time period, but faunal migrations imply a Bering land bridge 80 million years ago. The magnetic dating associated with the ridges in the eastern Pacific imply the decrease of EF. The magnetic dating and fault structure of the Indian Ocean show that Australia has moved slightly north of west (as we go backward in time) in relation to Africa in the given time period. Since Africa must simultaneously move slightly north compared with Asia, as demanded by the ridges in the Indian Ocean and the Red Sea, the link ABwas apparently shorter. This is consistent with the accepted biological evidence that the marsupials arrived in New Guinea and Australia by way of a land connection to mainland Asia (and not from South America by way of Antarctica) and that this land connection was broken 70 million years ago or before (13). The reconstruction of Fig. 1 also leads to this conclusion. The evidence for the decrease of each of these linkages as we go back in time is rather strong, and it seems highly improbable that the area enclosed by the perimeter was ever as large as half the earth's present area in the last 150 million years.

The topological argument given above is independent of possible downwelling of the ocean floor. It is also apparently independent of shrinkage of the continents associated with mountain formation since the important mountain regions of the perimeter could be included without significant increase in the perimeter. The argument is not very sensitive to the exact time scale or to variations in the rate of oceanfloor spreading, as long as these were reasonably monotonic in the period in question, and could be adapted to most proposed reconstructions of a single supercontinent.

The only hypothesis that has been suggested thus far that resolves the paradox described above is that in the past the earth's interior has expanded considerably (the inverse process of a contraction of the crust of this magnitude has not been seriously suggested). It is conceivable that a rather small expansion, as suggested by Dicke (14) and by Wilson (15), might be consistent with the above argument. The most direct interpretation of the evidence, however, seems to be that a large expansion of the earth's interior has taken place in the last 150 million years. The nature of the physical process that could have led to such an expansion is highly conjectural, but

such a process cannot be excluded on the basis of present physical knowledge. Because of the radical implications of the expansion hypothesis, the assumptions of the argument presented above will need to be examined with care and objectivity.

R. MESERVEY

Francis Bitter National Magnet Laboratory, Massachusetts Institute of Technology, Cambridge 02139

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Shallow Scattering Layer in the Subarctic Pacific **Ocean: Detection by High-Frequency Echo Sounder**

Abstract. Shallow scattering layers consisting mainly of Calanus cristatus were detected on a trans-Pacific crossing to depths of 60 meters with a high-frequency echo sounder. Biomass estimates of these layers indicate concentrations of zooplankton that are greater and more extensive than previously reported in the open ocean.

The extensive use of low-frequency sounders in the marine environment has shown the presence of deep scattering layers in many parts of the hydrosphere (1). These layers generally exist below 100 m in the oceans, but at least parts of the layers migrate at night from depths of 300 to 500 m into the surface waters. Thus far only limited use has been made of high-frequency echo sounders in plankton studies (2). The major limitation of high-frequency sounders in comparison to low-frequency sounders is that the signal of the former, which is very efficient at picking up small targets, has an effective range of no more than 200 m, whereas the latter unit, which is generally limited to large targets, commonly has a range in excess of 1000 m.

A high-frequency (200-khz) echo sounder (3) was operated continuously during two crossings of the Pacific Ocean, from 18 March to 5 May 1969, on board the Canadian research vessel Endeavour. The crossings (Fig. 1) followed an approximate great circle route through the subarctic Pacific between Esquimalt, British Columbia,

Canada, and Tokyo, Japan, and from Hakodate, Japan, to Esquimalt.

A dense shallow scattering layer was observed to occur during daylight hours over most of the Pacific at varying depths and concentrations. Illustrated in Fig. 1 are the relative positions and daily occurrences of the scattering layers within the upper 100 m from 0600 hours to 1800 hours.

Night observations of the layer indicated that it was closer to the surface and was comprised of a variety of plankton species. Net tows at night yielded mixed catches of nekton and euphausiids, and other zooplankton. During daylight the layer varied in depth and thickness from 10 to 60 m; the intensity of the echo varied from no response at relatively few locations to a very heavy echo response corresponding to a layer thickness of approximately 40 m. The layers were usually arrayed between depths of 20 and 40 m.

