regard these zones as equivalent to the Early Weichselian interstadials. If pollen zones 9, 10, and 11 were to be correlated with these interstadials, we should conclude that a large hiatus exists between the end of the Eemian and the Amersfoort in the Netherlands, but evidence in support of this conclusion does not appear to exist. The radiocarbon time scale used earlier for the Weichselian stratigraphic events has the Amersfoort starting at 68,200 ± 1100 years, the Brörup at 64,400 ± 800 years, and the Odderade at 60,500 ± 600 years B.P. (*12*). If this chronology is correct, our ^{14}C date of $69{,}500 \pm {}^{3800}_{2600}$ years B.P. for the end of zone 8 supports the correlation between zones 9, 10, and 11 and these Early Weichselian interstadials (Fig. 2). Further data are needed to resolve this dilemma.

The pollen and ^{14}C data taken together enable us to attempt correlations between the Grande Pile continental sequence and the ocean records (Figs. 1 and 2). Three minima in the time series for total tree and shrub pollen indicate three maximum cold periods, zones 1, 12, and 18, which can be correlated with the prominent ice-growth phases reflected in deep-sea sediments by oxygen isotope stages 6, 4, and 2, respectively. Absolute datings from land and ocean, respectively, fix the cold maximum (zone 12) initiating the Middle Weichselian between about 62,000 and 70,000 years B.P. and deep-sea stage 4 between 61,000 and 73,000 years B.P. Both interglacial maxima (pollen zones 2 and 21), identified as the Eemian and Holocene interglacials, are well correlated with oxygen isotope substage 5e and stage 1, respectively. The former correlation has recently been demonstrated (*4*). The Middle Weichselian, located here between 29,000 and about 62,000 years B.P., can be regarded as the equivalent of oxygen isotope stage 3. Pollen zones 3 to 11 then might correlate with the deep-sea substages 5d through 5a. The correlations suggested in Fig. 1 within this interval are, however, still unproved.

The results of our study show a good agreement between land and sea chronologies, reflecting a primary change from "interglacial" to glacial conditions at about 70,000 to 73,000 years B.P. This time corresponds to the start of the Middle Weichselian at Grande Pile and to the boundary between oxygen isotope stages 5 and 4 in the oceanic records (*17*). Uncertainty remains about the correlations between our pollen zones 4 to 11 and the classical stratigraphy: (i) zones 4, 6, and 8 as well as zones 9, 10, and 11 do not resemble the pollen records of the Early Weichselian interstadials; if zones 9, 10, and 11 correspond to these interstadials, a hiatus exists at Amersfoort and other places. (ii) If the present knowledge about the Early Weichselian ages is accepted as correct, zones 4, 6, and 8 cannot represent the classical interstadials Amersfoort, Brörup, and Odderade. (iii) Our continental record is in good agreement with the deep-sea record to about 70,000 years B.P. (that is, oxygen isotope stage 4), but we are still uncertain about how to correlate the classical interstadials with the substages of oxygen isotope stage 5.

GENEVIÈVE M. WOILLARD*
Institut Botanique, Laboratoire de
Palynologie et Phytosociologie,
4, place Croix-du-Sud,
1348 Louvain-la-Neuve, Belgium
WILLEM G. MOOK
Isotope Physics Laboratory,
University of Groningen,
Westersingel 37,
9718 CM Groningen, Netherlands

