics of the South Indian Ocean has been demonstrated by numerous oceanographic investigations over the last few years. These features include Agulhas rings, shear edge features of the landward side of the Agulhas Current, eddies shed across the Subtropical Convergence and eddies found in the vicinity of the Mozambique ridge. To this collection a new feature may now be added. We report here observations of an extensive warm eddy east of the southern Agulhas Current. It was observed to be shed from the seaward front of the Agulhas Current, a mesoscale process that has not been observed before.

Eddies and similar mesoscale disturbances to the mean flow have been observed in almost all components of the circulation of the oceans adjacent to southern Africa.[1] They are shed as large warm rings from the western termination of the Agulhas Current, the Agulhas retroflection,[2] whence they drift into the South Atlantic Ocean.[3,4] They are also found as the main disturbances of the general flow in the central South West Indian Ocean[5] and they regularly form at the Subtropical Convergence south of Africa.[6] Small eddies observed on the landward side of the Agulhas Current[7] are probably generated by that current. Off Natal, such eddies, by a process of vortex shedding,[8] may cause important and geographically extensive changes to the flow regime downstream.[9]

Eddies are important for a number of reasons. They carry vast amounts of heat, which may influence local weather and climate. They also carry large numbers of organisms from one ocean area to another, thus dispersing biota. Moreover, they influence the behaviour of currents[9] and are a central constituent of ocean dynamics as a whole.

Eddy generation by the Agulhas Current has been thought to be restricted to its southern termination, the Agulhas retroflection, and its landward side. Upstream of Port Elizabeth the location of the Agulhas Current is very stable, showing little meandering from side to side.[10] Its inshore front is sharp and, except for small shear features, usually stable. The seaward side is usually less distinct. Contrary to comparable currents such as the Gulf Stream and the Kuroshio, the Agulhas Current has till now not been observed to shed eddies or any coherent bodies of water along its length.

Data

We have used satellite remote sensing to monitor the seaward edge of the Agulhas Current. The data used in this study were a series of thermal infrared images derived from the NOAA-11 weather satellite. This satellite, with its sun-synchronous, near-polar orbit, makes several passes per day over southern Africa. Radiance measurements over swaths of 2 300-km width are made by the Advanced Very High Resolution Radiometer (AVHRR) on board. The orbit has a 9-day repeat cycle; the spatial resolution along the sub-satellite track being 1.1 km at nadir. The AVHRR has five spectral bands, measuring in the range 0.58 to 12.5 μm. Radiance measurements taken in the first two channels provide reflected sunlight (colour) data, while the remaining three channels provide thermal infrared (TIR) data.

Since these TIR bands of the AVHRR provide data both about heat radiated from the earth's surface and about absorption within the atmosphere primarily due to water vapour, an algorithm can be applied to provide detailed atmospherically corrected images of ocean surface temperature accurate to within 0.5°C rms. The visible, reflected light channel (band 1) was used to establish the geographic areas of cloud cover. The images were then all geometrically rectified to a uniform Mercator projection enabling consecutive images to be overlain.

These corrected images served as input to a computer program with which data missing due to cloud cover or a shifted satellite swath could be filled in with the most recent available data, latitude–longitude grids overlain, and the images further enhanced to provide detailed ocean surface temperature maps (4-km resolution) of the area of interest, extending from 28°S to 40°S and 13°E to 33°E.[11]

The daily TIR images for April/May 1991 were used to derive the position and direction of the Agulhas Current and associated mesoscale features. Although the distribution of surface temperatures only are indicated, experience from numerous *in situ* measurements has shown that in general, surface thermal expressions in the area are representative of a significant part of the upper water column.[6,9] This may be, depending on circumstances and the phenomenon in question, anywhere between 100 m and 2 000 m.

