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ECOLOGICAL AND DEVELOPMENTAL DYNAMICS OF A HOST-PARASITE SYSTEM INVOLVING A SEA ANEMONE AND TWO CTENOPHORES

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ABSTRACT: The lined sea anemone *Edwardsiella lineata* has evolved a derived parasitic life history that includes a novel body plan adapted for life inside its ctenophore hosts. Reputedly its sole host is the sea walnut, *Mnemiopsis leidy*i, a voracious planktivore and a seasonally abundant member of many pelagic ecosystems. However, we have observed substantially higher *E. lineata* prevalence in a second ctenophore species, the ctenophore predator *Beroë ovata*. The interplay among these 3 species has important conservation consequences as *M. leidyi* introductions are thought to be responsible for the severe depletion of numerous commercial fisheries in the Mediterranean basin, and both *E. lineata* and *B. ovata* have been proposed as biological controls for invasive *M. leidyi*. Over a 3-yr period (2004–2006), we collected 8,253 ctenophores from Woods Hole, Massachusetts, including *M. leidyi*, *B. ovata*, and a third ctenophore, *Pleurobrachia pileus*, and we recorded *E. lineata* infection frequencies, parasite load, and parasite location. We also conducted laboratory experiments to determine the likely mechanisms for parasite introduction and the effect of each host on parasite development. We observed peak *E. lineata* infection frequencies of 0% in *P. pileus*, 59% in *M. leidyi*, and 100% in *B. ovata*, suggesting that *B. ovata* could be an important natural host for *E. lineata*. However, in laboratory experiments, *E. lineata* larvae proved far more successful at infecting *M. leidyi* than *B. ovata*, and *E. lineata* parasites excised from *M. leidyi* exhibited greater developmental competence than parasites excised from *B. ovata*. Although we show that *E. lineata* is efficiently transferred from *M. leidyi* to *B. ovata* when the latter preys upon the former, we conclude that *E. lineata* larvae are not well adapted for parasitizing the latter species and that the *E. lineata* parasite is not well adapted for feeding in *B. ovata*; these developmental and ecological factors underlie the host specificity of this recently evolved parasite.

Parasitism has profoundly impacted biodiversity and organismal evolution (Hudson et al., 2006; Lafferty et al., 2006; Smith et al., 2006). Parasites are implicated in the evolution of sex (VanValen, 1973), they have driven the evolution of immune systems (Klein and Nikolaidis, 2005), and they continue to exert pervasive influence on contemporary mating systems (Becheikh et al., 1998; Thomas et al., 1999; Moore and Wilson, 2002). Furthermore, in the midst of the ongoing biodiversity crisis, parasites have assumed a prominent position in the field of conservation biology. In concert with other causal factors, parasites can contribute to precipitous declines in locally threatened populations (Lafferty and Kuris, 1999; Daszak et al., 2001; Smith et al., 2006), and the impact of parasites may be magnified by global climate change (Poulin and Mouritsen, 2006). At the same time, parasites are being evaluated as potential biological controls against destructive invasive species (Thresher et al., 2000; Goddard et al., 2005; Toepfer et al., 2005). Indeed, whether an introduced species exhibits reduced vulnerability to attacks from natural enemies, including parasites, may determine whether it becomes a destructive invader (Mitchell and Power, 2003; Torchin et al., 2003).

Critical determinants of a parasite's ecological impact include its abundance, mode of transmission, host specificity, and trophic level (Poulin, 2007). The mode of transmission and host specificity are reflected in a parasite's life history and how its ontogeny responds to relevant environmental cues from potential hosts (Thomas et al., 2002). Therefore, the development of a parasite is inextricably linked to its ecological impact as the flexibility of the developmental program will partially determine the flexibility of the parasite's host usage.

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The lined sea anemone, *Edwardsiella lineata*, previously known as *Fagesia lineata* or *Edwardsia leidyi* (Verrill, 1873; Daly, 2002), is a recently evolved parasite that affords several important advantages for studying the linkage between development and ecology. *Edwardsiella lineata* is known to parasitize the ctenophore *Mnemiopsis leidyi* (Crowell, 1965, 1976; Bumann and Puls, 1996) and has also been reported to occur within the ctenophore *Beroë ovata* (Bumann and Puls, 1996). It is potentially the only parasitic species in the Edwardsiidae. However, there is a single published report of a larva later identified as *Edwardsia carnea* being recovered from the ctenophore *Bolinopsis* sp. (Stephenson, 1935). *Edwardsiella lineata* has retained the ancestral adult body plan (the benthic polyp) and major elements of the ancestral developmental program (development of the polyp from a planula larva), but it has also evolved the ability to assume a novel body plan that is clearly adapted for parasitizing its ctenophore host (Fig. 1) (Crowell, 1965, 1976; Crowell and Oates, 1980).

Three factors make *E. lineata* a particularly informative and tractable model parasite for studying the interplay of development and ecology. First, the parasitic form of *E. lineata* can be easily collected in infected ctenophores. Second, we have discovered that when *E. lineata* is excised from its host, it undergoes a rapid developmental transformation, where it morphs from the nonciliated, vermiform body plan it exhibits as a parasite into the ciliated, fusiform body plan typical of a planula larva (Reitzel et al., 2006). Third, the subsequent development of this planula is plastic: (1) if provided with a second host, the planula can reinfect another ctenophore and revert to the parasite body plan; (2) if it is denied a second host, the planula can develop into a free-living polyp (Reitzel et al., 2006).

Edwardsiella lineata may have a profound effect on coastal ecosystems (Bumann and Puls, 1996), particularly if it acts to depress the population of *M. leidyi*, a voracious planktivore that is widely invasive and is implicated in the crash of commercially important fisheries (Finenko et al., 2006). However, we

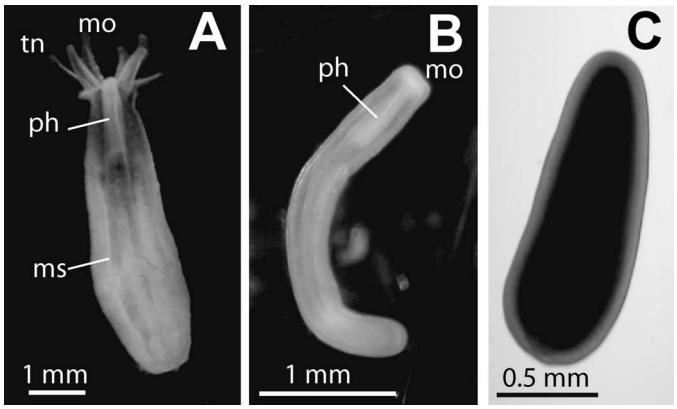

FIGURE 1. Three stages in the life history of the lined sea anemone, *Edwardsiella lineata*. (**A**) The adult polyp. (**B**) The parasite. (**C**) The planula larva. (Abbreviations: mo = mouth, ms = mesentery, ph = pharynx, tn = tentacle.)

currently have little empirical data on *E. lineata*'s abundance, mode of transmission, host specificity, or trophic level. At least 3 potential ctenophore hosts exist in its native range, and these ctenophores occupy 2 different trophic levels. Likewise, there are no data describing how *E. lineata*'s ontogeny is impacted by its host or hosts.