References and Notes

1. G. J. Kukla, *Earth-Sci. Rev.* **13**, 307 (1977).
2. G. M. Woillard, *Acta Geogr. Lov. 14* (1975); in "International Geological Correlation Programme Project 73/1/24 Report 4," V. Sibrava, Ed. (Stuttgart-Hohenheim, Prague, 1977), p. 72; *Quat. Res. (N.Y.)* **9**, 1 (1978); *ibid.* **12**, 154 (1979); in *Palaeoecology of Africa*, E. M. van Zinderen Bakker and J. A. Coetzee, Eds. (Balkema, Rotterdam, 1978), vol. 10, p. 125; *Bull. Soc. Belg. Geol.* **88**, 51 (1979); *Nature (London)* **281**, 558 (1979); in "International Geological Correlation Programme Project 73/1/24 Report 6," V. Sibrava, Ed. (Ostrava, Prague, 1980).
3. W. H. Zagwijn, *Meded. Geol. Sticht.* **14**, 15 (1961).
4. J. Mangerud, E. Sønstegaard, H. P. Sejrup, *Nature (London)* **277**, 189 (1979).
5. N. J. Shackleton and N. D. Opdyke, *Quat. Res. (N.Y.)* **3**, 39 (1973); ——, R. K. Matthews, *Nature (London)* **268**, 618 (1977); W. F. Ruddiman, *Science* **196**, 1208 (1977).
6. J. D. Hays, J. Imbrie, N. J. Shackleton, *Science* **194**, 1121 (1976).
7. M. A. Kominz, G. R. Heath, T. L. Ku, N. G. Pisias, *Earth Planet. Sci. Lett.* **45**, 394 (1979).
8. J. Mangerud and B. E. Berglund, *Boreas* **7**, 179 (1978).
9. Ar. Leroi-Gourhan, *Colloq. Int. CNRS* **219**, 61 (1973); —— and J. Renault-Miskovsky, in *Approche écologique de l'Homme fossile*, p. 35.
10. T. van der Hammen, C. C. Maarleveld, J. C. Vogel, W. H. Zagwijn, *Geol. Mijnbouw* **46**, 79 (1967); T. van der Hammen and T. Wijmstra, *Meded. Rijks Geol. Dienst* **22**, 55 (1971).
11. W. H. Zagwijn and R. Paepe, *Eiszeitalter Ggw.* **19**, 129 (1968).
12. P. M. Grootes, thesis, University of Groningen (1977); *Science* **200**, 11 (1978).
13. J. Mangerud, S. T. Andersen, B. E. Berglund, J. J. Donner, *Boreas* **3**, 109 (1974).
14. H. J. Beug, *Geol. Bavarica* **80**, 91 (1979); E. Grüger, *ibid.*, p. 5; *Quat. Res. (N.Y.)* **12**, 152 (1979).
15. S. T. Andersen, *Dan. Geol. Unders. Afh. Raekke 2* **75**, 1 (1961).
16. F. R. Averdieck, in *Frühe Menschheit und Umwelt*, K. Gripp, R. Schütrumpf, H. Schwabedissen, Eds. (Cologne, 1967), vol. 2, p. 101.
17. W. F. Ruddiman, A. McIntyre, V. Niebler-Hunt, J. T. Durazzi, *Quat. Res. (N.Y.)* **13**, 33 (1980).
18. The pollen curve is based in part on published data (*2*). It has been established with the four parallel cores I, XVIII, XIX, and X (core I being 350 m apart from the others), connected by palynology; a regular scale of depths has been applied in each core to draw the curve. About 500 pollen grains were counted in each of 370 samples; 120 taxa were recognized. Methods of processing the samples were described earlier in (*2*).
19. The radiocarbon samples were treated with acid, alkali, and acid prior to combustion of the residue. For the enriched date of $69{,}500 \pm {}^{3800}_{2600}$ years B.P. (GrN-9187), a 15-cm section was taken from the three parallel cores XVI, XVII, and XIX. The enrichment sample was rigorously extracted with alkali. The alkali extract was dated at > 49,000 years B.P. (GrN-9383). The alkali treatment was omitted for the radiocarbon sample dated at 11,170 ± 100 years B.P. (Lv-1046) because of the low content of organic material (too small a sample).
20. C. Emiliani, *J. Geol.* **63**, 538 (1955).
21. N. J. Shackleton, *Proc. R. Soc. London Ser. B* **174**, 135 (1969).
22. We are grateful to H. J. Streurman who carried out the ^{14}C enrichment and the GrN ^{14}C datings and to E. Gilot who obtained both Lv ^{14}C datings. We thank W. Mullenders, B. Frenzel, J. Mangerud, and A. V. Munaut for critical review of the manuscript. In 1980, G.M.W. was a research fellow of the Alexander von Humboldt Foundation at Hohenheim University, Stuttgart.

* Dr. Woillard died on 7 July 1981.