Two types of apparatus for the sampling of zooplankton were used to examine the layers. One type was the Miller sampler (4), ten of which were



Fig. 1. Cruise track of R.V. *Endeavour* showing periods of daylight observation with a high-frequency echo sounder and the relative intensity of the shallow scattering layer during two crossings of the north Pacific Ocean. The solid line joining vertical strokes indicates the daily distance traversed between 0600 and 1800 hours on the east-west crossing, Esquimalt to Tokyo, and the broken line joining circles represents the daily distance traversed between Hakodate and Esquimalt.

spaced at 25-m intervals on a hydrographic wire and towed horizontally at a speed of 2 m per second and a depth range of 0 to 125 m. The second apparatus was a Longhurst-Hardy recorder (5), which was lowered into the shallow scattering layer and towed horizontally at 1 m per second while sampling was done automatically every 2 minutes. Representative results from midday tows with these instruments are shown in Fig. 2, A and B, together with the respective high-frequency recordings made at the same time.

In all cases, the animals caught in the shallow scattering layers during day-

light were 99 percent Calanus cristatus Kr., with very small numbers of euphausiids, amphipods, and chaetognaths making up the remainder of the catch. No larger animals were caught, even when an Isaacs-Kidd mid-water trawl was lowered in place of the plankton nets. The maximum in copepod numbers (Fig. 2A) coincided with the maximum response from the 200-khz sounder during the sampling period. In terms of biomass, the maximum numbers of *C. cristatus* copepodite stage V corresponded to about 1.5 g/m³ (wet weight).

From the horizontal tow (Fig. 2B), which represents individual samples col-



Fig. 2. (A) Depth profile of *Calanus cristatus*. (B) Numbers of *C. cristatus* in a horizontal tow. The actual echogram recorded during these two sets of observations is shown above each figure.

lected over 25-m intervals, it is apparent that the layer which appeared more or less continuous on the echo sounder was subject to small-scale horizontal patchiness with C. cristatus numbers ranging from 2 to 150 per cubic meter. Two reasons for this difference in the continuous trace of the echo sounder and the patchiness recorded on the Longhurst-Hardy apparatus are (i) that the echo sounder "sees" about three orders of magnitude more surface area of water than is in the path towed through by the net; and (ii), although the Longhurst-Hardy sampler records depth, there is no guarantee that the net, which was towed from the stern of the vessel, was continuously in the densest portion of the shallow scattering layer during sampling.

Previous sampling of zooplankton in the north Pacific Ocean has been carried out by North American, Japanese, and Soviet scientists with oblique or vertical net hauls, and their results have shown that an average standing stock of zooplankton of approximately 0.1 g/m^3 (wet weight) is representative for the subarctic Pacific (6). However, in a study on the food requirements of fin whales, Klumov (7) determined that zooplankton concentrations would have to exceed 1.5 g/m^3 (wet weight) in order to support the feeding of the fin whales. At the time of Klumov's report (7), a zooplankton concentration of 1 g/m³ (wet weight) was considered exceptionally high, and, in general, it appeared to Klumov that data on the standing stock of zooplankton in the North Pacific gave concentrations that were too low. From the results reported here it appears that seasonal concentrations of zooplankton, as suggested by Klumov (7), do actually exist in dense near-surface layers.

The detection of the shallow scattering layer may serve as a basis for a reappraisal of the possibility of commercial exploitation of zooplankton. This idea (8) has thus far been considered uneconomical (9). Among the reasons offered were that zooplankton could not be detected by echo sounders, the composition of the stock was not uniform, and the zooplankton were not concentrated. None of these reasons appears correct from the data presented here.

W. E. BARRACLOUGH R. J. LEBRASSEUR, O. D. KENNEDY Pacific Oceanographic Group, Biological Station, Fisheries Research Board of Canada, Nanaimo, British Columbia

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Seawater Teleosts: Evidence for a Sodium-Potassium Exchange in the Branchial Sodium-Excreting Pump

Abstract. The net sodium extrusion rate by the gill of the seawater-adapted euryhaline flounder is identical to the potassium influx. The excretion of sodium is blocked in K^+ -free seawater solutions. The instantaneous sodium outflux readjustment pattern of flounders transferred from seawater to solutions of various sodium chloride or potassium chloride concentrations is consistent with the hypothesis of a linkage between Na^+ outflux and K^+ influx through a common exchange carrier. External Na^+ and K^+ compete for this common carrier. It is suggested that the exchange diffusion mechanism (linkage of sodium influx and outflux) and the high internal sodium turnover rate which characterizes all seawater teleosts are the results of this competitive process. The sodium-potassium dependent adenosine triphosphatase system occurring in the gill of the seawater teleosts may play a central role in this sodium-potassium exchange pump.

