An overview of the role of morphology and feeding behavior of copepod in sustaining its population

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Introduction

The world's oceans, lakes and its tributaries are inhabited by a numerous species of plankton. A tropical ocean, for one, is considered to have limited ecological niches. But why are there so many species thriving ? How is it possible for these organisms to coexist in an unstructured environment and share or compete for the same materials ? There are several theories that tried to answer these questions but will not be discussed here. One theory postulates that fluid turbulence causes variability in the environment preventing the formation of stable niches that could be dominated by a single species. Another study suggests "coexistence principle" which is based on the general ecological observation that taxonomically similar species often demonstrate similar distribution patterns. These theories and arguments could go on and on but one question remains and calls to be answered. "How do the many species of copepods exist, co-exist, and persist in an environment that is nutritionally dilute ? "

Feeding strategies of copepods was a subject of debate for many decades. Do copepods feed non-selectively by ingesting every particle it captures, or selectively, by evaluating the suitability of individual particles as food ? Cowles (1979) argued that feeding strategies varied with food environment – copepod feed selectively when food is abundant and non-selectively when food is scarce. Other authors use algal size classes to characterize copepod grazing (Paffenhöfer, 1984; Berggreen *et al.*, 1988; Zurek and Bucka, 1994). Studies on feeding behavior of copepods have become more significant when feeding structures were investigated through scanning electron microscopy (SEM) (Weatherby *et al.*, 1994; Ohtsuka *et al.*, 1997), and feeding behavior, feeding currents and cell capture of copepods were studied in detail using advanced optical techniques and high-speed cinematography (Price *et al.*, 1983; Paffenhöfer 1994, 1998; Jiang *et al.*, 1999; Mazzocchi and Paffenhöfer, 1999).

Copepod and its surrounding environment

Sometime in 1999, I attended a series of lectures by a very famous professor (Dr. Rudi Strickler) working on the swimming and feeding behavior of copepods and *Daphnia*. His lectures were focused on the interactions of copepods with the surrounding water by showing video clippings of his observations. Copepods live in a viscous environment. The viscousity of their surroundings may affect their swimming and feeding behavior. Copepods exhibit a particular behavior depending on their purpose of movement, either to feed, escape predator, or search a mate, among others. Copepods change their body position to keep itself afloat and prevent itself from sinking continuously. The swimming legs are the ones performing the task when copepods swim, by adjusting the angle of bending to accommodate or to push the water out. Perhaps one will ask, "How much energy does a copepod spend in its lifetime ? " Only at the initial action does more energy is required but it gradually decreases or dissipates into heat as the movements progress.

How efficient is the feeding mechanism of copepods in the presence of turbulence ? How do these animals cope with turbulence and viscousity of their environment ? Copepod is denser than the surrounding water. Unlike fish, copepods do not have swim bladders rather, they have a storage of oil in the form of wax esters present in their bodies which may aid them to keep afloat. To keep up with their biological demands as well as of their surroundings, copepods need to be neutrally buoyant. In turbulent water, copepods are capable of orienting their body position not only to catch up with the food particles passing nearby, but also to maximize utilization of food within a space.

Hydrodynamic interactions

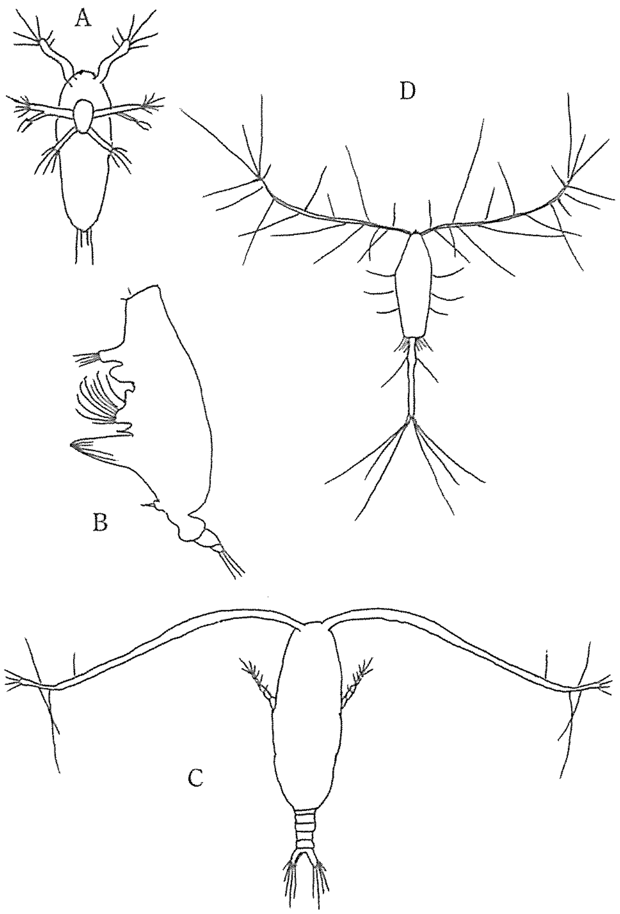
Physiological, behavioral, and morphological studies have revealed that copepods are able to perceive food particles, prey, predators and conspecifics through mechanoreception and/or chemoreception (Mauchline, 1998; Jiang *et al.*, 2002b; Jiang and Osborn, 2004). Since the water environment surrounds the copepods as well as their items of interest, the flow field created due to the presence of both parties will affect the generation and transmission of water-borne signals, whether the signals are mechanoreceptional or chemoreceptional.