Over a 3-yr period, we collected 8,253 ctenophores representing 3 different species from Great Harbor in Woods Hole, Massachusetts (7,472 *M. leidyi*, 181 *B. ovata*, and 600 *Pleurobrachia pileus*). We monitored the *E. lineata* infestation level in each ctenophore species as a function of date and ctenophore size, and we scored the location of parasites within hosts. We also performed laboratory experiments to identify the route(s) of infection, and we tracked the development of individual parasites excised from *B. ovata* and *M. leidyi* host ctenophores. Our results strongly suggest that *M. leidyi* is the preferred host and possibly the only suitable natural host for *E. lineata*. Although *B. ovata* can become more heavily infested with *E. lineata* than *M. leidyi* in the wild, *B. ovata* appears to be an inadvertent host that acquires *E. lineata* parasites principally, if not solely, from feeding on infected *M. leidyi*. Furthermore, *E. lineata*'s competence to complete development from the parasite to the adult polyp is affected by both its size and the terminal host it occupies. Development proceeds more quickly and successfully when *M. leidyi* is the terminal host. In light of these new data, we reevaluate the suitability of *E. lineata* as a biological control for invasive populations of *M. leidyi*, as has recently been suggested (Bumann and Puls, 1996).

MATERIALS AND METHODS

Ctenophore collection

Mnemiopsis leidyi, *Pleurobrachia pileus*, and *Beroë ovata* were collected from Great Harbor in Woods Hole, Massachusetts. Collections were made from a rock jetty that extends south-southeast for a distance of approximately 40 m from the shore. We made multiple sweeps with plankton nets along the jetty and gently lifted the ctenophores from the water. Although our collections may accurately represent the species composition of the ctenophore fauna in the vicinity of the jetty on each collection day, we did not attempt to standardize our collection effort across collection days, so we cannot directly compare ctenophore abundance at different times. Ctenophores were placed in containers of seawater for transport to the laboratory of the Boston University Marine Program located in Boston, Massachusetts. Upon returning to the laboratory, ctenophores were sized and scored for parasitic infections.

Ctenophore size measurements

To determine the relationship between host size and parasite load, we measured the body length of *M. leidyi* and *B. ovata*. We did not measure *P. pileus* because we did not recover any individuals infested with *E. lineata*. The body length of *M. leidyi* was measured as the straight-line distance from the apical organ to the tip of 1 of the oral lobes. Where the 2 lobes varied in size, the larger lobe was used for the measurement. The body length of *B. ovata* was measured as the straight-line distance from the apical organ to the tip of mouth. Previous research has shown that ctenophore body length is significantly correlated with ctenophore mass for both of these species (Anninsky et al., 2005).

Analysis of parasite location within ctenophores

Freshly collected, parasite-infected *M. leidyi* and *B. ovata* were placed in finger bowls containing 50 ml of artificial seawater. The location of each parasite's mouth within the ctenophore host was scored with the aid of a dissecting microscope. The 2 species of ctenophores differ in morphology, especially in the digestive tract. *Mnemiopsis leidyi* has a long pharynx that extends over most of the body length. In contrast, *B. ovata* has a large mouth cavity and a very short pharynx (Fig. 2). We scored whether parasites were located in primary digestive structures (pharynx, stomach) or secondary digestive structures (radial canals).

Parasite infection experiments

Individual, parasite-free *M. leidyi* (n = 50) and *B. ovata* (n = 16) were placed in finger bowls containing 100 ml artificial seawater, along with individual *E. lineata* parasites that had been previously excised from other hosts. Following excision, the parasites were kept in isolation from potential ctenophore hosts for approximately 1 day; this causes the vermiform parasites to develop into mobile ciliated planulae larvae (Reitzel et al., 2006). In addition, we placed parasite-free *B. ovata* in bowls of 300 ml seawater with infected *M. leidyi* (n = 7). *Beroë ovata* ate the infected *M. leidyi* within 5 min of introduction. For all trials, observations were made at 24 hr.

Parasite development experiments

Edwardsiella lineata parasites were removed from freshly caught *M. leidyi* (n = 46 parasites) and *B. ovata* (n = 93 parasites). Parasite length (straight-line distance along the oral-aboral axis) was measured with the aid of a dissecting microscope. After being measured, specimens were individually cultured at room temperature (18 C) in artificial seawater (salinity = 33 parts per thousand). The parasites were monitored daily for 1 of 2 outcomes, i.e., settlement as a benthic polyp or death. Tentacle number and polyp length (straight-line distance from the tip of the mouth to the base of the foot) were recorded at the time of settlement.

Data analysis

Parasite load and localization: We analyzed the relationship between host size and parasite load using linear regression. We also sorted parasites according to their location (primary digestive structures [pharynx, stomach] versus secondary digestive structures [radial canals]) and according to the parasite load of their hosts (lightly infected hosts [=1–4 parasites per host] versus heavily infected hosts [≥5 parasites per host]). To determine whether parasite number influenced parasite location within each species, we performed chi-squared tests using Pearson statistics (JMP). All relationships that were found to be significant ($P \leq 0.05$) using Pearson tests were also significant according to likelihood ratio tests.

Developmental outcomes: To determine the effect of host species on developmental outcome of the parasite, we regressed the percentage of parasites that were able to develop into polyps against the time since the parasite was extracted from the host. Data from *M. leidyi* and *B. ovata* were separately fit to Boltzman functions using OriginPro (v. 7.5885; Origin Lab Corporation; Northampton, Massachusetts). To determine the relationship between parasite length and developmental outcome, we regressed the percentage of parasites that were able to develop into polyps against parasite body length. Separate regressions were per-