16 January 1981; revised 21 August 1981

The Coalescence of Two East Australian Current Warm-Core Eddies

Abstract. *Two warm-core eddies coalesced in about 20 days as their centers rotated around a point on the contracting line that joined them. In the process of forming the new eddy, the subsurface isothermal-isohaline "signature" layer of one eddy was uplifted and somewhat depleted while that of the other was depressed.*

The warm-core eddies that are a notable feature of the East Australian Current (EAC) system were first described by Hamon (*1*). Since then they have been studied sporadically, sometimes as part of broader EAC studies (*2*) and sometimes in their own right (*3, 4*). The picture that emerges from the studies may be summarized as follows: (i) warm-core eddies about 250 km in diameter form from the pinch-off of EAC meanders; (ii) they have lifetimes of about 1 year; (iii) they can drift along complicated paths; (iv) they can rejoin EAC meanders; (v) the surface layers of an eddy cool and mix down to ~350 m in winter to form an isothermal core; and (vi) the formation of a summer surface "cap" of warmer water insulates this core from further changes so that it becomes, in effect, a signature for subsequent identification.

The first suggestion that warm-core eddies may coalesce came during 1979–1980 when the evolution of eddy J near

0036-8075/82/0108-0161$01.00/0 Copyright © 1981 AAAS

Sydney was closely followed starting in March 1979 (*5*). Winter cooling and deep mixing proceeded until the end of September to produce an isothermal-isohaline signature layer that was 365 m thick at the eddy center. A "cap" then formed from the combined effects of summer heating and surface flooding by EAC waters, so that in December the signature layer was up to 170 m thick in the depth range from 100 to 300 m; the eddy was then at 35°S. Curiously, when eddy J was surveyed at 36°S in early February 1980, its signature layer was found to lie on top of another quite different isothermal-isohaline layer. At the eddy center, the upper layer extended from 110 to 190 m and the lower one from 280 to 470 m. If we accept that such thick mixed layers form from the winter cooling of warm-core eddies (*4, 6*) and that in July 1979 a wide-ranging survey showed that there were only two eddies, eddy I and eddy J adjacent to the continent between 33° and 39°S, it seemed not unreasonable to identify the lower layer as the signature layer of eddy I. This identification raised questions about the nature of the apparent coalescence and whether it could be expected again.

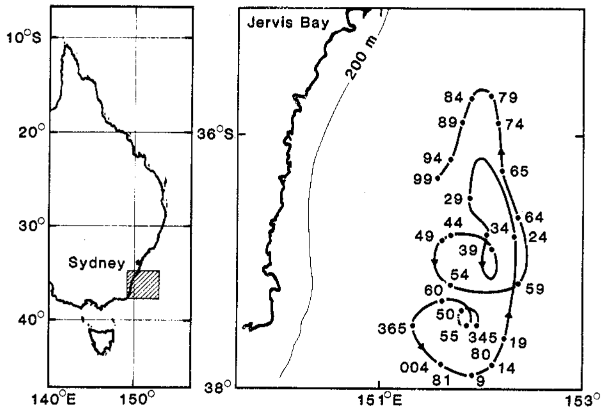

Fig. 1. The study area and the movement of the center of eddy Leo between day 345 in 1980 and day 99 in 1981.

In July 1980 two new eddies, Maria and Leo, were situated off eastern Australia at 33° and 36°S, respectively. The paths of pairs of satellite-tracked buoys released on brief surveys by R.V. *Sprightly* (en route to and from refit) in December 1980 and January 1981 ap-

