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COMMENT

Calanoid copepods: linking lower-higher trophic levels by linking lower-higher Reynolds numbers

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The copepods are said to be the most abundant multicellular animals on earth, with an estimated species number of 11500+ (Humes 1994). The most typical form of planktonic copepods in the oceans is the calanoids, which makes up >70% of all net-collected zooplankton (e.g. Lalli & Parsons 1993).

Why are the calanoids so abundant and successful? A clue to the answer to this question is the size (and the moving speed) of the calanoids, as shown in the life strategies of many animals (e.g. McMahon 1973, Schmidt-Nielsen 1984). The size of calanoids ranges roughly from 0.5 to 5 mm, and lies on the border that separates the aquatic habitats into 2 parallel worlds: the inertial and viscous worlds (Purcell 1977; Fig. 1). In the inertial world, the combat between prey and predators is primarily a matter of speed in escape and attack (Kerfoot 1978). By contrast, viscosity predominates over speed in the viscous world, where a moving object drags water and a water current drags objects.

The inertial and viscous worlds are described by the Reynolds number (Re), which is the dimensionless ratio of inertial and viscous forces as follows:

$$\mathrm{Re} = \frac{\text{inertial drag}}{\text{viscous drag}}$$

A simplified formula of the Reynolds number (Zaret 1980) can be written as:

$$\mathrm{Re} = \frac{\rho}{\eta} \cdot L \cdot U$$

where L (m) is the body length of an object moving at speed U (m s^{-1}). For seawater at 20°C, ρ (fluid density; kg m^{-3}) and η (fluid viscosity; kg m^{-1} s^{-1}) are 1.025×10^3 and 1.1×10^{-3}, respectively. Then the term ρ/η is roughly estimated to be 10^6.

The body length (prosome length) and the 'cruising' speed of the calanoids are on the order of 10^{-3} m and 10^{-3} m s^{-1}, respectively (e.g. Enright 1977, Gerritsen 1980). Thus the Reynolds number is estimated to be approximately 1, which lies on the border of the inertial and viscous worlds. However, Re of 1 is not the sole 'magic' number. Another border number is Re = 2000, which separates the conditions for laminar and turbulent flows (Vogel 1981); thus conditions in which Re = 1 to 2000 may be considered as 'transient'. This comment primarily discusses the uniqueness and significance of living on the border at Re = 1, as Re = 2000 is beyond the range of calanoid biology.

Feeding by calanoids takes place in the viscous world of Re < 1, because the prey are smaller (lower L) and slower (lower U). In the viscous world, 'attack' is not necessary to catch prey. Instead, the calanoids vibrate small appendages to generate a feeding current. The current is a laminar flow of viscous water that, like a conveyor belt, drags the prey to the calanoid mouth (Alcaraz et al. 1980, Koehl & Strickler

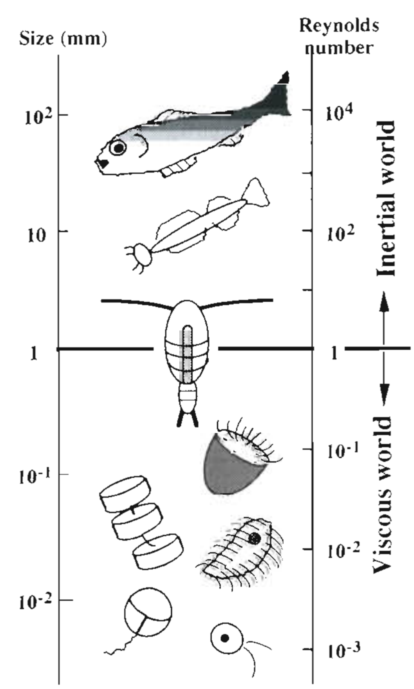

Fig. 1. Sizes and trophic levels of representative marine pelagic organisms, and the associated Reynolds numbers (Re). The viscous world (Re < 1) and the inertial world (Re > 1) are linked by the calanoid copepods

1981) and allows the calanoids to survive in nutritionally dilute pelagic environments (Strickler 1982).