1. morphology and activity

For copepods, the utilization of appendages and their sensors is essential in feeding and escaping predators. Nauplius of a copepod generally has three pairs of appendages to use for motion while copepodid stages possess six pairs of cephalic appendages (antennule, antenna, mandible, maxillule, maxilla, and maxilliped) and swimming legs. The latter is rarely used for feeding, except for some species of *Acartia* which operate both maxilla and swimming legs synchronously. In the nauplius, motion of the appendages not only propels but can also create feeding currents. The nearly continuous motion of most calanoid nauplii makes them vulnerable to predation because all three pairs of appendages are usually moving. On the other hand, nauplii of cyclopoid which only move occasionally are not so vulnerable to predation (Paffenhöfer, 1998). For most copepodid and adult calanoid copepods, motion of the cephalic appendages (such as antenna, mandibular palps, maxilla and maxilleped) results in feeding currents. Copepodid and adult cyclopoids (*e.g. Oithona plumifera*) is often characterized by numerous setae (mechanoreceptors), some approaching the length of prosome, in the entire antennule (see figure below). Numerous mechanosensors arranged in three dimensions on the antennule could perceive the precise location of moving prey of more than one body length away. This characteristic of an antennule has more advantage in detecting remote hydrodynamic signals unlike the antennule of a calanoid (See figure in the next page for the illustration of cephalic appendages of a nauplius and adult calanoid and cyclopoid copepods).

2. chemoreception

Chemoreception is one of the strategies that copepods employ to detect individual food particles remotely. Successful chemoreception must consist three components. First, chemical signals surrounding a particle such as an alga must be at the perceptible level (above the threshold level of detection) of the copepod. A living alga is surrounded by a 'phycosphere' within which the concentrations of certain chemical compounds, such as amino acids and sugars and/or other excreted matter, such as pheromones, exceed background levels (Bell and Mitchell, 1972; Maier and Müller, 1986). If the concentrations of chemicals within the phycosphere surrounding an algal particle are large enough to initiate a behavioral



Morphology of naupliar and adult stages of calanoid and cyclopoid copepods: (A) typical morphology of a calanoid nauplius with three pairs of appendages utilized for motion; (B) lateral view of an adult calanoid showing some cephalic appendages and four pairs of swimming legs joined together; (C) general aspect of an adult calanoid with an extended antennule; (D) *Oithona plumifera* showing the numerous setae on the antennule which function as mechanoreceptors. (Modified from Paffenhöfer, 1998)

response in a grazing copepod, the phycosphere may act as an 'active space' containing the chemicals perceptible by a copepod.

Second, a copepod must be equipped with chemoreceptors in its body. Morphological studies have already shown that chemoreceptors are found on the setae and sensilla or aesthetascs of the antennules, other cephalic appendages and mouthparts of copepods (Weatherby *et al*., 1994; Paffenhöfer and Loyd, 2000).

Third, physical processes are needed to transport chemical signals within the active space to the places where copepod's chemoreceptors are located, and after that facilitate the physical encounter between individual molecules of the chemical signal and the apical pores on the setae.

3. mechanoreception

Mechanoreceptors have been implicated in mediating responsiveness to presence of predators, prey or food particles and potential mates. The antennules of copepods are equipped with mechanoreceptors that are sensitive to small movements and high frequencies. Perception is usually followed by alternation of slow motion and use of sensing appendage (by extending the antennule) or by no motion at all. Through mechanoreception, copepods are able to distinguish a predator or a potential mate and could make necessary decision whether to escape, move closer or stay in its position. Making a wrong response would be energy costly, thus copepods have a way of increasing their perceptive ability in order to respond correctly to a stimulus. Mechanoreception is commonly employed by copepods that are not actively moving and do not create feeding currents.

