## The planktonic life of octopuses

Sir - The common octopuses of the world's oceans are bottom-living cephalopod molluscs. In more than half of the species known, hatchlings are planktonic ${ }^{1}$ and swim by jet propulsion ${ }^{2-4}$. The swimming behaviour and duration of this planktonic phase before settlement have been a subject of debate. Field plankton samples very rarely contain specimens at advanced stages, and it has not been possible to determine the age of octopods using statoliths or other hard structures


FIG. 1 Reared individuals of 0 . vulgaris at ages 1,20 , 30, 42, 50 and 60 days (upper right to lower left). The size expressed in dorsal mantle length (ML, distance from the mantle end to the midpoint between eyes) is $2.0,3.0,4.3,5.9,6.6$ and 8.5 mm , respectively. Individuals were photographed under anaesthesia, at the same scale.


FIG. 2 Cruising speed during swimming (solid line) and relative swimming speed (dashed line) are plotted against age and dorsal mantle length for $O$. vulgaris individuals aged 1, 15, 30, 42 and 60 days, giving mean and standard deviation. Values in parentheses in the top part are maximum swimming speeds (in mm $\mathrm{s}^{-1}$ ). Data were collected from digitized video records of groups of five individuals, filmed in still water in a circular tank 250 mm in diameter, with a water level of 30 mm . Settled individuals aged 60 days swim only when gently disturbed (crawling speed on the ground $\sim 12 \mathrm{~mm} \mathrm{~s}^{-1}$ ).
undergoing appositional growth. Conversely, the only successful rearing experiment leading to settlement was made with the northwest Pacific form of Octopus vulgaris and indicated that the animals remain in the plankton up to the age of 33-43 days ${ }^{5}$.

Rearing experiments ${ }^{6}$ were carried out with Mediterranean $O$. vulgaris at a mean temperature of $21.2^{\circ} \mathrm{C}$ to fit the inshore conditions in the northwest Mediterranean during summer, when most of the octopuses hatch ${ }^{7}$. At day 1 the individuals measure about 2.9 mm in total length, weigh 1.4 mg and have short arms with only three suckers each (Fig. 1). They grow exponentially, doubling their weight in roughly 8.5 days, with relative daily growth rates of $5.5-11.5 \%$. At 60 days the settled individuals measured 18.1 mm in total length and had a mean weight of 173.2 mg ( 125 times their weight at hatching). The duration of the planktonic phase before settlement varied between 47 and 54 days, $10-15 \%$ of the estimated longevity of $O$. vulgaris (12-18 months ${ }^{7}$. The high planktonic mortality is counterbalanced by high fecundity, which ranges from 1 to $5 \times 10^{5}$ eggs per female. This critical period of early life history gives this short-lived species a considerable dispersal capacity.
To quantify swimming activity, groups of individuals aged $1,15,30$, 42 and 60 days were recorded by video, using frame-by-frame tracking at $40-\mathrm{ms}$ intervals. Although the animals can turn their funnel tube in any direction for jetting, for $99 \%$ of the recorded time they jetted backwards. Relatively high swimming speeds were recorded in backwards jetting (Fig. 2). This backwards escape may allow animals in the sea to actively avoid traditional plankton nets.

It is significant that maximum jetting speed during backwards escape increased up to age 30 days, where the growth rate was highest, then declined to settlement (Fig. 2, top). This break occurred during the phase when the arms are drastically enlarged relative to the propulsive mantle, due to the highly disproportionate arm growth during the second half of planktonic life (Fig. 1). It is in this period that the animal changes shape from squid-like to the benthic octopus form. In contrast to the maximum speed plot, the relative cruising speed decreased
from 1 to 30 days of age and afterwards increased to settling, whereas cruising speed increased from hatching to settling (Fig. 2). Thus, the jet swimming of octopuses during planktonic life seems to be quite similar to the locomotion of squids, suggesting that it could enhance the dispersal capacity and colonization potential of this bottom-living species.

## Roger Villanueva

Institut de Ciències del Mar, CSIC,
Passeig Joan de Borbó s/n,
08039-Barcelona, Spain

## Christian Nozais

## Sigurd v. Boletzky

Observatoire Océanologique de Banyuls, CNRS URA 117,
F-66650 Banyuls-sur-mer, France

1. Hochberg, F. G. et al. Smithson. Contr. Zool. 513, 213-279 (1992).
2. Packard, A. Nature 221, 875-877 (1969).
3. Wells, M. J. Can. J. Zool. 68, 815-824 (1988).
4. O'Dor, R. \& Webber, D. M. J. exp. Biol. 160, 93-112 (1991).
5. Itami, K. et al. Bull. Japan Soc. scient. Fish. 29, 514-520 (1963)
6. Villanueva, R. Aquaculture 128, 143-152 (1994).
7. Mangold, K. \& Boletzky, S. v. Mar. Biol. 19, 7-12 (1973).

## Glacial cycles and orbital inclination

SIR - According to the Milankovitch theory, the 100 -kyr glacial cycle is caused by changes in insolation (solar heating) brought about by variations in the eccentricity of the Earth's orbit. There are serious difficulties with this theory: the insolation variations appear to be too small to drive the cycles, and a strong $400-$ kyr modulation predicted by the theory is not present. Moreover, the amplitude of the glacial cycle has been large at times ( 400 years ago and today) when the eccentricity modulation has been near zero; this conflict is also called the 'Stage-11 problem' ${ }^{11}$. In addition, improved measurements have uncovered an apparent causality problem: the sudden terminations of the glacial cycles appear to precede the increases in insolation ${ }^{2,3}$, although this interpretation has been disputed ${ }^{4}$. We suggest that a radical solution is necessary to solve these problems, and we propose that the $100-\mathrm{kyr}$ glacial cycle is caused, not by eccentricity, but by a previously ignored parameter: the orbital inclination, $i$, the tilt of the Earth's orbital plane.

Ancient climate is recorded in sediment through change in the oxygen isotope ratio, $\delta^{18} \mathrm{O}$, which is believed to

[^0]
[^0]:    1. Imbrie, J. et al. Paleoceanography 8, 699-735 (1993). 2. Broesker, W. S. Nature 359, 596 (1993).
    2. Landwehr, J. et al. Science 368, 594 (1994).
    3. Imbrie, J. et al. Nature 363, 531-533 (1993).
    4. Imbrie, J. J. et al. in Milankovitch and Climate Pt 1 (eds Berger, A. L. et al.) 269-305 (Reidel, Dordrecht, 1984). 6. Quinn, T. R., Tremaine, S. \& Duncan, M. Astr. J. 101, 2287-2305 (1991).
    5. Ruddiman, W., Raymo, M., Martinson, D., Clement, B. \& Blackman, J. Paleoceanography 4, 353-412 (1989).