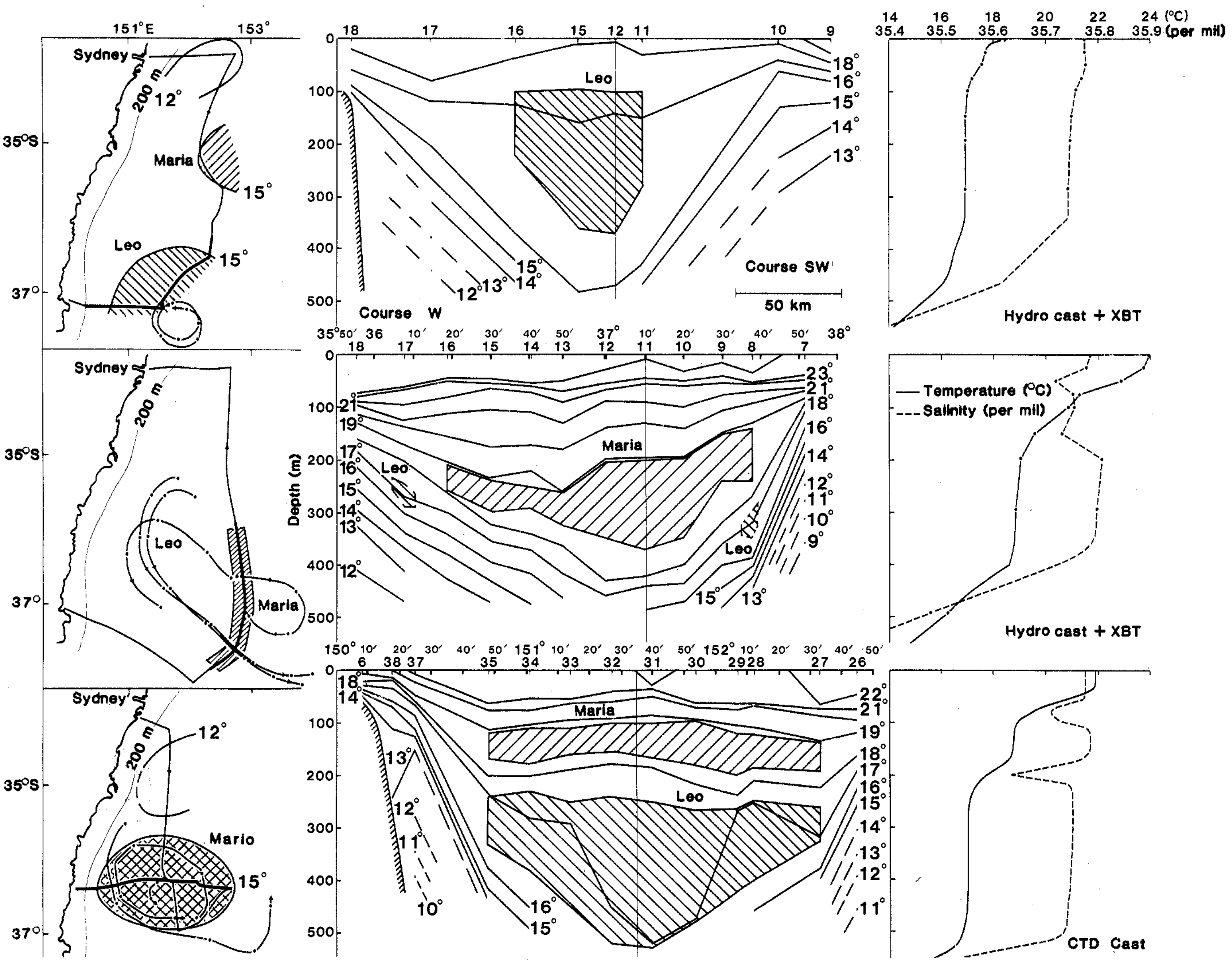

Fig. 2. Results of the ship surveys of December 1980 (top), January 1981 (middle), and April 1981 (bottom). In column 1 buoy tracks for several days before and after the surveys are marked; regions having 250-m temperatures exceeding 15°C are shaded; the 12°C isotherm for 250 m is marked. The thickened ship tracks define the temperature sections in degrees Celsius in column 2 where the signature layers of eddies Leo and Maria are shaded. The vertical lines in column 2 indicate the positions for the temperature and salinity profiles of column 3.

peared to be just adequate to document the rapid and complex coalescence of these eddies in January–February 1981. A hydrology survey in April 1981 confirmed the coalescence.

The buoys are torpedoes (1.5 m long by 0.4 m in diameter), each with a polyethylene rope 200 m long by 0.012 m in diameter tethered to an 8-m cargo parachute sea anchor (7). They are position-fixed six times per day (to ±1 km) by the ARGOS System. Instrumentation on the *Sprightly* included a surface thermosalinograph, Niskin bottles for hydro casts, and expendable bathythermographs (XBT's). A Neil Brown salinity, temperature, and depth profiler (CTD) was operated on the April 1981 survey.

Between the December 1980 and April 1981 surveys of the *Sprightly*, seven buoys were released into eddy Leo and the eddy that resulted from its coalescence with Maria. The buoy tracks made it possible to follow the center of eddy Leo as it traced anticlockwise arcs that were occasionally interrupted by northward translations (Fig. 1). The maximum speed of movement was 18 km day^{-1} between 19 and 25 January. The water in the eddy generally rotated with a period of 3 to 4 days as indicated by buoys that were within 30 km of the center. One of the buoys that was about 50 km from the center after coalescence indicated a period of 5 to 6 days.