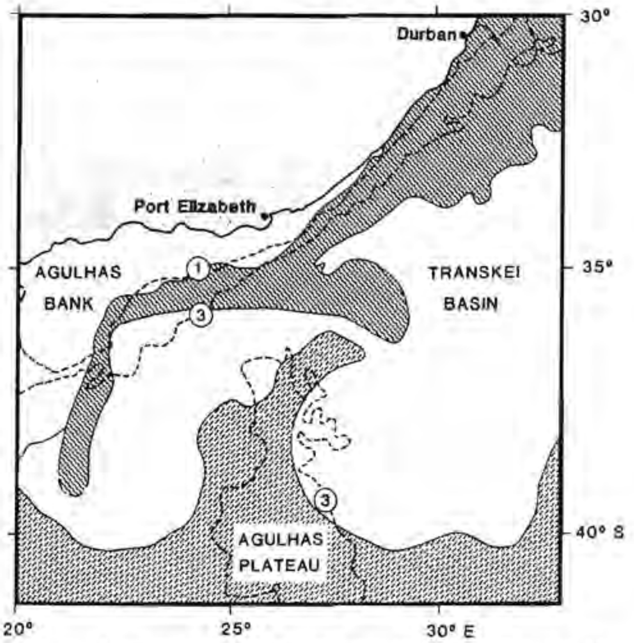

Fig. 1. Line drawing of the thermal infrared image for 21 April 1991 from the NOAA-11 satellite. The image portrays the surface expression of the Agulhas Current south of Durban, the hatched area representing Agulhas Current water of temperature greater than 24°C, while the shaded area represents cold Sub-Antarctic Surface Water of temperature less than 18°C. South of Port Elizabeth, a large pool of warm (> 24°C) Agulhas water is seen to leak in an eastwards direction along the northern edge of the Agulhas Plateau and into the Transkei Basin, while an extrusion of cold, sub-Antarctic water is shown to occur over the Agulhas Plateau. Isobaths in km delineate the main topographic features of the sea bottom.

Shedding of an eddy

The formation and subsequent shedding of a large, warm body of water from the seaward side of the Agulhas Current was observed in the April 1991 series of TIR images. Three cloud-free TIR images have been selected to demonstrate here the sequence of events which preceded and followed this occurrence.

The TIR image for 21 April 1991 (Fig. 1) shows the remarkably stable path configuration of the Agulhas Current as it closely followed the shelf edge of the southern African continent downstream of Durban. On reaching the southern tip of the Agulhas Bank, the Current continued in a southerly direction, retroflecting at about 21.5°E. However, a significant perturbation was observed south of Port Elizabeth, where warm (> 24°C) Agulhas water covering a large surface area was seen to protrude in an eastward direction along the northern edge of the Agulhas Plateau and into the Transkei Basin (Fig. 1). A prominent elongation of the Subtropical Convergence Rossby wave simultaneously occurred over the Agulhas Plateau, extending in a north-easterly direction towards the Transkei Basin (Fig. 1).

The TIR image for 24 April (Fig. 2) shows the abovementioned body of warm water as having become detached from the seaward side of the Agulhas Current proper to form a separate warm (> 24°C) pool of dimensions 160 × 170 km. This body of water, now centred at 35.7°S, 29.6°E, moved in an easterly direction at an average rate of 45 km per day during

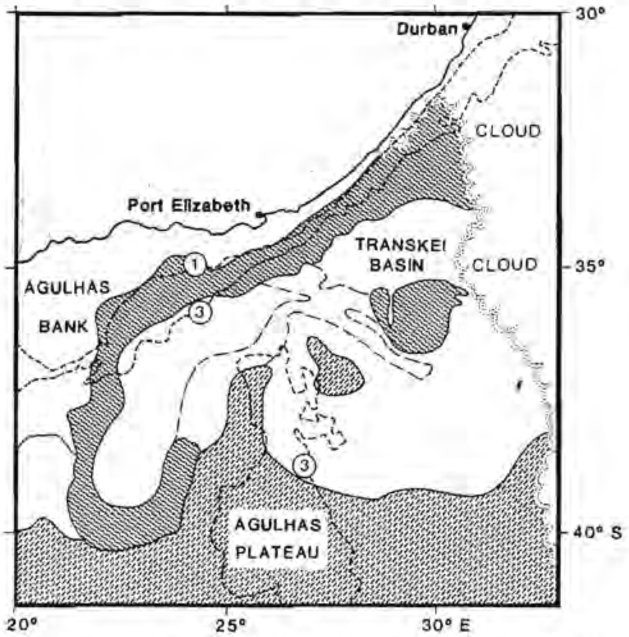

Fig. 2. Line drawing of the TIR image for 24 April 1991, as for Fig. 1, showing the large pool of warm water as having been shed from the seaward side of the Agulhas Current proper, the filaments which appear to be streaming from it suggesting an anti-cyclonic motion. The sub-Antarctic extrusion is also seen to have spawned a cold, tear-shaped eddy in the lee of the Agulhas Plateau.

the 3-day period. During the same period, the eastward extrusion of cold sub-Antarctic water spawned a cold, tear-shaped eddy[6] in the lee of the Agulhas Plateau, such that it lay alongside the large warm pool. The warm filaments which extended from the body of the warm pool strongly suggest that it was an eddy with an anticyclonic motion.

