SWIMMING DYNAMICS OF ZOOPLANKTON

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Summary

The swimming dynamics of zooplankton is the result of severe constraints that the aquatic medium and the ecological structure and functioning of pelagic systems have imposed in their evolution. The low productivity of the oceans, which constitute, in general, a poor, food-diluted environment for zooplankton, and at the same time being very heterogeneous in space and time, together with the lack of physical support for the structuring of communities, have forced zooplankton to swim to increase encounter rates with conspecifics and prey, in order to be able to accomplish sexual reproduction and feeding respectively.

Thus, foraging and reproduction are essential functions intimately related to swimming in zooplankton. The absence of cover in the pelagic realm has also obliged zooplankton to exhibit special morphological and behavioral adaptations to reduce the risk of predation. Most zooplankton show rapid swimming escape responses, triggered by the presence of potential predators. Finally, the high viscosity of water, together with the

range of sizes and speeds of zooplankton have also imposed relevant hydrodynamic constraints to their swimming and feeding, which fluctuate between the viscous and the inertial realms.

The different groups of zooplankton have found different solutions, sometimes convergent, involving morphological, physiological and behavioral traits, to a similar set of constraints. Most zooplankton can be divided into three groups regarding their foraging tactics: raptorial, entangling and suspension feeders. These foraging tactics are intimately linked to their swimming ability and mechanisms. Thus, two major swimming strategies appear in zooplankton, ambush and cruising behaviors. These two strategies are not rigid patterns, yet they are actually the extremes of a continuum, with some zooplankters exhibiting intermediate patterns. Swimming strategies do not vary only between groups or species, but they can also change through development or as a function of prey type within the same predator species.

1. Introduction

Plankton is commonly defined as those organisms unable to maintain their distribution against the movement of water masses. In spite of this definition, many planktonic organisms, and specifically those of zooplankton, have the capability to move in both the horizontal and the vertical plane, even performing extensive vertical displacements of hundreds of meters, from deep waters to the surface. Swimming in zooplankton is associated with functions essential for the success of the species. Pelagic primary production is concentrated in a superficial, lighter, (relatively) thin layer in the upper parts of the oceans. Most zooplankton activity is restricted, or dependent, in one way or another, on this photic layer. As most zooplankton are negatively buoyant, an obvious primary function of swimming will be to avoid sinking, i.e. leaving this epipelagic, upper layer. But swimming is also intimately associated with other crucial functions of zooplankton, like their feeding and reproduction, and avoidance of predation.

Swimming can be necessary for getting food. Although the epipelagic areas of the oceans are a vast environment, and may constitute a limitless food supply for the individual zooplankter, overall they are very diluted and, at the same time, not homogeneously distributed, with food dispersed in patches of different sizes. For their survival, zooplankton require the ability to cope with this patchiness and to be able to concentrate food in such diluted “soup”. Thus, zooplankton have developed different ways of moving through water, different foraging tactics to find their food, and different feeding behaviors to collect food particles.

Most zooplankton, at some point in their life, have sexual reproduction, requiring mating or the swarming of conspecifics for the successful continuation of the species. In such a vast environment as the pelagic seas, finding mates may be difficult and evolution has selected strategies and mechanisms to optimize mating. The low abundance of zooplankton in the water column make necessary the existence of special physiological adaptations and behaviors in order to meet each other and recognize partners.

Finally, swimming must be contemplated from the perspective of predation avoidance. The absence of physical cover in the pelagic areas of the oceans, in comparison with terrestrial ecosystems, has forced a convergent evolution in different taxa into strategies to avoid being detected by potential predators. These strategies include the size and transparency of organisms, rhythms of activity and vertical migration. Swimming makes an animal more conspicuous, both visually and hydrodynamically, to potential predators, but swimming can provide escape ability to the zooplankter facing an approaching predator. The strong selective force of predation has determined, in part, the broad repertoire of different swimming behaviors that can be found in zooplankton.

The term zooplankton encompasses an assorted group of organisms, with a broad range of sizes (from the smallest microzooplankton, 20-200 µm, to the larger megazooplankton, 20-200 cm), very diverse phylogenetically, and playing very different trophic roles in marine food webs. It is obviously difficult to describe such a variety in a single article. Instead of attempting such an enterprise, here I will focus first on a brief description of the locomotion of some characteristic groups (how do they swim?); later, some more general aspects about swimming behavior will be discussed (why do they swim?).

Throughout this contribution basic concepts and general patterns will be given, without intending to be exhaustive, nor to provide numerous exceptions to the generalities. When possible, argument is backed up with detailed and concise examples, in order to give the reader some figures and orders of magnitude of the processes involved with the swimming dynamics of zooplankton. Examples are restricted to a few groups of zooplankton (e.g. copepods, fish larvae), essentially because these groups have been studied in more detail and provide easier and clearer examples for the reader. These detailed descriptions must be viewed, thus, as illustrative.