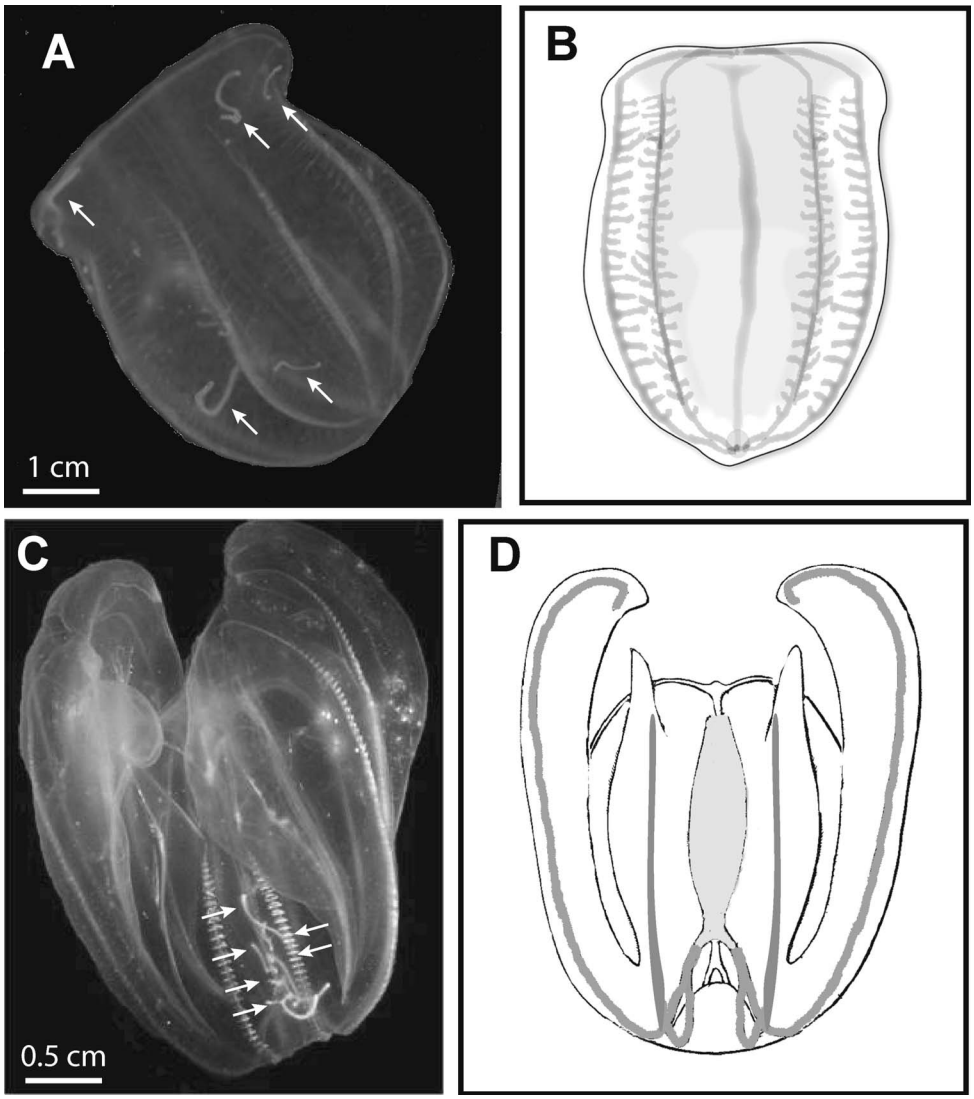

FIGURE 2. Two ctenophore species monitored in this study. (**A**) *Beroë ovata* infected with 5 *Edwardsiella lineata* parasites (arrows) scattered about the body, primarily along the radial canal system. (**B**) Diagram of *B. ovata* showing large oral cavity. (**C**) *Mnemiopsis leidyi* infected with several *E. lineata* parasites (arrows) clustered around the stomach. (**D**) Diagram of *M. leidyi* showing relationship of pharynx, stomach, and radial canals.

formed on data from *M. leidyi* and *B. ovata*. In addition, we log-transformed the body length data and determined 95% confidence intervals around each regression (JMP, v. 5.0.1). We tested for differences in the slopes of the regressions fit to the *M. leidyi* and *B. ovata* data using a *t*-test (Kleinbaum et al., 1988). Additionally, the syslin procedure (SAS; SAS Corp., Cary, North Carolina) was used to fit regression lines to each relationship via the ''iterative seemingly unrelated regressions'' (ITSUR) method. We tested the null hypothesis that the 2 models are equal using an *F*-test (SAS Institute, 1999; Nichols et al., 2004). We also regressed the time to settlement and the size of the polyp at the time of settlement against the size of the excised parasite.

RESULTS

Ctenophore abundance and parasite infection frequency

Along the coastline of New England, *M. leidyi* becomes seasonally abundant during the late summer, and its numbers decline markedly by the early winter (Fig. 3). Our ctenophore collections were conducted at Woods Hole, Massachusetts, on 45 days over a 3-yr period, including 10 days in 2004 (beginning on 24 August and ending on 5 December), 24 days in 2005 (beginning on 29 May and ending on 6 November), and 11 days in 2006 (beginning on 7 July and ending on 20 October). Overall we collected 7,472 *M. leidyi* (1,469 in 2004, 4,138 in 2005, 1,865 in 2006).

Our most thorough sampling of *M. leidyi* occurred in 2005, when we attempted to collect ctenophores on a roughly weekly basis from late May through late November (Fig. 3). We first succeeded in collecting *M. leidyi* in late June, after 4 failed attempts in late May and early June. Our collection data suggest that the *M. leidyi* population may have peaked in late September or early October, after which it underwent a dramatic decrease. We were able to collect in excess of 500 *M. leidyi* on 26 September, while we collected only 12 on 16 October. Interestingly,

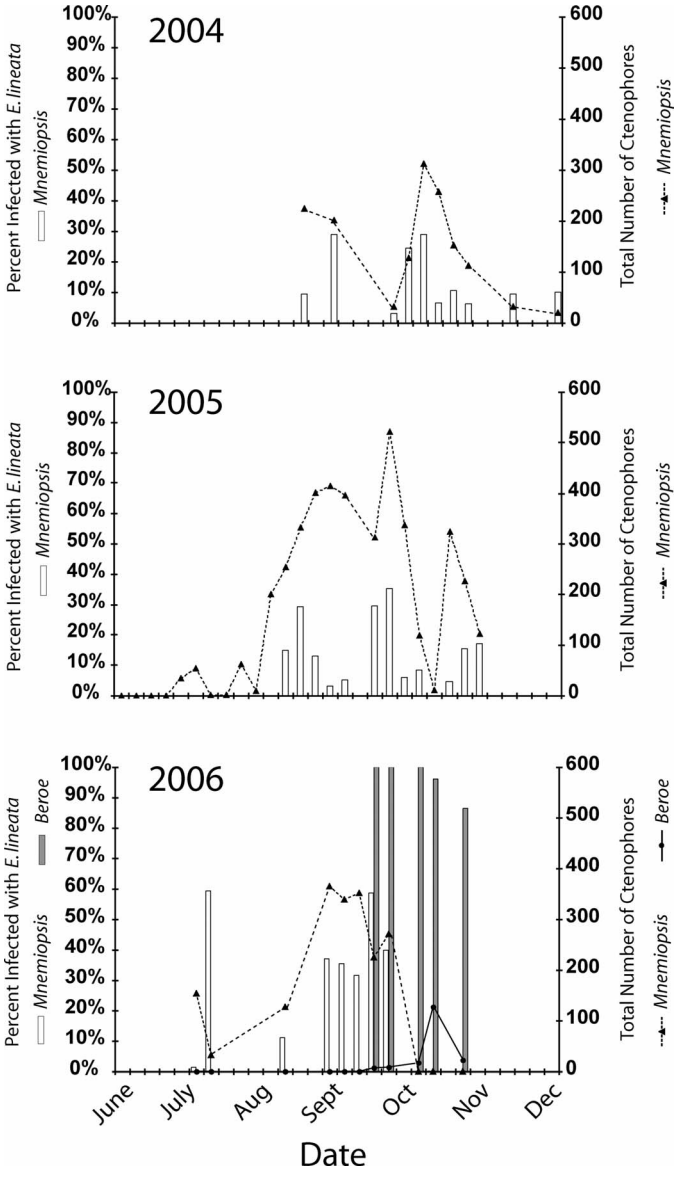

FIGURE 3. Field observations of the number of ctenophores collected in 2004–2006 and their frequency of infection with *Edwardsiella lineata* parasites.

the population appeared to rebound somewhat after this date (Fig. 3).

The first 372 *M. leidyi* we collected (between 26 June and 9 August) were entirely free of parasites (Fig. 3). The prevalence then climbed on 2 successive collection days (to 15% on 16 August and 29% on 21 August), and then fell on 2 successive collection days (to 13% on 6 September and 5% on 12 September). The prevalence then climbed dramatically again over the next 3 collection days, reaching a peak prevalence of 35% on September 26. The prevalence fell yet again, and on 15 October we collected 12 *M. leidyi* that were entirely free of *E. lineata*.

In 2004 we did not begin collecting *M. leidyi* until mid-August, and at this time the ctenophore was already very abundant (Fig. 3A). Both the abundance of *M. leidyi* and the prevalence appeared to vacillate in a manner similar to 2005 with an increase in parasite infection followed by a decline through November.

In 2006 *M. leidyi* appeared to peak earlier than in 2004 or 2005, i.e., in late September or early October, and it disappeared by early October (Fig. 3). During our collection of 9 October 2006, we were unable to collect any *M. leidyi*, and we did not observe the species again through our final sampling time point in late October. The rapid and apparently early decline of *M. leidyi* in 2006 coincided with a rapid increase in the apparent abundance of *B. ovata*, a major predator upon *M. leidyi*. Woods Hole lies just north of *B. ovata*'s usual range, and in a typical summer, this predacious ctenophore does not make an appearance (S. Tamm and M. Martindale, pers. comm.). However, in 2006 we began to observe *B. ovata* in small numbers in mid-September. Its abundance appeared to peak in early October. Through October, *B. ovata* declined sharply, but it persisted for several weeks after the apparent disappearance of its prey, *M. leidyi*.

