Infestation with larvae of the sea anemone *Edwardsia lineata* affects nutrition and growth of the ctenophore *Mnemiopsis leidyi*

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SUMMARY

The lobate ctenophore *Mnemiopsis leidyi* is a periodically abundant and voracious plankton predator in coastal waters along the east coast of the United States. In the 1980s it was accidentally introduced to the Black Sea where it caused a dramatic reduction in fisheries. We investigated how *M. leidyi* is affected by infestation with parasitic larvae of the sea anemone *Edwardsia lineata*. Infested *M. leidyi* contained 1–30 (median 7) *E. lineata* larvae. Within *M. leidyi* most larvae had their mouth in the gastrovascular system near the aboral end of the pharynx. Parasitic *E. lineata* ingested all food previously ingested and pre-digested by *M. leidyi*. Non-infested *M. leidyi* had higher growth rates than infested individuals, which had zero or negative growth rates. Egg production was similar for infested and non-infested *M. leidyi* of similar size. Simulation based on the empirical data suggests that growing, non-infested, *M. leidyi* are expected to have a larger life-time egg production than infested shrinking individuals. *E. lineata* could be at least partially responsible for the sharp decline of *M. leidyi* populations in fall in US coastal waters. Advantages and disadvantages of *E. lineata* as a potential candidate for the control of the artificially introduced *M. leidyi* population in the Black Sea are discussed.

Key words: Ctenophora, Anthozoa, plankton, Black Sea, seabather's eruption.

INTRODUCTION

The lobate ctenophore (comb jelly) *Mnemiopsis leidyi* is periodically abundant in coastal waters along the east coast of the United States, from North Carolina to Cape Cod (Kremer, 1994). *M. leidyi* appears to be a polymorphic species and specimens previously described as separate species (*M. mccradyi*, *M. gardeni*) are probably variants of *M. leidyi* (see Harbison & Volovik, 1994*a*; Seravin, 1994*a*, *b*).

Due to its exceptionally high growth rates and mass reproduction, *M. leidyi* responds quickly to zooplankton blooms with a large increase in population (Reeve & Walter, 1978; Reeve, Walter & Ikeda, 1978) and can control the abundance of both zooplankton and phytoplankton (Burell & van Engel, 1976; Reeve & Walter, 1978; Deason & Smayda, 1982). The potential environmental impact of *M. leidyi* became especially evident when it was accidentally introduced into the Black Sea (Vinogradov *et al.* 1989) in the 1980s. A bloom in 1989 dramatically changed this already disturbed ecosystem and led to a sharp reduction in local fish populations (Kideys, 1994).

In late summer and fall *M. leidyi* populations along the US coast are heavily infested by brown or pink larvae of the sea anemone *Edwardsia lineata* (formerly called *Fagesia lineata*, previously called *Edwardsia leidyi*) (Fig. 1) (Crowell, 1965, 1976; Williams, 1979; Crowell & Oates, 1980; Melville & Smith, 1987). After leaving *M. leidyi*, the planula larvae of *E. lineata* swim around for a few weeks before they settle and metamorphose into the adult anemone (Crowell, 1976; Crowell & Oates, 1980; Freudenthal & Joseph, 1993). The free-swimming larvae can cause seabather's eruption, an annoying dermatitis (Freudenthal & Joseph, 1993).

To determine the relationship between the parasitic larvae of *E. lineata* and their host, *M. leidyi*, we compared nutrition, growth, and egg production, for infested and non-infested *M. leidyi*.

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MATERIALS AND METHODS

M. leidyi were collected from the shore in Woods Hole, MA, in September 1995. They were transferred to sterile-filtered (0·2 μm) seawater and kept at 20–22 °C. The distance between mouth and aboral end was used for body length determination (range of 8–45 mm).

The number and position of *E. lineata* within *M. leidyi* was determined with a dissecting microscope for 72 infested *M. leidyi* (total number of *E. lineata*: 570).

