Feeding efficiency of the larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata)

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Larval stages of the ctenophore *Mnemiopsis leidyi* rely on metazoan prey, such as *Acartia tonsa* nauplii and copepodites, to support high growth rates. However, *M. leidyi* larvae <0.5 mm (total length) had low retention efficiencies (REs) (proportion of encountered prey actually ingested), 5.78 ± 2.6% (mean ± SE), of nauplii and were often damaged by their encounters. REs of nauplii rapidly increased, 38.94 ± 3.73%, as larvae grew to a size of ∼2.0 mm. For larvae >2.0 mm, nauplii REs plateaued at a mean of 91.03 ± 1.70%. All larvae <0.80 mm were incapable of successfully consuming copepodites. REs of copepodites increased, 23.04 ± 4.68%, as ctenophore larvae developed to ∼2.5 mm. Ctenophore larvae >2.5 mm reached a maximum copepodite RE of 63.75 ± 3.01%.

INTRODUCTION

The ctenophore, *Mnemiopsis leidyi* A. Agassiz 1865, is an abundant and a voracious planktonic predator known to regulate zooplankton communities and influence ecosystem dynamics in estuaries along the Atlantic coast of the Americas (Burrell and Van Engel, 1976; Kremer, 1979, 1994; Deason and Smayda, 1982a,b) and in the Black Sea and Azov Sea where it is an invasive species (Studenikina et al., 1991; Shiganova, 1998; Shiganova and Bulgakova, 2000; Shiganova et al., 2001). In these regions, juvenile ctenophores may seasonally dominate overall abundances of ctenophore populations (Kremer and Nixon, 1976; Deason, 1982; Shiganova, 1998; Mutlu, 1999; Finenko and Romanova, 2000; Shiganova et al., 2001). However, little is known about *M. leidyi* early life history and larval feeding ecology. Feeding ecology is a fundamental issue, because larval ctenophores occur at sufficient abundances capable of impacting prey populations (Sullivan and Gifford, 2004). Furthermore, because ctenophores are holoplanktonic, survival of larvae directly influences the population dynamics of adult *M. leidyi* blooms.

Larval stages of the ctenophore *M. leidyi* are omnivorous and require microplankton prey (20–200 µm) for growth and development (Stanlaw et al., 1981; Stoecker et al., 1987; Sullivan and Gifford, 2004; Rapoza et al., 2005). Three distinct life-history stages have been identified in the development of *M. leidyi* larvae (Sullivan and Gifford, 2004). Upon hatching, tentaculate stage *M. leidyi* larvae exhibit a classic cydippid morphology. Larvae then enter a transition stage at ∼5.0 mm possessing both tentacles and small oral lobes. Finally, tentacles are resorbed by the tentacle bulbs at the lobate stage.

Larval ctenophores forage with their tentacles and branching tentillae extended similarly to a seine. Prey become ensnared in the tentillae by the release of...
colloblast filaments (Main, 1928; Reeve and Walter, 1978). Upon prey capture, the larval ctenophore rapidly retracts the tentacle with captured prey, manipulating it toward the mouth for prey transfer, whereas the second tentacle remains extended in the fishing position. Tentaculate stage and early transition stage larval M. leidyi have only one obvious capture surface, the tentacles. Upon hatching, tentacles stretch only one to two times the total larval length and possess few branching tentillae; however, they extend rapidly in length with only a small increase in total larval size. Tentacles may stretch several body lengths and possess several to hundreds of branching tentillae off the main tentacles adding to capture surface area and aiding in retention (Reeve and Walter, 1978).

Mesozooplankton (0.2–20 mm) cause injury and mortality of small tentaculate stage cydippids (<1.0 mm length) (Greve, 1977; Stanlaw et al., 1981). Although ctenophore larvae can survive and grow when fed in situ assemblages of non-crustacean microzooplankton (Sullivan and Gifford, 2004; Sullivan and Gifford, unpublished data), Stoecker et al. (Stoecker et al., 1987) reported that a combined diet of ciliates and copepod nauplii supported the highest growth and survival rates. Furthermore, analysis of in situ gut contents of M. leidyi tentaculate stage and transition stage larvae by Rapoza et al. (Rapoza et al., 2005) revealed a diet dominated by small cells, but the diet was supplemented with metazoan prey including copepods and nauplii. We hypothesize that although unicellular microplankton are required in the first days following hatching, mature larvae require the higher nutritional content of nauplii, or other planktonic metazoans, to fuel the rapid growth of small tentaculate stage larvae. The objective of this study was to determine feeding efficiencies on both nauplii and copepodes by tentaculate stage and early transition stage ctenophore larvae.