The data from the three research vessel surveys are summarized in Fig. 2: column 1 gives the vessel tracks, the 250-m temperatures with regions exceeding 15°C shaded to identify the eddies, and the tracks of buoys for short periods around the time of the surveys. Column 2 gives XBT temperature sections for the thickened parts of the vessel tracks in column 1; signature layers isothermal to ±0.1°C are shaded according to whether they are characteristic of eddy Leo or eddy Maria. Column 3 gives temperature and salinity profiles at the positions marked by the vertical lines in column 2; these profiles are from hydro casts (and a CTD cast in April 1981), with XBT data being used in places to bridge gaps between bottles.

The December 1980 data of Fig. 2 show that the ship passed the western side of eddy Maria and released buoys about 35 km northwest of the center of eddy Leo. The signature layer there ranged from 100 to 370 m and had a temperature and salinity of 16.9° ± 0.1°C and 35.75 ± 0.01 per mil, respectively. The January 1981 data have been interpreted to show that the ship crossed the Maria part of a Leo-Maria couple that had centers separated by 160 km. The XBT section revealed an asymmetric signature layer for eddy Maria together with an apparent encircling subsurface filament of eddy Leo's signature layer; eddy Maria's signature layer had a temperature and salinity of 18.9° ± 0.1°C and 35.80 ± 0.01 per mil, respectively, and occurred in the depth interval from 200 to 370 m. Buoy data were used in April to fix the eddy center, and then the ship made meridional and zonal eddy sections. These showed two signature layers, with the upper one being characteristic of eddy Maria and the lower one of eddy Leo.

An interesting feature of the coalescence is revealed by the eddy center temperature and salinity profiles for April: the Leo and Maria signature layers have between them at 200-m depth a salinity minimum of 35.64 per mil with a corresponding temperature of 17.6°C. This temperature-salinity combination did not occur anywhere in the eddy Leo hydro cast in December, and so we must look closely at eddy Maria in January. Using a reasonable interpolation, we can see that this temperature-salinity combination occurred beneath the Maria signature layer at a depth of ~ 430 m. In other words, the lower boundary of eddy Maria's signature layer was uplifted 230 m by the coalescence event. The thickness of this signature layer decreased from 170 m in January to 70 m in April. By comparison, there was no measurable change in the vertical extent of Leo's signature layer between December (100 to 370 m) and April (250 to 530 m). In December the bottom of the layer was measured at 370 m some 35 km from the eddy center. Allowing it to be at most 50 m deeper at the center suggests that eddy Leo's layer may have been depressed by at least 100 m as a result of the coalescence.

The buoy data for late January–early February (Fig. 3) are complex, and the tentative interpretation made is that eddy Leo was initially perturbed by the arrival of eddy Maria, that the two eddy centers then moved anticlockwise about a point on the line joining them, and that this line contracted as the eddies coalesced. Figure 3a shows eddy Leo being perturbed and accelerating to the northwest. Perhaps it then lost part of its volume because both buoys escaped to the southeast. Figure 3b shows eddy Leo moving down to the south with three different buoys documenting the move. (When two buoys were released on 27 January, buoy B6 moved around eddy