Homer Smith (1) showed that marine teleosts maintain their water balance by drinking, absorbing water and electrolytes in the gut, and eliminating the monovalent ions by the gills. More recently, dynamic studies of salt balance, made by using radioactive tracers (2), demonstrated that sodium and chloride turnovers involve amounts of salt more than ten times greater than can be accounted for by gut absorption and gill excretion. My observations concerning the mechanism of the branchial sodium pump have been obtained on the seawater-adapted flounder Platichthys flesus.

The most recent evaluations of the drinking rate of flounder (3) give a value of $192 \pm 35 \ \mu l \ hr^{-1}$ per 100 g of body weight (mean and S.E. for N =11) at 17°C, the temperature at which all the present flux measurements have been made. Assuming that all the Na+ swallowed is absorbed, the Na+ concentration of the seawater in our tanks being 520 mmole/liter, the gut absorption and gill excretion rate of Na+ amount to $100 \pm 18 \ \mu \text{mole hr}^{-1}$ per 100 g. All the subsequent flux values will be given in these units. The gill sodium outflux (f_{out}) as deduced from the turnover rate (4) amounts to 2600

 μ mole and direct measurement of this outflux (5) gave a closely similar value: $2623 \pm 90 \ \mu \text{mole} \ (N = 12)$. The net flux of sodium across the gill represents therefore only about 3.5 percent of the unidirectional fluxes, and the ratio $f_{\rm in}/f_{\rm out}$ is nearly 1.

By rapid transfer experiments permitting the comparison of the sodium unidirectional fluxes in media of various sodium concentrations, Motais, Garcia Romeu, and Maetz (4) demonstrated that about 85 percent of the sodium outflux as well as the total sodium influx are dependent on the external sodium concentration in a manner suggesting Michaelis-Menten saturation kinetics. An exchange-diffusion carrier with a low affinity for sodium (K_m about 400 mmole) allowing for the coupling of sodium influx and most of the sodium outflux has been suggested.

According to this hypothesis, adaptation of the fish to any change of external salinity would be accompanied by a variation in the quantity of available carrier in the gill epithelium. Indirect evidence suggests a close correlation between the exchange-diffusion process and the sodium-excreting pump (6). This pump is a potassium-sodium

exchange pump. External sodium, the concentration of which is about 50 times that of potassium in seawater, competes for this exchange carrier. The exchange-diffusion effect arises as a result.

The K+ influx, measured with the help of the tracer ⁴²K added to the outside medium in a closed circuit (7), was found to be $120 \pm 23.5 \ \mu$ mole (N = 4), a value identical to the net sodium excretion rate given above.

Rapid transfer experiments were performed on flounders alternately placed in K+-seawater and K+-free seawater for comparison of the sodium outfluxes in these media (8). A small but consistent reduction of the sodium outflux was observed in the absence of external potassium (-2.95 percent) ± 0.44 ; N = 6; P < .01). This reduction amounts to $80 \pm 12 \mu$ mole, a value similar to the net extrusion rate of sodium. If the animals are kept for 24 hours in renewed K+-free seawater, an increase of the internal sodium is observed, the plasma sodium level augmenting by 17.5 ± 2.42 mmole/liter (N = 8; P < .001). The sodium space also increases: 46.1 ± 3.63 ml/100 g compared with 34.2 ± 2.55 (N = 8; P < .05), the value previously reported for the seawater-adapted flounder (4). The rate of increase of the internal sodium is about 110 μ mole hr⁻¹ per 100 g, a value that would be expected if the sodium-excreting mechanism failed. After return to K-seawater for 48 to 72 hours, the internal sodium concentration declines by 27.8 ± 6.32 mmole/ liter, the decrease being highly significant (P < .01; N = 8). This decline can be explained by the sodium pump being "turned on" again upon addition of external potassium. The sodium turnover rate remains high in K-free seawater, for the sodium outflux of the fish kept in this medium was $2125 \pm$ 354 μ mole (N = 7) which is only a slightly smaller value than that reported for control fish (see above), the difference not being significant. Furthermore a net potassium loss of 36 ± 5.5 μ mole (N=7), is observed in Na-free seawater. It is evident that suppression of external potassium does not abolish the sodium-sodium exchange mechanism, but this is not the vital mechanism for the osmoregulation of the fish.

The existence of a K-Na exchange mechanism is further demonstrated by rapid transfer experiments of the fish permitting the comparison of the sodium outfluxes in seawater, in deion-