The parasite prevalence differed dramatically between *M. leidyi* and *B. ovata* in 2006 (Fig. 3). Of 150 *M. leidyi* collected on 3 July 2006, only 3% were infected with *E. lineata*. The percentage of *M. leidyi* that harbored parasites increased to nearly 60% by 16 July, and, thereafter, the observed prevalence ranged between 35 and 60% until *M. leidyi* disappeared from Great Harbor in late October. This range of infection frequencies is broader, but substantially overlaps the infection frequencies we observed in 2004 and 2005. In contrast, 100% of the *B. ovata* we collected on 18, 21, and 23 September were infested with *E. lineata*. Only after *M. leidyi* disappeared from Great Harbor did the proportion of infected *B. ovata* drop below 100%, down to 96% on 9 October and 86% on 20 October.

A third ctenophore was abundant in Great Harbor in 2004, 2005, and 2006, i.e., the tentaculate cydippid, *P. pileus*. On both 26 June 2005 and 30 October 2005, we collected 300 *P. pileus* and scored them for the presence of *E. lineata* parasites. None of these 600 animal harbored parasites, despite the fact that 15% of 226 *M. leidyi* collected on 30 October 2005 were infested. During subsequent collections in 2005 and 2006, we continued to inspect the *P. pileus* we captured, and we never observed a parasitized individual.

Parasite number and ctenophore size

Most of the infected ctenophores that we collected harbored multiple *E. lineata* parasites. While the overall size range of the 2 ctenophore species was similar, the mean number of parasites per individual and the relationship between host size and parasite load varied substantially between ctenophore species. The infected *M. leidyi* contained an average of 1.97 ± 0.92 parasites per ctenophore in 2004 (range = 1–9, n = 84), 2.27 ± 0.52 parasites per ctenophore in 2005 (range = 1–7, n = 359), and 3.41 ± 2.96 parasites per ctenophore in 2006 (range = 1–20, n = 252). The infected *B. ovata* contained an average of 13.88 ± 14.59 parasites per ctenophore (range = 1–64, n = 124).

In *M. leidyi*, we observed no correlation between ctenophore size and the number of parasites per host (Fig. 4A; n = 507, $R^2 = 2.77 \times 10^{-7}$, $P = 0.99$). Among parasitized *B. ovata*, there was a significant positive correlation between ctenophore size and the number of parasites per host (Fig. 4B; n = 138, R^2 =

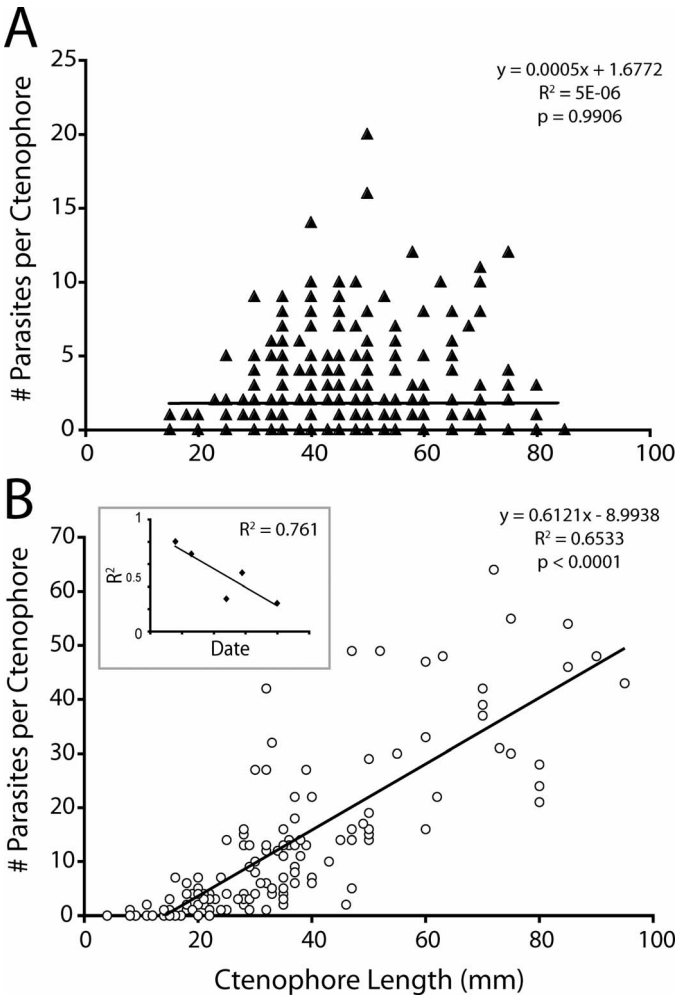

FIGURE 4. Relationship between ctenophore size and parasite load for (**A**) *Mnemiopsis leidyi* (n = 507, $R^2 = 5 \times 10^{-6}$, $P = 0.99$) and (**B**) *Beroë ovata* (n = 138, $R^2 = 0.65$, $P < 0.0001$). The explanatory power of ctenophore size to predict multiplicity of infection decreased during the season (18 September to 20 October) after the disappearance of *M. leidyi* (inset).

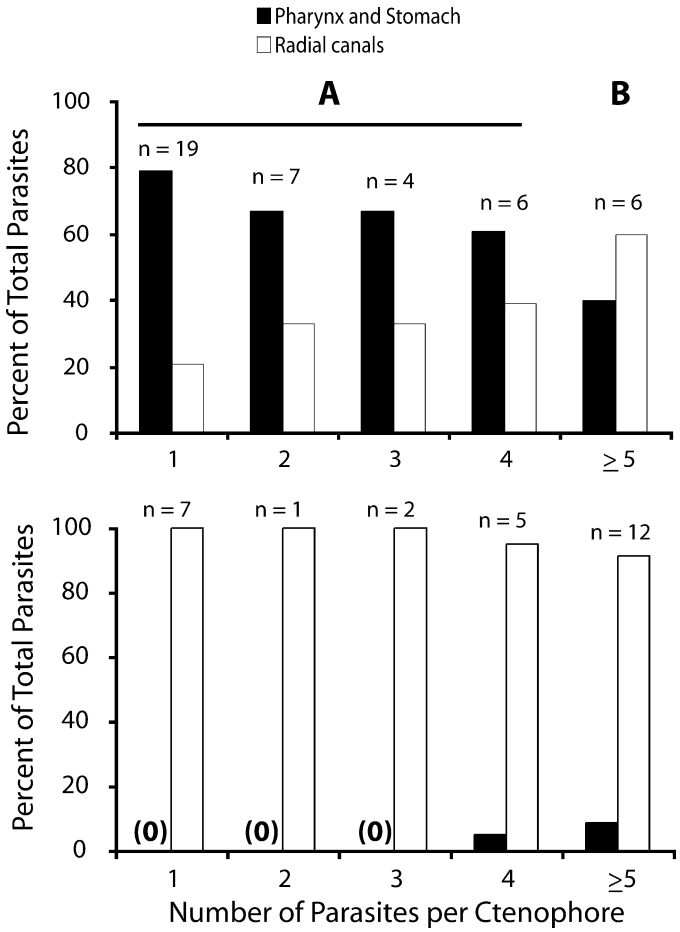

FIGURE 5. Parasite location as a function of parasite load in *Mnemiopsis leidyi* (top panel) and *Beroë ovata* (bottom panel). There was a significant difference in the percentage of parasites that occupy the pharynx/stomach or the radial canals in (**A**) *M. leidyi* parasitized by 4 or fewer anemones versus (**B**) those parasitized by 5 or more anemones (df = 1,106, $\chi^2 = 7.133$, $P = 0.0076$). No significant relationship between the number of parasites per ctenophore and parasite location was observed in *B. ovata* (df = 1,159, $\chi^2 = 1.66$, $P = 0.197$). The sample size above each bar (n) indicates the number of ctenophore hosts examined.