2. How do they swim?—The study of zooplankton locomotion

Two major swimming modes will be considered here. In most zooplankton, swimming is intimately related to feeding. Many zooplankters must move to find individual potential prey or to concentrate particulate matter. Zooplankters spend much time foraging, and therefore, feeding-related swimming modes contribute to a high percentage of their life time allocation. Avoiding predation is another important issue in a zooplankter life, and most of them perform quick escape responses under imminent attack by a predator. The mechanics behind these two different swimming modes are different. But before embarking on such matter, some basics concepts on small-scale physics of water are required.

2.1 Physics of water

When studying plankton swimming, a main consideration to take into account is the fact that plankton is small and water is viscous. Although human beings experience water as wet, and water flows easily between our fingers when we attempt to grab it, zooplankton experience a completely different medium. A body moving in water experiences two main types of forces (disregarding gravity and buoyancy to simplify): inertial forces, related to momentum, and viscous forces, related to the tendency of the fluid to resist deformation.

The dominance of either type of force depends on two properties of the body, its velocity and its size, and two properties of the medium, density and viscosity. This empirical relationship can be described by a dimensionless variable, the Reynolds number (*Re*),

$$Re = \frac{\ell \times u}{\nu / \rho} \qquad (1)$$

where ℓ is a characteristic length of the body, usually taken as the length along the flow direction, u is the speed of the body, ν is the fluid viscosity, and ρ is the fluid density.

At high Reynolds number (>1000), inertial forces dominate, and locomotion is based on accelerating fluid backwards in order to gain forward momentum. Big organisms live in this inertial world.

However, small organisms, because of their small sizes and low velocities, live at lower Reynolds number, spending their life in their entirety or part of it in a viscous regime, where water could be felt like “thick and sticky” (similar to the feeling that swimming in honey or syrup would produce for us). Viscous forces gain greater importance and moving a volume of water is very difficult and costly. One might describe small organisms as “walking” in the water, pushing against the medium to move in the opposite direction.

Most zooplankton live at the transition between the dominance of viscous and inertial forces, coping with the advantages and drawbacks of both regimes. Thus, for instance, a swimming copepod will experience the viscous regime while slowly swimming for suspension feeding, and will change to the inertial regime while swimming fast to escape a potential predator.

Ontogenetic changes in zooplankton, with accompanying increases in size and speed, also may involve relevant changes in Reynolds number. Experiencing the viscous environment has many implications, not only for swimming but also for feeding and the capability of chemical remote detection. Many of the hairy appendages found in zooplankton, ornamentation of finely spaced setae, actually act more like a blade than like a sieve.

2.2 Description of the locomotion

2.2.1 Appendicularians

Appendicularians produce a mucous feeding house wherein they stay and filter-feed, until the house is clogged and discarded, whereupon the appendicularian secretes a new house. Appendicularians use rhythmic bursts of tail beating (inside the house) to suck water into the house through the bilateral inlet funnels and create a feeding current flowing through the several internal very fine sieves of the house, where particles are withdrawn (Figure 1).

The jet of water coming out of the house drives the animal (and house) slowly forward. When disturbed or discarding the house, they rapidly emerge from the house and exhibit frenetic short bursts of the tail to maintain position in the water column until a new house is built.

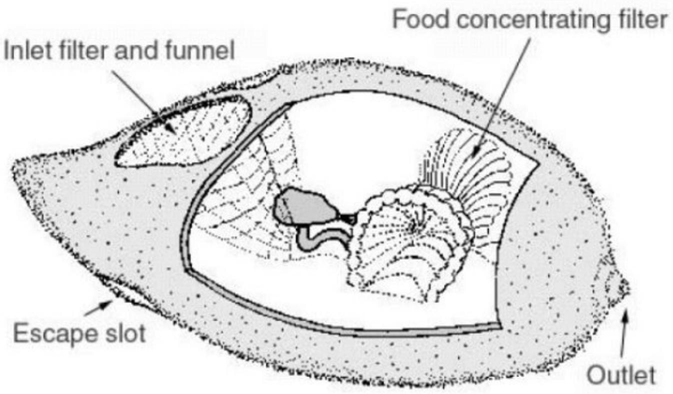

Figure 1: Conceptual drawing of an oikopleurid appendicularian with its house. The body of the animal, formed by a trunk and a tail, and the house wall, are showed in gray. *Based on drawings in Alldredge, A.L. (1977), House morphology and mechanisms of feeding in the Oikopleuridae (Tunicata, Appendicularia), J. Zool. 181: 175-188, and Fenaux, R., Les appendiculaires des mers d'Europe et du bassin méditerranéen, Maison et Cie., Paris, 1967.*

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Biographical Sketch

Enric Saiz, Born in 1962. Ph.D. in Biology in 1991, under the supervision of Prof. M. Alcaraz.

Research interests deal with, in a broad sense, the role of microzooplankton and mesozooplankton in planktonic food webs, and the study of the factors that control their activity, with special emphasis on behavior, small-scale processes and individual-based approaches. Main topics include: secondary production, predation effects on zooplankton, the effects of small-scale turbulence on zooplankton, trophic interactions between classical food webs and microbial food webs, functional diversity, food quality and quantity, patchiness, etc