

PERSPECTIVES: OCEANOGRAPHY

Is the Deep Sea on a Diet?

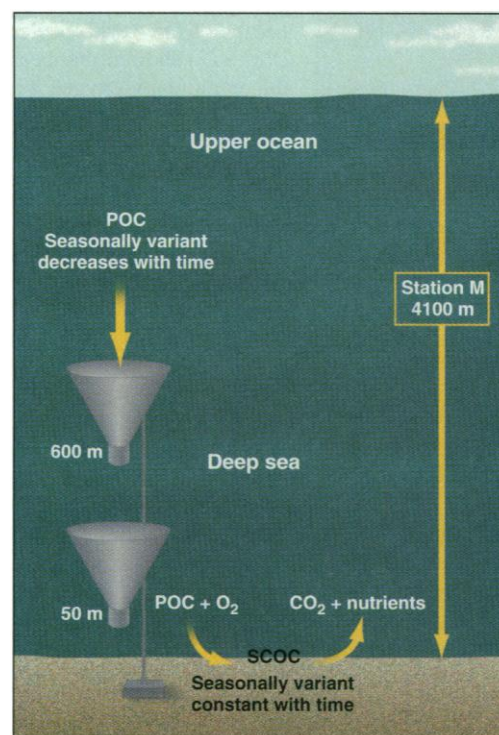
Ellen R. M. Druffel and Bruce H. Robison

Most of the animals that live on the deep-sea floor rely on a food chain that begins thousands of meters above them in the ocean's upper layers. Photosynthesis driven by sunlight supports microscopic plant life (phytoplankton) near the sea surface, which in turn supports animal and microbial communities throughout the ocean's depths. During the descent of phytoplankton and other organic matter to the sea floor, mid-depth communities filter and recycle sinking detritus that consists of phytoplankton cells, fecal pellets, and myriad forms of organic debris. The end result is that organic matter collects at the interface between the ocean and the sea floor. Here it is eaten by sediment-dwelling (benthic) organisms (including bacteria) that emit carbon dioxide and nutrients as waste products into the seawater (see the figure). Food supply and food demand are presumed to be in balance. If these processes become unbalanced, the oceanic carbon cycle may be disrupted and the stability of benthic fauna threatened. On page 1174 of this issue, Smith and Kaufmann (1) report a surprising finding about the balance between food supply and demand. Studying a station in the Northeastern Pacific (off the central California coast) between 1989 and 1996, they found that despite a pronounced decline in food supply, the food demand of the deep-sea benthic community remained relatively constant. They attribute the decrease in food supply to the well-documented increase in sea-surface temperature and decrease in plankton biomass in the Northeastern Pacific. But the paradox of constant food demand has yet to be explained.

Oxygen and organic matter, the basic essentials to sustain benthic organisms of the ocean floor, are thought to be available in plentiful supply. Oxygen is replenished in the deep sea through the sinking of oxygen-rich surface waters at higher latitudes. The flux of organic matter, however, can apparently dwindle to small values that appear inadequate to support the benthic communities. Using particle traps shaped like huge inverted cones placed 50 and 600 m off the ocean bottom (see the figure), Smith and Kaufmann monitored a 7-year decline in sinking organic matter (a mea-

sure of food supply). In contrast, oxygen consumption (a measure of food demand) in the benthic community living at 4100 m below the ocean's surface was unchanged.

Why was there no apparent effect of the decreased food supply on the community of the ocean floor? Are these deep-living creatures slowly being starved and, if so, how long can they survive? Perhaps one answer is that the detrimental effect is manifest in some process, such as reproduction, that is not measured by oxygen consumption.



Sampling a deep-sea menu. Processes involved in the transfer of particulate organic matter (POC), a measure of food supply, in the deep ocean. POC flux was measured using particle traps deployed at 50 and 600 m above the ocean floor in a section of the Northeastern Pacific. POC decreased steadily over 7 years. In contrast, sediment community oxygen consumption (SCOC), a measure of food demand by benthic organisms living in the sediment of the ocean floor (at 4100 m depth), remained constant.

However, if reproduction was deferred in response to low food availability, we would expect that cumulative mortality would have led to a decline in sediment community food demand, at least in the later years of the time series.

Another explanation could be that the impact of reduced food supply is borne by other constituents of the deep-ocean benthic

community. The mobile megafauna (which include epibenthic organisms such as sea cucumbers and brittle stars) do not figure into the measurements of sediment community food demand because they are too rare. The megafauna may be affected by the reduction of organic input, however, because their feeding strategies are better suited to concentrated food sources. But there was no evidence of a reduction in the abundance of mobile megafauna at Station M (the station at 4100 m depth where food supply and demand was measured) (2), and so this option does not appear to be a viable answer to the conundrum.

The case for alternative food sources must also be considered. Dissolved organic matter is available in high concentrations (0.5 mg/liter) in the seawater surrounding the study site (3) and may serve as a source of food for benthic microorganisms such as bacteria. There is also some evidence for the horizontal transport of organic material from the continental shelf and slope of the California coast, east of Station M, especially during early summer (4–6).