The calanoids' principal prey is phytoplankton, which are non- or slow swimmers. Phytoflagellates swim as slowly as 10^{-4} m s^{-1} (e.g. Morris 1980). Assuming the size of the prey phytoplankton to be 10^{-4} to 10^{-5} m, the associated Reynolds number is estimated as 10^{-2} to 10^{-3} or lower. Planktonic ciliates are occasional prey (e.g. Stoecker & Sanders 1985, Turner et al. 1993). They swim at approximately 10^{-3} m s^{-1}. *Paramecium* swims typically at 1.2×10^{-3} m s^{-1}, ranging from 0.8 to 3×10^{-3} m s^{-1}, with a body size of 10^{-4} to 10^{-5} m (Wichterman 1986). The associated Reynolds number is thus estimated as 10^{-1} to 10^{-2}, though certain ciliates such as *Mesodinium rubrum* may achieve higher Reynolds numbers during escape.

The velocity of the feeding current generated by a calanoid is 7 to 56×10^{-3} m s^{-1}, varying from one appendage to another. The associated Reynolds number is approximately 10^{-1} to 10^{-2} (Koehl & Strickler 1981), which overlaps those associated with phytoplankton and ciliates. Feeding currents of lower velocity (i.e. lower Re) may be sufficient to maintain growth as well; however, the efficiency of prey catch per unit time will decrease accordingly. The observed current velocity may be practically the maximum for feeding.

The calanoids are eaten, in turn, in the inertial world of Re > 1, as the predators are larger (higher L) and faster (higher U). For example, the Reynolds number associated with a 5 cm fish swimming at 1 cm s^{-1} is 500. Fish of such size and arrow worms attack calanoids. The calanoids escape from predation by making a 'jump', which is an acceleration lasting less than 0.1 s. An acceleration of 12 m s^{-2} (e.g. Strickler 1977) makes the top speed as fast as 0.5 m s^{-1}, resulting in an associated Reynolds number of as high as 500 to 1000 (e.g. Kerfoot et al. 1980, Zaret 1980).

Other major groups of mesozooplankton, such as cyclopoid copepods and cladocerans, do not jump as fast as the calanoids do (Kerfoot et al. 1980). As a result, cyclopoids and cladocerans are vulnerable to predation, while calanoids are resistant (Drenner & McComas 1980). A calanoid jump costs 400 times more energy than cruising (Strickler 1977). The jump, however, is worth the high energy cost for the escape from predation.

As a hypothetical conclusion (Fig. 1), the flourishing dominance of the calanoids is based on the advantage of living on the border of different worlds. On the one hand, they catch prey in the viscous world, by generating a feeding current at a practically maximum velocity. The calanoids are the major 'top predator' in the viscous world. On the other hand, they are attacked in the inertial world, but can effectively escape by jumping, which is high Reynolds number behavior. This may be a clue to explaining why the calanoids are so abundant and successful. A similar example is that the most abundant and successful of the cephalopods are the ommastrephid squid larvae, which are the smallest and make both conveyor belts and jumps using their jet (O'Dor et al. 1985).

A consequence of ecological significance is that the calanoids link the viscous and inertial worlds. They link sizes, Reynolds numbers and trophic levels within the marine food chain. If fish and arrow worms had to feed directly on small-sized phytoplankton and ciliates, it would be difficult. The difficulty comes from the size difference of 10^2 (Eating a piece of bread is much easier than eating wheat grains one by one!) More difficulty comes from the separation between the inertial and viscous worlds. (Net-scooping would be harder in viscous molasses than in water.)

The calanoid copepods link lower-higher trophic levels through linking low-high Reynolds numbers. They link photosynthetic and fisheries production, and thus facilitate energy transfer in the marine food chains.

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