To compare digestion, 8 infested and 8 non-infested *M. leidyi* were fed with 2-day-old *Artemia salina* (brine shrimp) nauplii. Some *A. salina* were previously stained with 0·02 % Evans Blue to obtain a better contrast for nauplii swallowed by *E. lineata*.

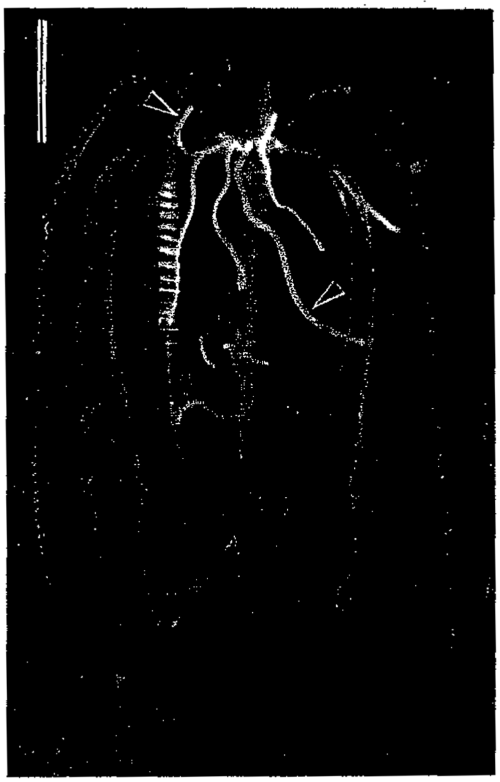

Fig. 1. The ctenophore *Mnemiopsis leidyi* infested with several parasitic larvae of the sea anemone *Edwardsia lineata* (arrowheads). This photograph was kindly provided by R. Harbison.

Growth rate and egg production of the simultaneous hermaphrodite *M. leidyi* (Strathmann, 1987) was compared at 8 dates in September 1995 for groups of 12 non-infested and 12 infested individuals. The length of each individual was determined, and infested and non-infested *M. leidyi* were chosen to have similar size distributions. The *M. leidyi* were placed individually in beakers each containing 800 ml of filtered seawater. After 24 h, the length was measured again and the seawater was slowly filtered through a 44 μm filter of 8 cm diameter to collect eggs.

Size distribution and egg production of infested and non-infested *M. leidyi* populations were simulated for a 7 day period based on our short-term data. Both populations were assumed to have initially the same size distribution which was obtained from measurements of individuals collected in September 1995.

RESULTS

Infested *M. leidyi* contained 1–30 (median 7) *E. lineata* larvae as observed earlier (Crowell, 1976; Oviatt & Kremer, 1977; Freudenthal & Joseph, 1993). Large *M. leidyi* contained more *E. leidyi* larvae than small individuals (data not shown; Kendall's rank correlation test, $n = 72$, $\tau = 0{\cdot}16$, $P < 0{\cdot}05$; Siegel (1956). Within *M. leidyi*, most *E. lineata* larvae had their mouth opening in the gastrovascular system close to the aboral end of the pharynx as observed earlier (Crowell, 1976).

Digestion in non-infested *M. leidyi* proceeded as described for other ctenophore species (Hernandez-Nicaise, 1991). Ingested *A. salina* nauplii were extracellularly digested in the flattened pharynx. In the aboral region of the pharynx, predigested but still almost intact *A. salina* nauplii were disrupted to small fragments (diameter < 30 μm) by strong ciliary currents. The fragments entered the canal system where absorption occurred. In infested *M. leidyi*, *A. salina* nauplii were extracellularly digested in the pharynx as in non-infested *M. leidyi*. However, before being disrupted all *A. salina* nauplii were swallowed by the parasitic *E. lineata*, which entered the pharynx from the canal system and approached the food. After feeding 50 *A. salina* nauplii *E. lineata* appeared bright orange due to the endogenous carotenoids of the prey while no staining of *M. leidyi* occurred indicating that almost all food was trapped by the parasite.