The TIR image for 29 April (Fig. 3) shows this warm eddy as having moved in a north-easterly direction at an average rate of 22 km per day during the 5-day period, while its border configuration had become much more diffuse. The cold eddy in turn had lost much of its surface expression. The seaward border of the Agulhas Current upstream of Port Elizabeth likewise appears to have become very indistinct at the sea surface with a diffuse surface thermal pattern throughout the area. This cannot, unfortunately, be clearly portrayed by a line drawing such as Fig. 3.

Subsurface measurements

Crucial to an understanding of the importance of these observations is information on the depth to which this warm feature extended. The occasional advection south-eastwards of some of the top 50 m of warm Agulhas water would certainly have important implications, but the shedding of a deep eddy would have considerably greater importance.

The supply and research vessel *S.A. Agulhas* was on a return voyage from Marion Island from 5 April 1991 and was able to lay out its returning leg so that it nearly intersected the warm eddy (Fig. 3). Expendable bathythermograph probes (XBTs) were launched at regular intervals, giving a vertical trace of the ambient ocean temperature at each station. This line of stations, portrayed in Fig. 3, was not occupied simultaneously with the acquisition of the satellite image itself. Stations 217 to 219, which seem closest to the warm feature, were occupied on 5 and 6 May, i.e. 6 days after the depiction of the sea surface temperatures in Fig. 3. A certain degree of movement in the main features can therefore be expected.

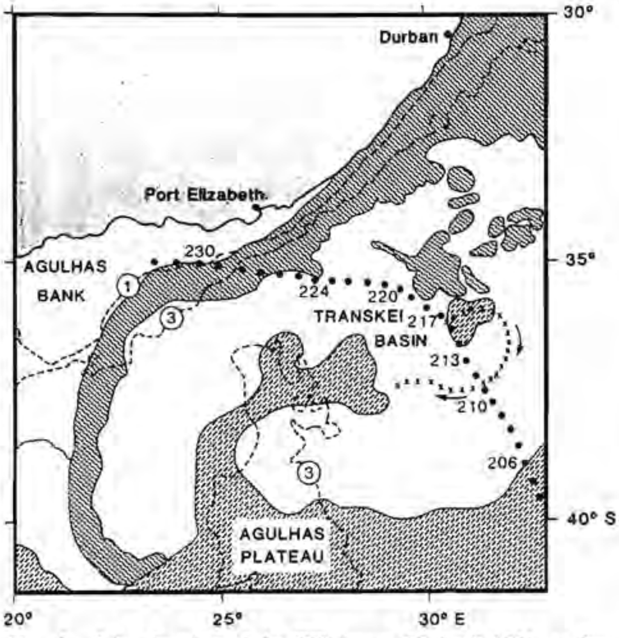

Fig. 3. Line drawing of the TIR image 29 April 1991, as for Fig. 1, showing the warm eddy as having moved in a north-easterly direction, while its border configuration has become much more diffuse. The surface expression of the cold eddy also had become less distinct, and a general diffuse surface thermal expression is seen throughout the area. The line of dots represents a sequence of expendable bathythermograph (XBT) stations undertaken from 5 to 6 May 1991. Numbers are to be compared with those used in Fig. 4. The line of crosses shows the initial path of a drifting buoy launched between stations 215 and 216.

Figure 4 shows the temperature section along this track. The strong horizontal temperature gradient between stations 206 and 207 locate the Subtropical Convergence. Its middle temperature was 18°C, warmer than the mean for this front.[12] Its position had not shifted markedly.

The cold eddy that had been spawned from the Subtropical Convergence is a distinct feature between stations 213 and 216. Its surface expression had rapidly been eroded,[6] but below the surface it clearly retained its sub-Antarctic characteristics. It bears a striking resemblance to the so-called Mozambique Ridge eddies[5] found about 600 km to the north-east. Having been observed to move about 400 km in about 8 days on this occasion (Figs 1–3), a cold eddy of this kind could well arrive at the usual location of these Mozambique Ridge eddies without too long a time elapsing. The so-called Mozambique Ridge eddies have their 10°C isotherm at about 350-m depth, whereas the feature discussed here has 10°C water extending to 200 m (Fig. 4). If some Mozambique Ridge eddies do have their origin in the sub-Antarctic, some spinning-down and mixing would therefore already have occurred. Recent studies[13] suggest a wide possible range of origins of Mozambique Ridge eddies including the region east of Madagascar. The possibility of a more southern origin has only been suggested so far.[14]

As depicted in Fig. 4, the warm surface water (> 22°C) of the Agulhas Current extended quite far seaward on this occasion. This agrees with the warm water leakage to the east, observed in the satellite observations described above. Even surface water warmer than 23°C was found on this line; at station 224 and between stations 222 and 223.