Feeding currents

Strickler (1985) addressed two hypotheses on feeding currents of copepods. First, feeding current enables the animal, using their mechano- or chemoreception, or both, to scan a large amount of water and hence benefit the animal's feeding success. Second, the feeding current also creates a hydrodynamic disturbance that may alert the animal's prey or may arouse its potential predator. Calanoid copepods commonly use mouth appendages in creating feeding currents, which is scanned for food items. How do they do that ? To capture food, the feeding appendages are extended laterally, opening up a cavity between them, thus drawing particles toward the copepod. This is referred to as the "fling and clap" mechanism which governs the well-organized "feeding machine" within a copepod (Strickler's lecture, 1999). The feeding current propels the animal forward and draws food towards the mouth appendages. The strength of the feeding current directly relates to the feeding rate. The feeding current also plays an important role in providing copepod with information about its environment and it transfers signals from the copepod to organisms in its vicinity (van Duren *et al.*, 2002). The feeding current is a viscous shear flow that is influenced by the shape of the copepod's body and the distribution of forces (Jiang, *et al.*, 1999). The latter represents the activities of the copepod that generates the feeding current. However, not all copepods produce feeding currents in order to feed (e.g. *Clausocalanus furcatus*, *Oithona plumifera*). Swimming behavior of many other copepod species as observed in the laboratory are summarized by Jiang *et al.*, (2002a).

Swimming behavior and feeding strategies

Copepods exhibit a certain behavior depending on the type of signal they perceive. Calanoids show two types of swimming behavior. The first is the behavior of swimming fast or jumping, which is performed faster than their usual activities. This type of swimming behavior is usually an escape reaction to take them away from the stimulus causing it. The second is the slow-swimming behavior involving the cephalic appendages. For most calanoids, the behavior of swimming slowly is connected with feeding (creation of feeding currents) (Jiang *et al.*, 2002a).

How does a certain species of copepod in an oligotrophic environment coexist and persist with other groups ? Copepods tend to employ certain feeding behavior that would make them survive and be more advantageous than the other co-inhabiting species. For example, *Clausocalanus furcatus* exhibit continuous swimming and occasional high speed somersaulting. It does not create feeding current. Food is perceived by direct encounter due to its highly mobile behavior which in turn makes it possible for this species to cross previous tracks and thus searching a larger area and water volume. The motion and feeding behaviour of *C. furcatus* show that the foraging tactic of this species is to explore small volumes of water rapidly (Mazzocchi and Paffenhöfer, 1999).

Paracalanus aculeatus, on the other hand, is a slow continuous swimmer that generates a feeding current to entrain food particles and perceives food at a distance by chemoreception (Paffenhöfer, 1984). It has a preference for small sized prey (8 – 12 μm).

Oithona plumifera is an ambush predator that uses its long antennule armored with many setae to sense remotely hydrodynamic signals of motile particles (Paffenhöfer and Mazzocchi, 2002). It has preference for large, fast sinking or motile prey. *O. plumifera* sink rather slowly while mainly in a horizontal position, which enhances the probability of encountering suitable food particles.

The fast and continuous ambit of C. *furcatus* leads to a preference for medium-sized prey (8 – 40 μm) while the feeding current and slow continuous motion of *P. aculeatus* results in a preference for the smallest cells (Wiggert *et al.*, 2005). At low prey concentrations, *O. plumifera* exhibits difficulty in maintaining optimum carbon uptake. This suggests that this species would most likely employ energy conserving behavior in food-limited environment. *P. aculeatus* would most likely persist even when oligotrophy becomes acute.

Those copepods which create a weak or intermittent feeding current can supplement nutrition with carnivory, which requires perception by the antennule such as that of *Centropages velificatus* adults (Paffenhöfer, 1998).

Other species switch between herbivory and carnivory such as *Calanus pacificus* (Landry, 1981). This behavior may be significant during the decline of phytoplankton blooms when phytoplankton densities are low and small animals are relatively abundant due to high birth rates during the bloom.

Conclusion

Copepods employ certain feeding strategies in order to survive in an environment where scarcity of food may sometimes occur and other inhabitants pose as possible competitors. Feeding currents make it possible for copepods to cover a larger volume of water to search for food and to increase encounter probability rates. Non-moving and extended sensors (setae) are best suited for mechanical/hydrodynamic perceptions in those copepods which hardly move and lack a feeding current. Utilization of their mechano-chemical perception helps copepods avoid useless energy spending by knowing precisely the location of food or mate than by swimming aimlessly around.

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