0.65, $P < 0.0001$). Although this relationship is significant for 5 of the 6 time points over which these data were collected (P-value range for each significant time point: $0.0000 < P\text{-value} < 0.0173$), the explanatory power of ctenophore length decreased as the season progressed, with R^2 decreasing from 0.80 on 18 September to 0.25 on 20 October (Fig. 4B, inset).

Parasite location within ctenophores

Parasite location was scored with reference to the gastrovascular system. Food enters the mouth and passes from the pharynx through the stomach to the radial canals, becoming progressively smaller due to both mechanical (ciliary) breakdown and enzymatic digestion. The radial canal system is much more extensive than the rest of the gastrovascular system combined, i.e., the 8 radial canals each run the entire length of the animal, under the overlying ctene rows (Fig. 2).

The parasite's feeding ability is limited by its small gape. Its location relative to the digestive system is, therefore, critical because this determines the size of the food particles that will be encountered. In singly infected *M. leidyi*, 79% of the parasites were located within the pharynx or stomach (15/19), while only 21% were located within the much more extensive radial canal system (Fig. 5A). The propensity of parasites to settle within the pharynx or stomach is consistent between hosts infected by 4, or fewer, parasites. We could detect no significant difference in parasite location among hosts infected by 1, 2, 3, or 4 *E. lineata*. However, parasite location differs significantly between ctenophores infected by 4 or fewer parasites (73 *E. lineata* in 36 hosts) and ctenophores infected by 5 or more parasites (35 *E. lineata* in 6 hosts), with a higher fraction of parasites located in the stomach or pharynx of ctenophores infected by ≤4 parasites (~67%) than in those ctenophores infected by ≥5 parasites (~40%; df = 1,106, $\chi^2 = 7.133$, $P = 0.0076$).

In contrast to *M. leidyi*, when *B. ovata* was infected by 3 or fewer *E. lineata*, the parasites were always located in the radial canals, never along the pharynx or stomach (Fig. 5B). In *B.*

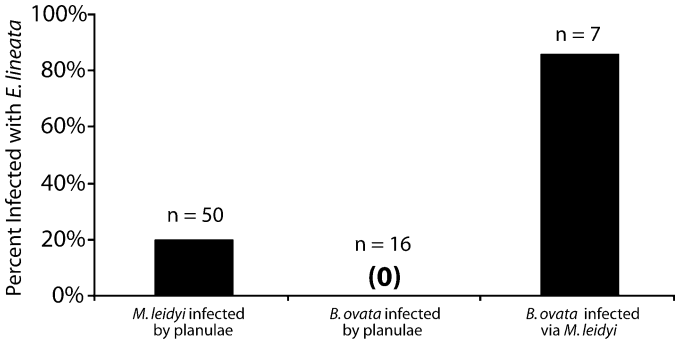

FIGURE 6. Infection frequencies observed during laboratory experiments in which *Mnemiopsis leidyi* were exposed to *Edwardsiella lineata* planulae, *Beroë ovata* were exposed to *E. lineata* planulae, or *B. ovata* were fed *M. leidyi* infected with *E. lineata* parasites.

ovata harboring a greater number of *E. lineata*, a small proportion of parasites (~8%, n = 146 parasites in 17 ctenophores) were located along the pharynx-stomach, but a majority of parasites were still located in the radial canals.

Laboratory infection of host ctenophores

Laboratory experiments indicate that infestation by *E. lineata* likely occurs via different routes in *M. leidyi* and *B. ovata* (Fig. 6). We excised *E. lineata* parasites from both *M. leidyi* and *B. ovata* and subsequently exposed them to uninfected ctenophores of the same species from which they were extracted. Within several hours of excision, the vermiform parasites developed into ciliated planula larvae. When single planulae were introduced into small finger bowls with live *M. leidyi*, nearly 20% of the ctenophores were infected with *E. lineata* after 24 hr (n = 50). We observed that the planulae could enter *M. leidyi* via 2 different routes, i.e., some entered via the mouth, and then burrowed through tissue in the pharynx, while others entered through the outer body wall and then burrowed through the mesoglea to settle adjacent to the gastrovascular system.

In contrast to *M. leidyi*, when *E. lineata* larvae were added to fingerbowls containing *B. ovata*, we observed no infected ctenophores after 24 hr (n = 16). Larvae were still swimming in the cultures after this period. However, when *M. leidyi* infected with *E. lineata* parasites were fed to *B. ovata*, approximately 80% of *B. ovata* were infected with *E. lineata* after 24 hr, and 64% of the parasites harbored by the infected *M. leidyi* had been successfully transferred to *B. ovata*.

Parasite development and settlement after excision from hosts

Previous literature suggests that if a parasite is excised from its host and allowed to develop in the absence of a second ctenophore host, it will typically develop into an adult polyp (Reitzel et al., 2006). We excised 46 parasites from *M. leidyi* and 93 parasites from *B. ovata* and cultured them in the absence of a second ctenophore host. The parasites extracted from *M. leidyi* were monitored over a period of 17 days, and the parasites extracted from *B. ovata* were monitored over a period of 54 days. Eighty-three percent of the parasites excised from *M. leidyi* survived for at least 17 days, and nearly 65% (30/46) successfully settled and underwent metamorphosis to form adult polyps (Fig. 7A). By contrast, only 48% (45/93) of the

