

end of the crossbridges, and that this region of the crossbridge remains well ordered with respect to the thick-filament periodicity during isometric contraction or slow shortening. After a quick length change, however, it is proposed that those crossbridges that are carried beyond the end of their working stroke remain rigidly attached to actin, causing a distortion of the myosin-based periodicity of the backbone end of the crossbridge and hence a drop in the 143 Å intensity.

The actin-based layer line pattern which is characteristic of rigor was not detected either during isometric contraction or after a rapid length change. The 143 Å reflection clearly does indicate, however, that changes in the crossbridges occur during contraction. There is still some controversy over how much of the 143 Å intensity arises from attached crossbridges, or indeed how many crossbridges are attached to actin filaments during normal contraction (for example, refs 5, 12).

The data of Huxley and colleagues provide further evidence for the cyclical attachment and detachment of crossbridges to the actin filaments, where the crossbridge is considered as a single particle which produces force during the cycle by tilting about an extensible hinge region¹³. It remains to be seen how this view of the crossbridge cycle, in which the outer end of the bridge moves with the actin filament and the inner end stays associated with the thick filament, can be correlated with the other large body of independent data on crossbridge structure obtained from looking at equilibrium states. It will probably be necessary to have more information about the weaker reflections in the X-ray pattern from contracting muscle, particularly those with actin-based periodicity, in order to compare such crossbridge structures with, for example, the AMPPNP state. □

Maxine Clarke is in the MRC Cell Biophysics Unit, King's College, Strand, London WC2B 5RL.

Ecology

Animals as nutrient carriers

from Peter D. Moore

It has long been recognized that the movement of grazing animals from one terrestrial ecosystem to another, feeding in one and defaecating in the other, may result in a significant movement of certain elements between them. What has now been made evident, in work on the coral reefs of the Virgin Islands¹, is that a similar process takes place in aquatic ecosystems.

If the grazing and defaecation processes were random, there would be no net transfer of elements between ecosystems, but very often the behavioural patterns of herbivores result in an imbalance. Take, for example, roosting birds. Work on roosts of the rook (*Corvus frugilegus*) in England² showed that over 4 kg sodium, 8 kg potassium and 75 kg calcium were deposited per m² in faeces during an 8-week observation period. When compared with the average input from rainfall for an equivalent period, this represents twice as much sodium, 10 times the potassium and 35 times the calcium derived from rain. In addition there were further inputs from regurgitated grit.

Clearly such enrichment will affect the vegetation of the roost site; but will the ecosystems from which the nutrients are derived suffer some degree of impoverishment? No certain answer can be given. The lack of nutrients in many heavily sheep-grazed chalk grasslands has been blamed upon the non-random pattern of grazing and defaecation³. In the New Forest's acid grasslands large herbivores such as cattle, ponies and deer use specific latrine areas⁴ which gain nutrients rapidly, but whether there is significant nutrient depletion elsewhere has yet to be demonstrated. The long-term harvesting of sheep from Penine moorland may have been responsible for the low nutrient status of the upland pastures⁵, but nutrient budget studies show the drain is negligible⁶ in comparison with other gains and losses.

Turning to aquatic ecosystems, the utilization of lakes for the aquaculture of fish can result in nutrient imbalance. Balance sheets for the culture of rainbow trout in cages in Polish lakes⁷ show the quantities of nutrients supplied to the fish in food exceed those recovered in the harvest of fish, the remainder entering the lake ecosystem in the form of waste food, dead (or escaped) fish and their faecal products. The recovery of elements such as phosphorus and nitrogen is only about 20 per cent of the input with the result that these elements are supplied to the lake at rates of about 0.6–1.0 g P and 2.7–4.4 g N m⁻² yr⁻¹. This is clearly an important source of eutrophication in the lake.