A distinct warm feature is also evident between stations 216 and 219 in Fig. 4. From its location in Fig. 3, it would seem that the XBT line had intersected the edge of the warm feature in question at this point. The crucial question now is whether there was evidence that this feature was deep. A distinct perturbation in the temperature field to the full depth measured (Fig. 4), based on at least two independent stations, strongly suggests that this feature was, first of all, an eddy and, second, vertically extended beyond the surface layer.

It is a great pity that a section through the presumed centre of the warm eddy, slightly further to the north, was not undertaken. The inferred core of the feature in the XBT trace is shown as a broken line in Fig. 4. It may be noted that this line

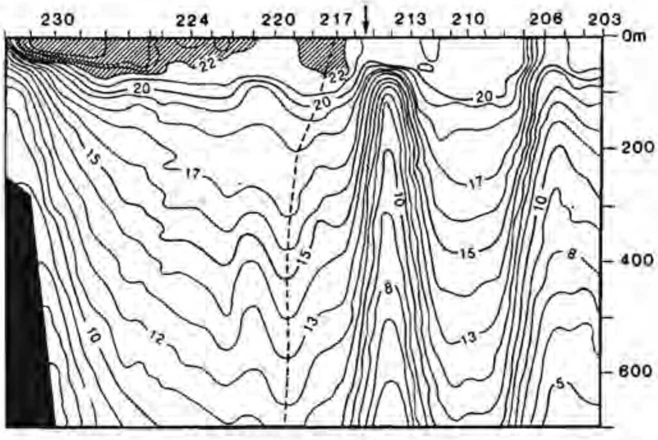

Fig. 4. Temperature section to 700 m depth from south of the Subtropical Convergence (right) to north of the Agulhas Current (left). The locations of the stations are given in Fig. 3. Water warmer than 22°C has been shaded. The core of the warm eddy is indicated by a near-vertical broken line. The arrow locates the launch position of the buoy (Fig. 3).

is not perfectly vertical but slopes eastwards above 300 m. It is not unusual for eddies, observed elsewhere, to exhibit such a slope.

Drifting buoy

A drifting weather buoy was placed in the water near station 215, at 36.3°S latitude, 30.5°E longitude on 5 May (Fig. 3). According to the thermal structure presented in Fig. 4, this would initially locate the buoy somewhere between the warm and cold eddy, but closer to the rim of the cold one. Subsequent drift behaviour of the buoy supports this interpretation. It drifted rapidly eastward, turned south before it reached 32°E and then west at about 37.5°S (Fig. 3). It subsequently followed the Subtropical Convergence along which it moved eastward (not shown).

These buoys are small and have a very small cross-sectional area above the water, thus minimizing windage. They may therefore be considered to follow the movement of the water masses in which they are embedded quite closely. They have, however, no deep drogue and therefore portray the movement of the upper few metres of the water column only, but this may be representative of much greater depths.

Unfortunately for this experiment the buoy was not trapped in either the cold or the warm eddy. Its motion is nevertheless in general agreement with the above interpretation of both the temperature section (Fig. 4) and the satellite imagery (Fig. 3). It seems to have slipped through the gap between the warm and cold eddy, to have then circled the cold eddy and finally joined the general ambient flow eastward.

One may consider these drift results as not adding much new information, but as giving general support to the interpretation of the other data sets.

Conclusions and implications

The observation of the loss of a coherent body of water from the seaward side of the Agulhas Current as an entity, is new and has some important implications. It suggests that amounts of salty, warm Subtropical Surface water may be injected into the South West Indian subgyre directly from the Agulhas Current. It also suggests that the mass flow of Agulhas Water may, on occasion, be somewhat reduced between Durban and the tip of the Agulhas Bank.

Such a leakage has been observed before as an early retroflection.[9] The leakage noted on this occasion may be part of the same mechanism, representing an uncompleted early retroflection. There is an important difference between the two phenomena, however. An early retroflection only shortens the route by which Agulhas water enters the South Indian Current which then carries it eastward. The feature reported here does not do that, but injects this water into the centre of the South West Indian Ocean subgyre where it may remain, thus adding to the salt and heat of the subgyre. Although the underlying mechanism for these two processes may therefore conceivably be the same, the results seem, on the basis of the limited results presented here, distinctly different.

The rapid disappearance of the surface expression of the feature may have been due to a number of possible factors. The heat loss from the ocean to the atmosphere in this warm feature may have been high, or insolation of surrounding surface water may have made it hard to continue to distinguish it in TIR imagery.

The fact that such bodies of warm, salty water, covering areas of more than 40×10^3 km^2, can become detached from the seaward side of the Agulhas Current and drift into the deep ocean, suggests a less cohesive seaward border to the Agulhas Current than conceptualized before.

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