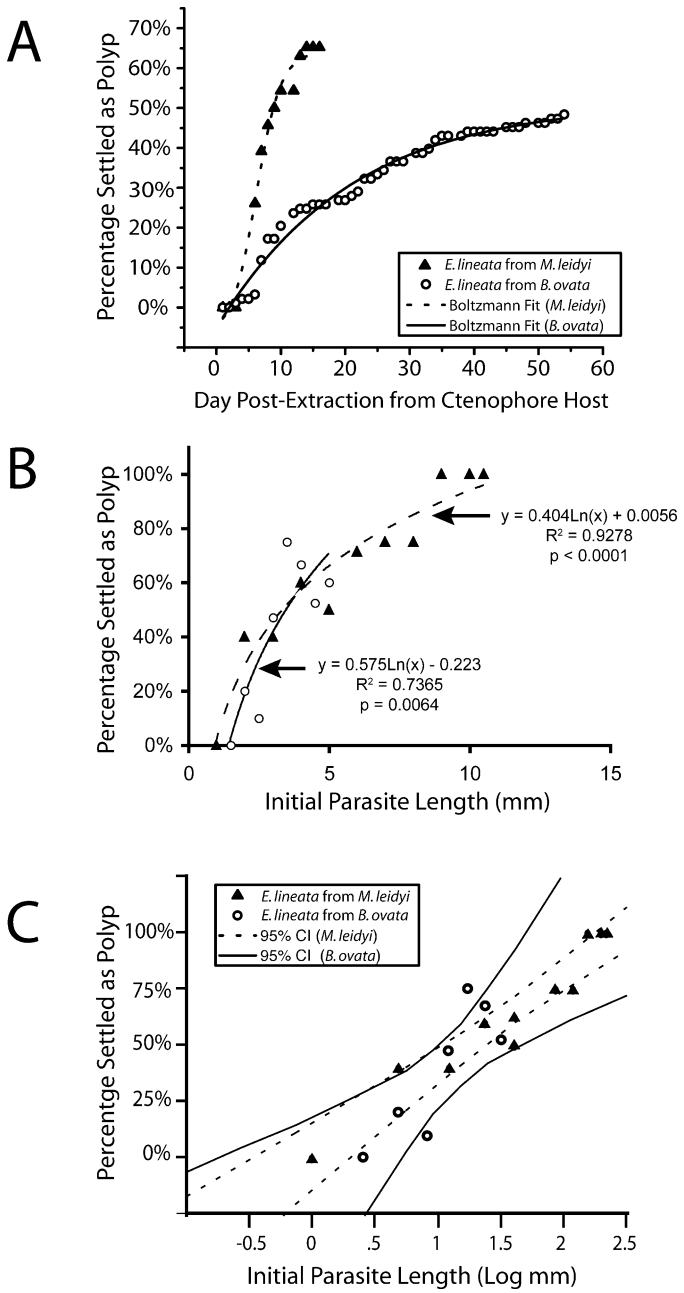

FIGURE 7. Development of *Edwardsiella lineata* after extraction from each host ctenophore. (**A**) There was a significant difference in the postparasitic developmental trajectories of parasites excised from *Beroë ovata* and those excised from *Mnemiopsis leidyi*. Parasites that resided in *M. leidyi* as a terminal host become polyps at a significantly more rapid rate. (**B**) There is a significant and predictive relationship between initial parasite length and the likelihood of settling as a polyp for both *B. ovata* ($R^2 = 0.737$, $P = 0.00639$) and *M. leidyi* ($R^2 = 0.928$, $P < 0.0001$). (**C**) The relationship between likelihood of settling as a polyp and initial size is independent of terminal host ($t = 1.06$, df = 15, $P = 0.3059$) with completely overlapping 95% confidence intervals surrounding the least squares regression best-fit lines for the relationship between metamorphosis success and log-normalized parasites lengths.

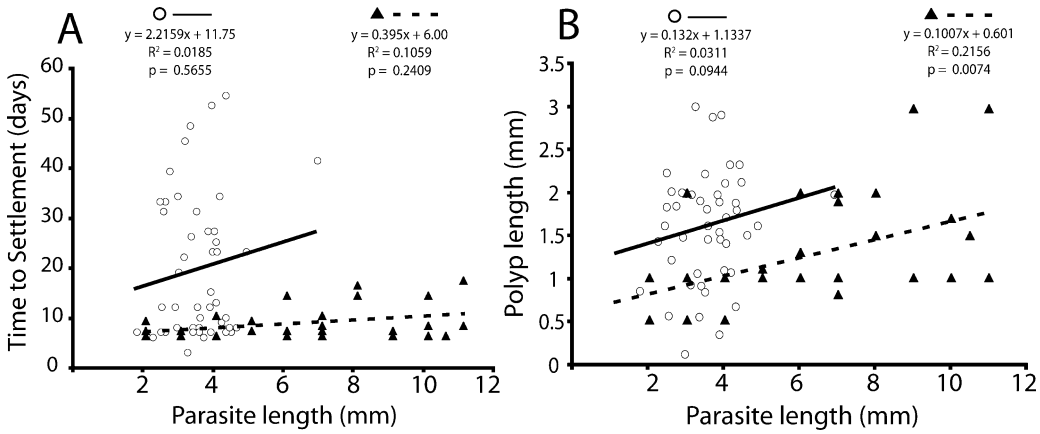

FIGURE 8. Time to settlement and length of polyp at the time of settlement as a function of parasite length. (**A**) Multivariate analyses indicated that terminal host species ($P < 0.0001$) but not parasite length ($P = 0.139$) significantly affected time to settlement (Model $R^2 = 0.2198$, df = 3,73, $P = 0.0004$). (**B**) Polyp length was a function of terminal host species ($P = 0.0017$) and parasite length ($P = 0.0491$; Model $R^2 = 0.1598$, df = 3, 73, $P < 0.0051$). For both models an interaction term was included in the model and failed to indicate a significant interaction. These multivariate analyses utilized only those data points within the overlapping *x*-axis range, i.e., 0–7 mm). Statistical values on the panels indicate the results of univariate analyses and include all data points in each scatter plot for both species. Although the relationships between the outcome variables (1) time to settlement and (2) polyp length were not a function of parasite length when *B. ovata* was the terminal host ($\alpha = 0.05$), the best-fit lines for these univariate relationships as per least-squares regression are provided for reference.

parasites excised from *B. ovata* survived and underwent metamorphosis over 54 days, with the rest dying during the course of the experiment.

Regardless of host species, *E. lineata* did not begin settlement for at least 3 days after extraction. Of the 30 parasites excised from *M. leidyi* that survived to metamorphosis, more than 50% had settled by 8 days post-extraction and 79% had settled by day 14. No additional individuals settled over the next 3 days prior to termination of the experiment. Parasites from *B. ovata* required more time to settle. Of the 45 parasites excised from *B. ovata* that survived to metamorphosis, only 32% had settled by day 14, 50% by day 23, and 79% by day 40 (Fig. 7A).

The size of parasites excised from each host species is a significant predictor of whether a parasite will settle into a polyp (Figs. 7B, C). Parasites excised from *B. ovata* (mean ± SD: 3.38 ± 1.93 mm) were significantly smaller than those excised from *M. leidyi* (5.74 ± 1.49 mm; df = 137, $t = -7.12$, $P < 0.0001$; *t*-test assumes unequal variance). For both *B. ovata* and *M. leidyi*, initial parasite length is a strong predictor of likelihood of settling as a polyp ($R^2 = 0.737$, $P = 0.006$ and $R^2 = 0.928$, $P < 0.0001$, respectively; Fig. 7B). This relationship was not significantly different between parasites extracted from each host (*t*-test of regression parameters: df = 15, $t = 1.06$, $P = 0.3059$; proc syslin: $F_{1,4} = 0.20$, $P = 0.670$). The lack of a host-effect is supported by overlapping 95% confidence intervals surrounding the regression lines for each host, which show *M. leidyi* confidence thresholds lie entirely within the 95% confidence interval range of *B. ovata* (Fig. 7C).

Time to settlement varied significantly between species (Figs. 7A, 8A). A multivariate regression was used to test for dependence of time to settlement upon (1) parasite length and (2) terminal host. Terminal host significantly affected time to settle ($P < 0.0001$) while neither parasite length ($P = 0.1392$) nor an interaction term ($P = 0.2706$) significantly affect the time it took an excised parasite to settle. Nonetheless, terminal host explains only a small fraction of the variation within the timing of parasite metamorphosis ($R^2 = 0.2198$; Fig. 8A).

For parasites extracted from *M. leidyi*, the body length of the excised parasite correlated significantly with the body length of the polyp that resulted after settlement (Fig. 8B, $R^2 = 0.216$, $P = 0.0074$). Conversely parasite length exhibited no relationship with polyp size for parasites extracted from *B. ovata* ($R^2 = 0.0311$, $P = 0.2409$). A multivariate analysis indicates that both parasite length and terminal host significantly affect polyp length (model $R^2 = 0.1598$, df = 3,73, $P = 0.0051$), with polyp length increasing by 0.12 mm for every 1 mm increase in parasite length ($P = 0.0491$) and polyps being larger on average by 0.32 mm in individuals extracted from *B. ovata* ($P = 0.0017$). There was no significant interaction effect between host and parasite length ($P = 0.8836$).

DISCUSSION

Gelatinous zooplankton: poorly understood pelagic hosts

Parasites are known to exert profound impacts on coastal ecosystems (Poulin, 2004), but the existing host-parasite data are biased toward terrestrial and freshwater systems (McCallum et al., 2004). One significant gap in our knowledge of marine systems concerns gelatinous zooplankton. Gelatinous zooplankton are a major component of pelagic food webs (e.g., Brodeur et al., 1999; CIESM, 2001), and their importance may be increasing because of ocean warming (Mills, 2001; Sullivan et al., 2001; Purcell, 2005). However, very few host-parasite studies have been performed on gelatinous zooplankton (Spaulding, 1972; McDermott et al., 1982; Arai, 2005). The present study is the first to directly monitor parasitic infection frequencies in gelatinous zooplankton in the wild and the first to directly investigate host specificity, a key determinant of a parasite's ecological impact.