Free-living fish can act as carriers of nutrients from one part of an aquatic eco-

system to another, as has recently been demonstrated by Meyer, Schultz and Helfman¹ in the coral reefs of the Virgin Islands. They have investigated the possibility that fish schools sheltering in coral reefs may enrich their environment with faecal and excretory products. Water samples were taken in coral heads where fish were resting and those in which they were not present and they found that levels of ammonium ions reached 0.9 μM in the former and only 0.2 μM in the latter. In addition, particulate matter rich in phosphorus and nitrogen was significantly more abundant when fish schools were present, presumably being derived from faecal material.

Both ammonium ions and the particulate matter form a readily available nitrogen source for the corals, but diffusion out of the vicinity, if rapid, could reduce these levels. Measurements of the diffusion rate, made by injecting dye into a coral head, showed that diffusion was, in fact, quite slow: it took over six minutes for the dye to be diluted to one-tenth its original concentration.

The total input of nitrogen by the fish is equivalent to 30–75 per cent of that derived from nitrogen fixation by blue-green algae. The question still remains, however, whether the additional nutrients permit higher growth rates among the corals. This was tested by marking selected coral heads and collecting the additional calcium carbonate deposited after a year had elapsed. Fish were then removed from certain heads and all corals were measured again after a further eight months. In heads where fish schools had been removed, coral growth was only 55 per cent that expected, indicating that the presence of the fish is advantageous for maintained growth.

Mobile animals in aquatic ecosystems clearly play a part in the spatial redistribution of nutrients and, in doing so, influence the growth and performance of other organisms. In this respect they resemble their terrestrial equivalents. One added complication in aquatic habitats is the three dimensional nature of the mosaic produced by fish defaecation. □

Peter D. Moore is Senior Lecturer in the Department of Plant Sciences, King's College, 68 Half Moon Lane, London SE24 9JF.

- Huxley, A.F. & Niedergerke, R. *Nature* 173, 971 (1954); Huxley, H.E. & Hanson, J. *Nature* 173, 973 (1954).
- Sleep, J.A. & Smith, S.J. *Curr. Topics Bioengng* 11, 239 (1981).
- Ford, I.E., Huxley, A.F. & Simmons, R.M. *J. Physiol., Lond.* 311, 219 (1981).
- Huxley, H.E. *et al. J. Molec. Biol.* 169, 469 (1983).
- Goody, R.S. & Holmes, K.C. *Biochim. biophys. Acta* 726, 13 (1983).
- Barrington-Leigh, J. *et al. Cold Spring Harb. Symp. quant. Biol.* 37, 443 (1972); Goody, R.S. *et al. Biophys. J.* 15, 687 (1975).
- Marston, S.B., Rodger, C.D. & Tregear, R.T. *J. molec. Biol.* 104, 263 (1976).
- Kuhn, H.J. *J. Muscle Res. Cell Motil.* 2, 1 (1982).
- Tregear, R.T., Milch, J.R., Goody, R.S., Holmes, K.C. & Rodger, C.D. in *Crossbridge Mechanisms in Muscle Contraction* (eds Sugi, H. & Pollack, G.) 407 (University of Tokyo Press, 1979).
- Tregear, R.T. & Marston, S.B. *An. Rev. Physiol.* 41, 723 (1979).
- Reedy, M.C., Reedy, M.K. & Goody, R.S. *J. Muscle Res. Cell Motil.* 4, 55 (1983).
- Huxley, H.E. *et al. Proc. natn. Acad. Sci. U.S.A.* 78, 2297 (1981).
- Huxley, H.E. *Science* 164 1355 (1969).

- Meyer, J.L., Schultz, E.T. & Helfman, G.S. *Science* 330, 1047 (1983).
- Weir, J.S. *Nature* 221, 487 (1969).
- Green, B.H. *Biol. Conserv.* 4, 378 (1972).
- Edwards, P.J. & Hollis, H.J. *appl. Ecol.* 19, 953 (1982).
- Pearsall, W.H. *Mountains and Moorlands* (Collins, London, 1950).
- Crisp, D.T. *J. appl. Ecol.* 3, 327 (1966).
- Penczak, T., Galicka, W., Molinski, M., Kusto, E. & Zaleski, M. *J. appl. Ecol.* 19, 371 (1982).