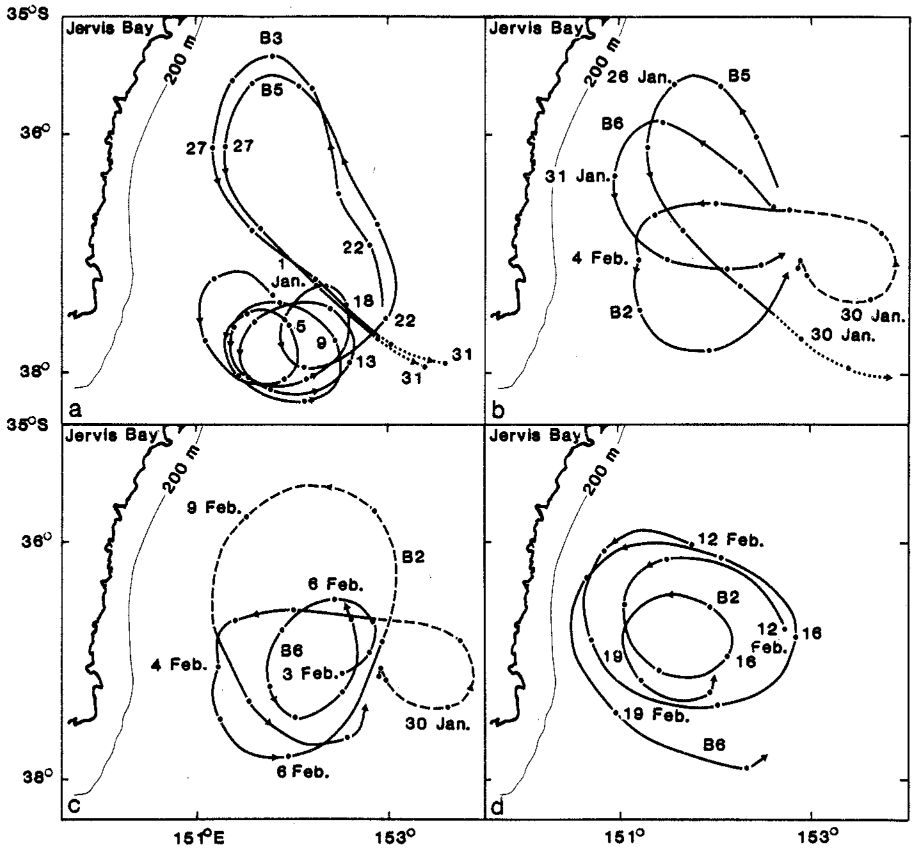

Fig. 3. The tracks of buoys B2, B3, B5, and B6 late January to early February 1981) interpreted to be in eddy Leo (solid line), eddy Maria (dashed line), or escaping from the eddy pair (dotted line). In (a) the track of buoy B3 is shown only from 22 January onward.

Leo and buoy B2 around eddy Maria.) Figure 3c shows eddy Maria moving around to the north and eddy Leo moving in a manner suggesting that the line between the eddies was shortening. In Figure 3d the buoys achieve a synchronism of rotation around a large feature that would seem to preclude the possibility that the centers of the two eddies were still separated. The new eddy was named eddy Mario (see Fig. 2).

Our observations support the idea that two eddies with characteristic signature layers coalesced in a process lasting about 20 days. During the coalescence, both eddies seemed to move around a point on the contracting line joining their centers. Part of the signature layer of eddy Maria was lost as a result of the coalescence, and the lower boundary was uplifted about 230 m. The signature layer of eddy Leo stayed mainly intact as it was depressed by at least 100 m beneath the uplifted part of eddy Maria's signature layer. The temperature and salinity structure of the combined eddy was very similar to that of an eddy observed 1 year earlier (eddy J) and believed to be the result of coalescence. The buoy tracks were reminiscent of the two-dimensional coupling of vortices revealed by computer simulation (*8*).

GEORGE R. CRESSWELL
Division of Oceanography,
Commonwealth Scientific and
Industrial Research Organization
Marine Laboratories, Box 21, Cronulla,
New South Wales 2230, Australia

References and Notes

1. B. V. Hamon, *Aust. C.S.I.R.O. Div. Fish. Oceanogr. Tech. Pap. No 11* (1961).
2. ———, *Deep-Sea Res.* **12**, 899 (1965); F. M. Boland and B. V. Hamon, *ibid.* **17**, 777 (1970); F. M. Boland and J. A. Church, *ibid.*, in press.
3. J. C. Andrews and P. Scully-Power, *J. Phys. Oceanogr.* **6**, 756 (1976); C. S. Nilsson, J. C. Andrews, P. Scully-Power, *ibid.* **7**, 659 (1977).
4. C. S. Nilsson and G. R. Cresswell, *Prog. Oceanogr.* **9**, 133 (1981).
5. The extensive data set for eddy J is presently being analyzed by D. Tranter, S. Brandt, and G. R. Cresswell.
6. A. Tomosada, *Bull. Tokai Reg. Fish. Res. Lab.* **94**, 59 (1978).
7. G. R. Cresswell, G. T. Richardson, J. E. Wood, R. Watts, *Aust. C.S.I.R.O. Div. Fish. Oceanogr. Rep. No. 82* (1978).
8. J. P. Christiansen, *U.K. At. Energy Auth. Res. Group Culham Lab. Rep. CLM-R 106* (1970).