Evidence of host specificity for *Edwardsiella lineata*

Edwardsiella lineata has only been observed to parasitize ctenophores. However, even if *E. lineata* is specific to this phylum, Woods Hole is inhabited by multiple ctenophore species that occupy different trophic levels, for example, *M. leidyi* and *P. pileus* feed on the planktonic larvae of fish and invertebrates, while *B. ovata* preys on other ctenophores, primarily *M. leidyi*. Over the previous century, a number of reports have described *M. leidyi* as a host for *E. lineata* (Hargitt, 1912; Crowell, 1965, 1976; Crowell and Oates, 1980; Bumann and Puls, 1996), and a single published report describes *E. lineata* infesting *B. ovata* (pers. comm. by A. Moss and S. Tamm, cited in Bumann and Puls, 1996). However, these studies provided no direct evidence regarding host preference or host specificity because they did not monitor *E. lineata* prevalence in the field, and they did not compare infection mechanisms or developmental outcomes across species.

By directly comparing the prevalence of infection in 3 different ctenophore species, we found peak prevalence (PP) and mean parasite load (MPL) in *B. ovata* (PP = 100%, MPL = 13.88, n = 181) to be substantially higher than peak infection and average parasite load in *M. leidyi* (PP = 60%, MPL = 1.97, n = 7,472) or *P. pileus* (PP = 0%, MPL = 0, n = 600). By themselves, these data would suggest that *E. lineata* is a semi-selective parasite of ctenophores in Woods Hole, with a greater effective host preference for *B. ovata* than for *M. leidyi*. However, our parasite infection experiments reveal that *E. lineata* planulae are far more adept or far more inclined to parasitize *M. leidyi* than *B. ovata*.

The data on parasite length and development suggest that *E. lineata* may not be well adapted for feeding in *B. ovata*. The mean body length of parasites embedded in *B. ovata* is significantly less than the mean body length of parasites embedded in *M. leidyi*. Because the principal mechanism by which *E. lineata* enters *B. ovata* is via ingestion of infected *M. leidyi*, the parasites must undergo shrinkage after coming to reside within *B. ovata*. Such shrinkage is clearly maladaptive, as parasite length is an important predictor of developmental competence, i.e., smaller parasites are less likely to complete development and form an adult polyp. However, while the likelihood of successful metamorphosis is solely a function of size, the speed of metamorphosis is solely a function of terminal host. Even small parasites extracted from *M. leidyi* that were able to survive and undergo metamorphosis did so more rapidly than parasites excised from *B. ovata*. The longer time period necessary for metamorphosis may reflect a poorer nutritional state of those parasites excised from *B. ovata*, or they may be somehow developmentally delayed.

It is also significant that parasite location differs dramatically between *M. leidyi* and *B. ovata* as parasite location relates to feeding efficiency. In *M. leidyi* the parasites exhibit a strong preference for locating themselves in the pharynx or stomach, particularly the stomach (Figs. 2C, 5); e.g., when only a single parasite is infecting a ctenophore, 80% of the time it will settle in the pharynx or stomach. The stomach is quite small, but all of the food that has been ingested must pass through this structure, and the food reaching this point has already undergone extensive mechanical and enzymatic digestion; the stomach, therefore, represents an ideal location for a gape-limited gut parasite. As the available space surrounding the pharynx and stomach decreases with a higher parasite load, an increasing fraction of parasites take up residence outside of this ''preferred location'' (Crowell, 1976), suggesting that parasites preferentially settle in certain portions of the ctenophore hosts. Parasites embedded in *B. ovata* do not exhibit a preference for the stomach or pharynx; they are more likely to be located adjacent to the radial canals, but this may merely reflect the fact that the radial canal system is far more extensive than the pharynx and stomach combined.

The likely influence of host feeding mode on parasitic infection

Sea anemone larvae (Cnidaria; Anthozoa; Actinaria) have evolved the ability to parasitize gelatinous zooplankton on at least 2 occasions. In addition to *E. lineata* (Edwardsiidae), the planula larva of *Peachia parasitica* (Haloclavidae) is parasitic on the scyphozoan *Cyanea* sp. (McDermott et al., 1982), and the larvae of *Peachia quinquecapitata* parasitize multiple species of hydromedusae (Spaulding, 1972). Planulae may be predisposed toward becoming parasitic on gelatinous zooplankton because they routinely gain access to the potential host's internal body cavity, and if they can avoid being digested, life inside a jellyfish could afford many advantages relative to a free-living existence, e.g., protection from some predators, greater dispersal ability, and an abundant supply of food.

The probability that a planula can gain entry into a ctenophore or cnidarian medusa is likely influenced by the potential host's feeding mode. The feeding mode of the 3 ctenophores tracked in this study differs significantly, likely impacting their susceptibility to *E. lineata* infection. *Pleurobrachia pileus* employs 2 long, pennate tentacles to snare small zooplankton including copepods, cladocerans, larval molluscs, larval fish, and fish eggs (Mutlu and Bingel, 1999). Captured food is brought to the small mouth via coordinated contractions of the tentacles and movements of the body (Tamm and Moss, 1985). Presumably, the mouth opens only briefly, and relatively little water is ingested during feeding. This feeding mode would limit the ability of *E. lineata* to infect *P. pileus* through the mouth. *Pleurobrachia pileus* has been shown to harbor the nematode *Hysterothylacium aduncum*, an important internal parasite of farmed sea trout, but the mechanism of introduction has not been identified (Mutlu and Bingel, 1999). Though it feeds on the same general type of prey as *P. pileus*, *M. leidyi* is an atentaculate, lobate ctenophore that utilizes a ram feeding mechanism (Costello and Case, 1998). When feeding, *M. leidyi* swims with its mouth open, ingesting water as it captures small planktonic animals, e.g., copepods and larval molluscs, (Mutlu, 1999). This feeding mode provides ample opportunity for *E. lineata* to enter the mouth of *M. leidyi*, one of the principal avenues by which the parasite was able to infect *M. leidyi* in our laboratory infection experiments. Finally, *B. ovata* employs gape-and-suck feeding to capture and ingest *M. leidyi* (Matsumoto and Harbison, 1993). The mouth is open only briefly, and that may partially explain why planulae did not successfully parasitize *B. ovata* during our laboratory infection experiments.

However, *B. ovata*'s predation on *M. leidyi* renders it extremely vulnerable to *E. lineata* infection from ingesting parasitized *M. leidyi*. Over the first 3 wk of its occurrence at Woods

Hole in 2006, 100% of *B. ovata* were infected with *E. lineata*, in most cases with 10 or more parasites. The prevalence only decreased after *M. leidyi* had disappeared from Woods Hole. In addition, parasite load was positively correlated with host size in *B. ovata*. Larger *B. ovata* have presumably ingested more infected *M. leidyi*, thereby acquiring more parasites. This correlation implies that the rate of parasite uptake exceeds the rate of parasite loss, an inference consistent with our laboratory infection experiments. We demonstrated that *E. lineata* parasites are efficiently transferred from *M. leidyi* to *B. ovata* when *B. ovata* feeds upon *M. leidyi*, and, once transferred, these parasites can remain stably embedded in their new terminal host for at least 48 hr. Interestingly, later in the season, after the disappearance of *M. leidyi*, the correlation between host size and parasite load begins to break down. Through October 2006 we collected many small (40–60 mm) but heavily infected *B. ovata*. We suspect that these represent formerly large adults that have undergone starvation-induced shrinkage. Adult *B. ovata* lose an average of 9.4% body mass per day when starved for 18 days in a laboratory setting (Anninsky et al., 2005).