**METHODS**

Nauplii, juvenile and adult (NI-CVI) *Acartia tonsa* Dana 1849 were obtained by culture. During July 2005, *A. tonsa* prey were collected by vertically towing a 0.5-m diameter, 64-µm mesh plankton net from a dock in Greenwich Cove, East Greenwich, RI, USA (42°35′N, 71°27′W). Adult *A. tonsa* were isolated from the plankton using a wide-bore pipette and transferred to an 8-L plastic container filled with 0.7-µm filtered seawater. Cultures of *A. tonsa* were maintained at 15°C and exposed to a 12:12 light : dark cycle. Every other day, they were fed an equal mixture by biovolume of phytoplankton cultures containing *Isochysis galbana*, *Thalassiosira weissflogii* and *Oxyrrhis marina*.

Adult *M. leidyi* were obtained from the field by hand dipping with a plastic ladle from surface waters at Greenwich Cove during the summer of 2005. Adult ctenophores were isolated in plastic containers of filtered seawater at in situ temperature (18–22°C) and salinity (27 p.p.t.). Fertilized eggs released during overnight hours were removed the following morning. These eggs required a further 24 h to hatch. Ctenophores were fed natural microplankton prey collected as whole water from the surface waters at Greenwich Cove. Feeding and water changes were conducted twice weekly.

Healthy larvae with intact ctene rows and tentacles were transferred by pipette to experimental chambers. Individual larvae were photographed using a B/W video camera (Spot Insight model 3.1.0) attached to a dissecting microscope (Nikon SMZ-U Zoom 1:10). Frame-grabbed images were processed by Spot Advanced v. 3.5.0 software for Mac OS 9.2 and measured for total larval length.

Copepod cultures were poured through a 200-µm mesh sieve to remove adults (CVI) and then through a 54-µm mesh sieve to retain nauplii and early stage copepodes. Stage NI–NII nauplii and stage CI copepodites were sorted under a dissecting microscope using a pipette. By choosing these stages, we avoided radical changes in the development because of possible molting during the experiments (i.e., nauplii did not transition into copepodites or copepodites into adults). Groups of either ~200 nauplii or ~100 copepodites were isolated for each experiment and added to a crystallization dish (Table I). An individual ctenophore larva was added to the crystallization dish under a dissecting microscope. Observations began after 5–10 min when the larva displayed routine feeding behavior with tentacles fully extended. Ctenophore–prey interactions were observed for 20 min during which time the following components of predation were recorded: tentacle contact, contact location, tentacle capture, ingestion and escape (Holling, 1959, 1966; Waggett and Costello, 1999). Tentacle retention efficiencies (REs) were calculated by (Waggett and Costello, 1999):

\[
RE = (\text{total tentacle captures/total tentacle contacts}) \times 100
\]

Analysis was performed using SigmaPlot v. 7.0. REs were fitted to a modified version of a Michaelis–Menten equation:

\[
RE = y_0 + \left[\frac{(RE_{\text{max}} \times L)}{(L + K_m)}\right]
\]
where $y_0$ is the theoretical RE of a 0.00 mm ctenophore larvae, $R_{E_{\text{max}}}$ the predicted maximum RE of an infinitely sized ctenophore larvae, $L$ the length of the ctenophore larvae and $K_m$ the half saturation constant for the ctenophore larvae.

**RESULTS**

*Mnemiopsis leidyi* larvae from all size categories (0.35–5.20 mm length) were capable of consuming early stage *A. tonsa* (NI–NII). However, prey capture was a destructive process among ctenophore larvae <0.65 mm, often resulting in the loss of a tentacle (21% of observations). A generalized model of tentacle RE for nauplii can be described using a modified version of a Michaelis–Menton curve where $RE = \frac{212.05}{L} \frac{L}{0.48 + L}$ (Fig. 1; $r^2 = 0.85$, $n = 76$, $P < 0.0001$). As ctenophore larvae develop to ~2.0 mm, a linear relationship is evident between larval size and their RE of nauplii. Larval ctenophores >2.0 mm had a mean tentacle RE of 91.03 ± 1.70% (mean ± SE; $n = 19$) when feeding on nauplii.

Interactions with *A. tonsa* copepodites often severely damaged ctenophore larvae <0.80 mm total length. Copepodites caused tentacle detachment and injured ctene rows and body structure. The smallest larva to successfully consume a copepodite was 0.80 mm total length. A generalized model of tentacle RE for copepodites can be described using a similar modification of the Michaelis–Menton equation where $RE = \frac{293.85}{L} \frac{L}{0.34 + L}$ (Fig. 2; $r^2 = 0.85$, $n = 25$, $P < 0.0001$). A linear relationship is evident between larval size and their RE of copepodites, as ctenophore larvae develop to a size of ~2.5 mm. Larval ctenophores >2.5 mm achieved a maximum tentacle RE of 63.75 ± 3.01% (mean ± SE; $n = 11$) when feeding on copepodites.