Smith and Kaufmann (1) effectively defend their measurements of particle flux and oxygen demand. For example, they state that sediment trap clogging could contribute to the discrepancy between food supply and demand. Then they correctly point out that for this to be an operative factor, the clogging rate should have increased between 1989 and 1996 to produce the observed results. However, increased clogging is a function of increased particle flux, which is counter to the productivity trends measured at the surface. Thus, clogging is not likely to be a source of error.

This reasoning assumes that the same kinds of particles are involved in both high and low levels of organic matter flux. If, however, there was a change in particle type due to reduced phytoplankton productivity and a shift from crustacean grazers such as krill to gelatinous grazers such as pelagic tunicates, which filter feed efficiently when phytoplankton are scarce, then clogging might be expected to increase because of more mucus-derived particle aggregations. There is no clear evidence of such a shift in the plankton data, only a pronounced decline in overall abundance (7, 8). Given the circumstances, we believe that Smith and Kaufmann's measurements are an accurate representation of deep-sea processes in the Northeastern Pacific.

Three different methods were used to measure the food demand of the sediment

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community, all of which required assessment of oxygen consumption in different enclosures for 1 to 6 days (1). Remarkable among these technologies is a new benthic research vehicle called ROVER (see the photograph). This autonomous undersea vehicle resembles a small, tracked forklift. It carries a suite of instruments and cameras, a navigation system, and a programmable control system with a limited decision-making capability. ROVER's endurance allows for 6-month deployments, but unlike its relative, Mars Sojourner, it can operate independently of real-time human control for its entire mission.

There is an important temporal aspect to this story with future implications for the stability of benthic communities. In the Northeastern Pacific, the past few decades have seen an increase in sea-surface temperature with a concomitant decrease in primary production and zooplankton abundance (7–9). These trends are linked to decreases in the abundance of seabirds and kelp production off the south-

ern California coast (10, 11) and are now joined by Smith and Kaufmann's measurements of decreased particulate organic flux in the deep sea during the 1990s.

What are the causes of these regional changes in water temperature, biology, and the supply of food to the deep sea? Is it a natural pattern, or is it partly related to human-induced increases in greenhouse gases in the atmosphere? We cannot yet answer this question, and Smith and Kaufmann leave it as a tantalizing tidbit for us to ruminate over. For the future, it will be important to determine whether these findings in the Northeastern Pacific are applicable to the other oceans of the world. Sayles *et al.* (12) showed that benthic community oxygen demand did not vary with the seasons in the Sargasso Sea (of the North Atlantic) and was constant from 1987 to 1993; these results are in contrast to Smith and Kaufmann's clearly seasonal data (particle flux and oxygen demand were highest in early summer and fall, and lowest in winter).

The findings of Smith and Kaufmann

will have far-reaching implications for oceanographers, biogeochemists, and climate modelers. We used to think of the deep sea as a highly stable, steady-state system, but with the advent of high-resolution, time-series data sets this picture is changing. Seasonal, annual, and decadal variability in mixing processes and exchanges with other systems appear to be the rule, not the exception. The ramifications of a declining food supply for benthic communities are a *sine qua non* for future studies of the oceanic carbon cycle.

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NOTA BENE: EVOLUTIONARY BIOLOGY

The Male's Dilemma

What is the cost of male sexual swagger? Exaggerated sexual traits, such as the peacock's tail or the bright coloration of guppies and sticklebacks, lack any obvious survival value. Indeed, these displays of vigor that help the female discriminate between suitors may drain the male's resources. But is there a still greater cost? Folstad and Karter (1) have proposed that sexual ornamentation comes at the expense of immune function, increasing the risk of infection and disease. Is there any evidence for this trade off? A recent study by Verhulst *et al.* suggests that there is (2).

In a unique set of experiments, these investigators established lines of domestic chickens (*Gallus domesticus*) bred for high or low antibody responsiveness to injected sheep red blood cells. After 15 generations of selection, specific antibodies could not be detected in the low-responder line but were greatly enhanced (compared with control chickens) in the high-responder line. Although this may seem like a bizarre trait on which to base selection, the titer of antibody to sheep erythrocytes is a good surrogate marker of humoral immune responsiveness. The authors compared the size of the sexual ornament—the fleshy serrated outgrowth that crowns the head, called the comb—in high and low responder male chickens. In support of Folstad and Karter's "immunocompetence handicap" hypothesis, they found that low-responder male chickens had larger combs than high responders. (The low-responder chick-

ens themselves were also larger, but comb-size differences persisted after controlling for body size.)

How might ornamentation and immune function be linked? The authors suggest that there might be energy-based competition, with both the heat loss through the comb and the effort required to maintain a constantly replenishing immune system draining energy resources. However, the energy costs involved in setting up and maintaining a sophisticated immune system have not yet been studied in detail.

Another explanation implicates testosterone, which is known to strongly influence comb size. In the Verhulst study, levels of this male hormone varied with anti-sheep erythrocyte antibody titer: high testosterone, low antibody; low testosterone, high antibody. However, the link between the three traits is not as straightforward as it might appear. Exogenous administration of testosterone to birds is not immunosuppressive (3) and male birds, which have more testosterone, are not more prone to infection than females (4). One intriguing possibility is that immune status modulates testosterone levels (rather than the other way around), which in turn influence sexual ornamentation. Clearly, there is a lot still to be learned about the interface between evolutionary biology, physiology, and immunity.

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