Although it is not yet known how *E. lineata* impacts the physiology or fitness of *B. ovata*, quantifying the parasite load allows us to estimate *B. ovata*'s consumption of *M. leidyi*. For example, we recovered individual *B. ovata* harboring as many as 64 parasites. Assuming 2.1 parasites per infected *M. leidyi* (the average parasite load over the period that *M. leidyi* and *B. ovata* co-occurred at Woods Hole in 2006) and a transfer efficiency of 64% (based on laboratory infection experiments), we estimate that this single *B. ovata* consumed at least 67 *M. leidyi*. The actual number is likely higher because this estimate does not account for parasite loss from *B. ovata*. This represents the first empirically based estimate of ctenophore on ctenophore predation in the wild. This is important because ctenophores represent an important component of pelagic food webs, and their trophic contributions have rarely been quantified (Finenko et al., 2006). Furthermore, *B. ovata* has been suggested as an important biological control for invasive populations of *M. leidyi* (Vinogradov et al., 2005).

Edwardsiella lineata as a biological control

Mnemiopsis leidyi is native to the east coast of North America, but it was introduced to the Black Sea in the early 1980s, presumably in ship ballast water. Lacking predators in its introduced range, this voracious zooplankton predator increased in density to >1 kg/m^2 by 1989 (Vinogradov et al., 1989). At the same time, commercially important fish populations experienced precipitous declines (Kideys, 2002). *Mnemiopsis leidyi* then spread from the Black Sea to other nearby seas, including the Caspian and Aegean (Vinogradov et al., 1989; Shiganova, Kamakin et al., 2001; Knowler, 2005; Finenko et al., 2006) and the Azov and Marmara (GESAMP, 1997). More recently, invasive populations of *M. leidyi* have spread to other northern European seas including the North (Faasse and Bayha, 2006), Baltic (Javidpour et al., 2006), and the Skagerrak (Hanson, 2006). A recent computer model based on data from the Caspian Sea indicates that, if unchecked, the *M. leidyi* density will tend to exceed the level at which pelagic fisheries could recover from ctenophore predation (Finenko et al., 2006). At the same time, persistent increases in ctenophore density in the waters off the northeast United States suggest that *M. leidyi* could begin to cause declines in commercially important fisheries within its native range (Link and Ford, 2006).

The consequences of *E. lineata* infection can mimic the effects of food deprivation in *M. leidyi*. *Mnemiopsis leidyi* adults are known to decrease in size and density following population crashes of their zooplankton prey. One laboratory study noted a 9.3% reduction in wet mass per day in starved *M. leidyi* during an 8-day study (Anninsky et al., 2005). Another laboratory study of infected *M. leidyi* found that *E. lineata* could successfully purloin all of the food eaten by its host, leading to starvation-induced shrinkage and a reduction in fecundity (Bumann and Puls, 1996); this study demonstrates that *E. lineata* could negatively impact the reproductive rate of *M. leidyi*. However, it is difficult to determine the actual impact of *E. lineata* on *M. leidyi* in the native range because there are little published data documenting the frequency and abundance of *E. lineata* parasites, and there are no data comparing the fecundity of parasitized and unparasitized ctenophores in the wild. Field data from Long Island, New York (Freudenthal and Joseph, 1993), and Woods Hole, Massachusetts (Crowell, 1976), report large variation in seasonal and interannual abundance of *E. lineata* larvae. Interestingly, our data from 2004 and 2005 seem to show that steep increases in the *E. lineata* prevalence foreshadow steep declines in the *M. leidyi* population (Figs. 3A–B).

The fact that *E. lineata* can infect *B. ovata* is a complicating factor when considering its possible utility as a biological control for *M. leidyi*. *Beroë ovata* is a selective predator on *M. leidyi* in locations where the native ranges of these animals overlap, and it has been suggested as a biological control for invasive *M. leidyi* in the Black Sea (Bumann and Puls, 1996; GESAMP, 1997). The data presented here suggest that a single *B. ovata* can consume more than 67 *M. leidyi* in a matter of days. Although the introduction of *B. ovata* was never officially sanctioned, its recent appearance in the Black Sea is credited for the precipitous decline of invasive *M. leidyi* populations and the associated recovery of the anchovy fishery (Shiganova, Bulgakova et al., 2001; Vinogradov et al., 2002; Finenko et al., 2003; Vinogradov et al., 2005).

If either *B. ovata* or *E. lineata* are to be considered as potential biological controls for invasive *M. leidyi* populations, we need to develop a better understanding of their direct and indirect ecological interactions. All 3 species may eventually cooccur outside their native ranges, if they haven't already; both ctenophores have already become established outside their native ranges, and as either ctenophore can harbor significant numbers of *E. lineata*, it is likely the parasitic stage of the sea anemone will be introduced outside its range. Whether the anemone can become established outside its range will depend upon whether the adult stage of the life history can survive and reproduce, thus completing the life cycle. The indirect interactions among these 3 species might also be influenced by the large number of organisms that may reside on or in *E. lineata*, *M. leidyi*, or *B. ovata*. Ctenophores are known to harbor numerous species of epibiont protozoa that are likely to be transported to new habitats (Moss et al., 2001).

The combined effects of *B. ovata* and *E. lineata* on *M. leidyi* populations are difficult to predict. The effects of *B. ovata* and *E. lineata* could be strictly additive, or the 2 species might act

synergistically to drive *M. leidyi* populations more sharply downward. However, if *E. lineata* has negative fitness consequences for *B. ovata*, particularly if *E. lineata* impacts *B. ovata* more negatively than *M. leidyi*, it is possible that the presence of *E. lineata* could undermine efforts to control *M. leidyi* using *B. ovata*. On the other hand, in the event that *E. lineata* has a similarly detrimental effect on both *M. leidyi* and *B. ovata*, the simultaneous deployment of *E. lineata* and *B. ovata* could serve as an effective control on *M. leidyi* populations that would be self-limiting, as *B. ovata* blooms could be controlled by the parasitic anemones. This third result seems particularly important given that *B. ovata* may generalize its ecological niche to include feeding on other gelatinous zooplankton, including native ctenophores and jellyfish.

Based on the many unanswered questions and based on our data regarding infection frequency, we have doubts regarding the utility of *E. lineata* as a biological control for invasive populations of *M. leidyi*. At Woods Hole, the infection frequency in *M. leidyi* seldom exceeds 40%, while the infection frequency in *B. ovata* consistently approaches 100%. Even though *E. lineata* has been shown to reduce the growth rate and fecundity of *M. leidyi* (Bumann and Puls, 1996), if *E. lineata* infection reduces the fitness of *B. ovata* even slightly, the effect of adding *E. lineata* to an ecosystem already harboring *M. leidyi* and *B. ovata* could be a net increase in the *M. leidyi* population. Additionally, before the introduction of *E. lineata* is seriously considered, the ecological impact of the adult polyp would have to be determined. Dense mats of adult *E. lineata* have been reported in some regions of North America (Crowell and Oates, 1980; Daly, 2002), but the feeding habits, population stability, and reproductive output of these adults are unknown. On top of all of these ecological uncertainties, *E. lineata* is implicated as a causative agent in seabather's eruption, a skin irritation in humans (Freudenthal and Joseph, 1993). The potential negative impacts of *E. lineata* on humans, *B. ovata*, and nontarget species do not currently recommend it as a biological control for *M. leidyi*.

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