![Fig. 1. Tentacle retention efficiencies (REs) of *Mnemiopsis leidyi* larvae feeding on *Acartia tonsa* nauplii. Each filled circle (•) represents the RE of a single larva. Curve represents the non-linear regression of the relationship between larval length and tentacle REs on nauplii.](https://academic.oup.com/plankt/article-abstract/28/7/719/1482797/b5142797)
DISCUSSION

The results of this study support previous work documenting the requirement of microplankton prey in the diet of young ctenophore larvae (Stanlaw et al., 1981; Stoecker et al., 1987). Larval ctenophores <0.50 mm length need to consume protistan prey, because metazoan prey, even early-stage copepod nauplii, damage the larvae. This damage may be fatal if metazoan prey are sufficiently abundant. Additionally, small ctenophore larvae have low REs when feeding on _A. tonsa_ nauplii and copepodites. However, those larvae that survive quickly develop the ability to capture and retain metazoan prey, achieving nearly 100% retention of nauplii and 65% retention of copepodites at a size of ~2.0 mm.

Small larval ctenophores have low REs when feeding on metazoan prey. The physical and metabolic cost of subduing and manipulating relatively large metazoan prey into the gut may outweigh any nutritional value to the small larval ctenophore. Upon hatching, larvae (300–400 μm diameter) are barely larger than _A. tonsa_ nauplii (NIII–NV: 100–300 μm) (Kiørboe et al., 1999). Larval tentacles remain relatively short (~1–2 body lengths) over the first few days and are ill equipped to capture motile prey of equivalent sizes. As larvae grow, their tentacles develop to extend several body lengths with hundreds of branching tentillae. This tentacle development increases their capture surface area and facilitates the retention of larger metazoan prey that become ensnared in a net of branching tentillae.

Metazoan prey supply a larger ration of carbon per capita than the smaller protistan microplankton and facilitates rapid growth of larval ctenophores. Stoecker et al. (Stoecker et al., 1987) reported higher growth rates of larval _M. leidyi_ when nauplii were included in their diet than those larvae fed ciliates alone. Stanlaw et al. (Stanlaw et al., 1981) found that larvae raised on a diet consisting solely of nauplii grew slower than those fed a diet supplemented with copepodites. This reinforces the idea that with an increase in size, larvae require larger prey to sustain high growth rates and to balance the energetic cost of foraging and capturing active prey. The high REs of ctenophore larvae >2.0 mm allow them to capture and retain more metazoan prey to support these high growth rates. Additionally, by feeding on metazoan prey, larval ctenophores >2.0 mm would be decreasing direct feeding competition with their newly hatched conspecifics.

Extant ctenophores are believed to have evolved from an ancestral cydippid ctenophore (Podar et al., 2001). Costello and Coverdale (Costello and Coverdale, 1998) proposed that the evolution of the lobate body plan allowed ctenophores to exploit the microzooplankton in addition to larger mesozooplankton; however, cydippid larval stages of lobate ctenophores are already capable of consuming both microplankton and mesoplankton prey (this study; Stanlaw et al., 1981; Sullivan and Gifford, 2004). This leads to the question of why ctenophores have evolved a lobate body plan when the cydippid form has persisted and succeeded. The cydippid ctenophore, _Pleurobrachia pileus_, may co-occur in coastal zones with lobate ctenophores such as _M. leidyi_ and _Bolinopsis infundibulum_ (Costello and Coverdale, 1998; Mutlu and Bingel, 1999). _Pleurobrachia pileus_ targets larger, more mobile zooplankters (e.g., crab zoea, gammarid amphipods and larger calanoid species) than its lobate counterparts (Lebour, 1922; Nagabhushanam, 1959; Bishop, 1968; Costello and Coverdale, 1998). This difference in prey selection may facilitate the coexistence of the ctenophore species by relieving direct competition and allowing the species to occupy separate ecological niches. Additionally, by eliminating the tentacle-to-mouth transfer of prey, lobate ctenophores should decrease the prey-handling time required of cydippids, a strategy that may allow lobate ctenophores to more easily exploit ephemeral plankton patches. The developmental ontogeny of _M. leidyi_ provides the same benefit. By partitioning of the available plankton (i.e., protists, nauplii and copepodites), _M. leidyi_ cydippid larvae and lobate adults are not in direct competition with each other. Such niche separation may further allow proliferation of the species during periods of low mesozooplankton abundance.
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REFERENCES


