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Planktonic Feeding and Evolutionary Significance of the Lobate Body Plan Within the Ctenophora

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Ctenophores are gelatinous marine invertebrates that prey upon zooplankton. The two main ctenophoran orders that affect planktonic communities are the Cydippida and the Lobata. The Cydippida possess two elongate tentacles. In the Lobata, two large lobes surround comparatively reduced tentacles, and water is drawn through the inter-lobe space by four flap-like ciliated auricles. Both groups are successful predators and are widespread in the world's oceans (1). In coastal regions, members of the genera *Bolinopsis* (Lobata) and *Pleurobrachia* (Cydippida) may co-occur and often reach high densities simultaneously.

The co-occurrence of *Bolinopsis* and *Pleurobrachia* suggests the possibility of dietary overlap and feeding competition between these genera, because both are commonly believed to consume copepods as their primary prey (2, 3). To examine this hypothesis, we recorded the gut contents of individuals from two species, *Bolinopsis infundibulum* (Lobata) and *Pleurobrachia pileus* (Cydippida); the animals were collected simultaneously on six dates between March and May 1998 from the Woods Hole Oceanographic Institution pier in Woods Hole, Massachusetts. *Bolinopsis infundibulum* preserved poorly (total disintegration within 24 h in 0.5% formalin solution), did not tolerate vessel containment well, and often regurgitated prey when held in a container for more than 30 min. As a result, ctenophore gut contents were observed microscopically and recorded at the sample site within 30 min of hand collection. Gut contents were easily observed in intact animals due to transparency of the body wall. On each sample date, 20–30 individual ctenophores of each species were sampled.

Although the day-to-day selection by the ctenophore predators was subject to the availability of specific prey types, a pattern of prey partitioning between the ctenophore orders was evident (Fig. 1). The cydippid *Pleurobrachia pileus* consistently consumed larger, more strongly swimming prey such as gammarid amphipods, crab zoea, calanoid copepods, and barnacle cyprid larvae. In contrast, the lobate *Bolinopsis infundibulum* selected smaller, more weakly swimming prey such as copepod nauplii, gastropod veligers, rotifers, and tintinnids.

Differences in patterns of prey selection reflected the mechanical bases of prey capture by each species. *P. pileus* sits motionless while its tentacles are extended and set in a wide net that ensnares highly mobile prey. *B. infundibulum* uses the ciliary lining of its auricles to create a feeding current that entrains low-speed and weakly swimming prey that are entrapped on a network of fine tentillae located near the oral region (4). The two mechanisms favor capture of a different fraction of the

available plankton and allow co-occurring ctenophores with different body plans to partition available prey.

Although the prey capture mechanism of cydippid ctenophores such as *P. pileus* have long been appreciated (3, 5, 6), the mechanics of lobates such as *B. infundibulum* have been less studied and are poorly understood. However, evidence on the mechanics of prey capture by lobates has been growing (Costello, unpubl. data) and now indicates that both of the lobate genera examined to date share the ability to utilize the smaller, less mobile fraction of plankton classified as microzooplankton. This ability is a consequence of the lobate body plan: funnel-like oral lobes; ciliated auricles; and in the genera *Bolinopsis*

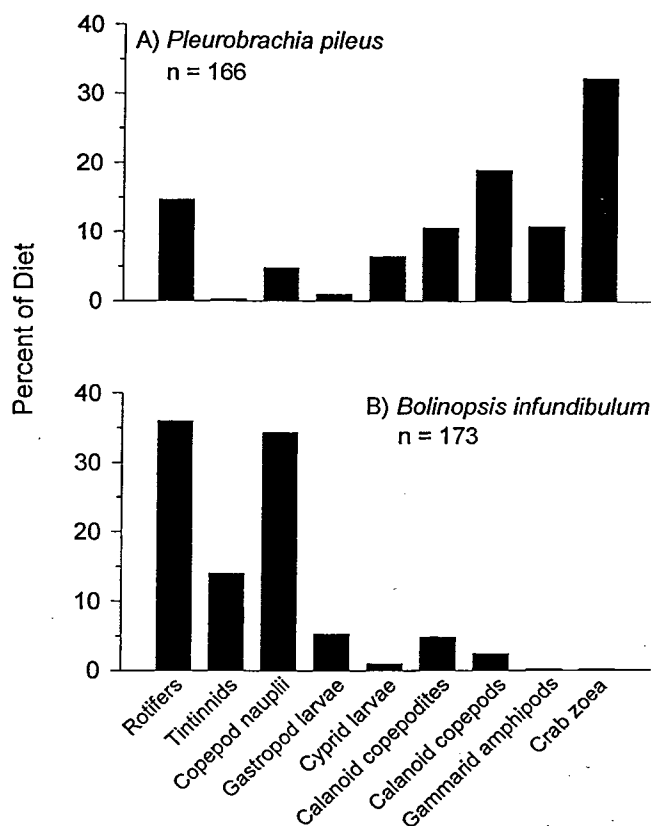


Figure 1. The percentages of various prey types in the gut contents of two ctenophores: (A) *Pleurobrachia pileus* (Cydippida) and (B) *Bolinopsis infundibulum* (Lobata). These values are based on the total prey numbers consumed over the 6-day sampling period. The ctenophores were collected adjacent to Great Harbor in Woods Hole, Massachusetts. The proportional contribution of each prey item was significantly different between the two ctenophores (χ^2 , $P < 0.01$ for all comparisons). Prey types are arranged sequentially by approximate length and varied from rotifers (0.15–0.35 mm) to crab zoea (1.5–3.0 mm).

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and *Mnemiopsis*, modification of elongate tentacles into a finely spaced sieve of tentillae.

We propose that the capacity to exploit the microzooplankton was a major selective force favoring evolution of lobate ctenophores from cydippid ancestors. Cydippid groups such as the Pleurobrachiidae are physically constrained by tentacle thread spacing from successfully preying on microzooplankton taxa. By making this prey group available, the lobate characteristics enabled a substantial radiation of forms within the Ctenophora, particularly in open-ocean communities, where the planktonic size spectrum is shifted downward relative to coastal and upwelling areas. Note that lobates, such as *Mnemiopsis*, never completely abandoned the capacity to prey on calanoid copepods and other macrozooplankton. Rather, they developed mechanosensory abilities and behavioral responses (Costello, unpubl. data) that allow predation both on macrozooplankton, using primarily the oral lobes, as well as on microzooplankton, using the tentacles (Costello and Waggett, unpubl. data). Thus, we suggest that the evolution of the lobate body plan allowed an expansion of prey niche dimensions rather than a complete reallocation of predatory effort. However, design options in-

volve tradeoffs in performance, and the *in-situ* gut contents data (Fig. 1) demonstrate that, while enabling feeding on microzooplankton, the lobate design may perform less favorably than that of the cydippid at capturing the larger, more mobile end of the zooplankton prey spectrum.

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