21 August 1981

The Chloride Cell: Definitive Identification as the Salt-Secretory Cell in Teleosts

Abstract. *Chloride-secreting isolated opercular membranes from the seawater-adapted teleost* Sarotherodon mossambicus *contain the several cell types also seen in the branchial epithelium. The vibrating probe technique has been used to localize conductance and chloride current specifically to the so-called chloride cells, thereby establishing these cells definitively as the extrarenal salt-secretory cells.*

Seawater-adapted teleost fish live in a dehydrating environment but cannot produce a concentrated urine. Numerous ion transport studies have made it clear that the branchial epithelium, in addition to serving as a respiratory organ, functions as the site of extrarenal salt secretion in these fish (*1*). It is generally accepted (*2*) that the anatomical basis of branchial salt secretion is chloride cells, large, granular, acidophilic cells originally described by Keys and Willmer in seawater eel gills (*3*). The gill epithelium is composed of four principal cell types (*4*), however, and each of these cell types has, at one time or another, been implicated as the salt-secretory cell type (*3, 5*). Despite numerous ultrastructural, enzymatic, and kinetic studies (*1, 2*), there is still no direct experimental support for the idea that the chloride cell is the site of branchial salt secretion.

We have used the vibrating probe technique (*6*) to localize current and conductance pathways in the opercular membrane isolated from the seawater-adapted euryhaline teleost, the tilapia *Sarotherodon mossambicus* (formerly *Tilapia mossambica*). This epithelium possesses a rich population of chloride cells characterized by an ultrastructure typical of branchial chloride cells (*7*) and displays ion transport properties that respond to various hormonal and pharmacological agents in a manner analogous to the branchial responses (*7, 8*). We provide here the first conclusive evidence that chloride cells are sites of active chloride secretion and high ionic permeability.

Opercular membranes were isolated from seawater-adapted tilapia as described in (*7*). The pigmented serosal connective tissue was gently removed with fine-tipped forceps, and the translucent epithelium was mounted horizontally, apical side up, in an Ussing chamber containing tilapia Ringer solution. The apical side was approached with the vibrating probe under visual control; we used bright-field optics at ×100 or ×320. The transepithelial voltage was measured with agar bridges, each within a few millimeters of either side of the tissue, and connected to calomel electrodes. The epithelium was voltage-clamped by standard techniques with series resistance compensation.

The vibrating probe apparatus developed by one of us (C.S.) is similar to that described by Jaffe and Nuccitelli (*6*), except that the tip was smaller (7 μm in diameter) and vibrated at higher frequencies (1.6 or 6 kHz) (*9*). The tip of a platinized gold electrode was vibrated along a line 10 to 15 μm long, and its signal was analyzed with computational circuitry to measure a weighted average of the voltage gradient along the line of vibration. We calibrated this measured voltage gradient and then converted it into current density by dividing by the medium bulk resistivity. It was assumed that the bulk resistivity closely approximated the medium resistivity near the tip because the acoustic streaming at the tip vigorously mixed the bulk solution with the solution at the tip (*6, 9*). With the assumption that chloride cells represent point sources of current density at the apical surface, we calculated the current per chloride cell by multiplying the current density above a chloride cell by the area of a hemisphere centered at the chloride cell with a radius equal to the height of the probe above the surface. We checked the probe signal corresponding to zero current density periodically throughout the experiments by moving the probe into an area of the bath where there was no current. The signal drift was usually negligible during an experiment and corresponded to no more than 5 percent of the current density measured over a chloride cell.

The short-circuit current (I_{sc}) across the tilapia opercular membrane represents chloride-carried negative charge flow into the apical solution (*7*). To investigate the distribution of current sources on the epithelium, the vibrating probe was positioned so that the closest excursion of its vibration was 5 to 10 μm above the apical surface with the line of vibration at a 60° angle with the surface. Under short-circuit conditions, the vibrating probe output revealed peak negative current densities over 90 to 95 percent of the chloride cells examined in eight different opercular membranes. Current density peaks were never observed over nonchloride cells. Figure 1 is a typical transect in which the vibrating probe was moved at a constant height (20 μm) above the tissue between two chloride cells. Negative current density is greatest when the tip of the probe is

0036-8075/82/0108-0164$01.00/0 Copyright © 1981 AAAS