Growth rates of non-infested *M. leidyi* were higher than those of infested individuals of the same populations, which had zero or negative growth rates (Fig. 2A; sign test, 8 out of 8 trials, $P < 0{\cdot}01$; Siegel (1956). Even infestation with a single *E. lineata* eliminated the positive growth of *M. leidyi* (Mann-Whitney-U test, $n_1 = 96$, $n_2 = 8$, $U = 152{\cdot}5$, $P < 0{\cdot}01$; Siegel (1956). Among non-infested *M. leidyi* small individuals had higher absolute growth rates than large individuals (Fig. 2B; Mann-Whitney-U test, $n_1 = 19$, $n_2 = 28$, $U = 129$, $P < 0{\cdot}01$; Siegel (1956) as previously observed (Reeve, Syms & Kremer, 1989; Kremer & Reeve, 1989). For infested *M. leidyi* no significant size-dependent differences were observed (Mann-Whitney-U test, $n_1 = 21$, $n_2 = 30$, $U = 279$, $P < 0{\cdot}5$; Siegel (1956). The high scatter in growth rates for the different trials could be related to the strong tidal currents in the Woods Hole region so that *M. leidyi* populations collected there might have experienced different environments in their past few days (i.e. Martha's Vineyard sound or Buzzards Bay). Since both infested and non-infested *M. leidyi* were collected from the same populations this scatter did not affect the comparison of growth rates between infested and non-infested *M. leidyi*.

Egg production had a high scatter as previously observed (Baker & Reeve, 1974) but was not significantly different for non-infested and infested *M. leidyi* of similar size (Fig. 3).

No direct information about long-term effects of infestation on growth rates and egg production has been obtained in this study since we employed only short-term experiments to minimize artificial lab-

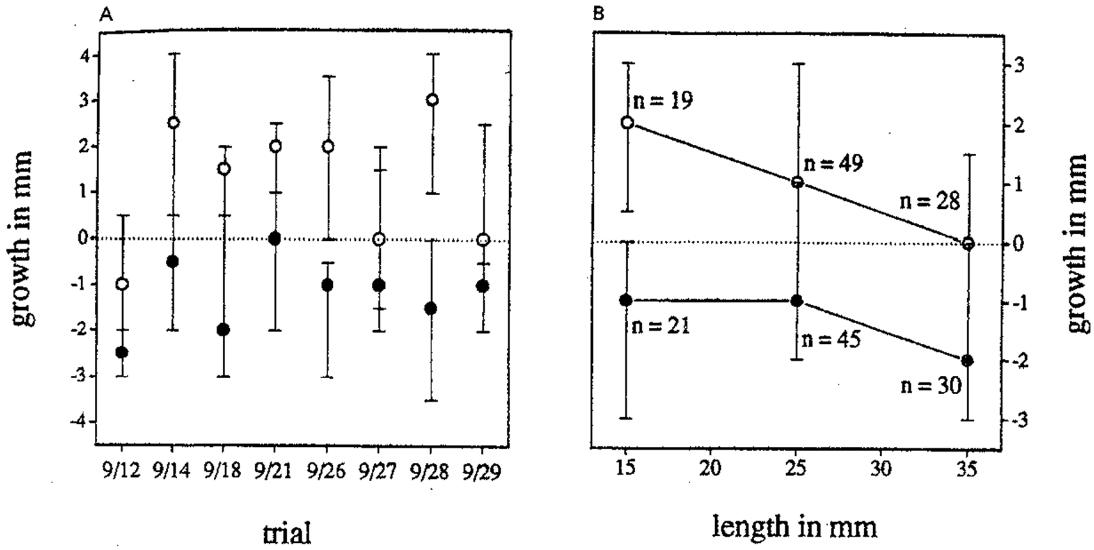

Fig. 2. Comparison of growth during 20 h for infested (●) and non-infested (○) *Mnemiopsis leidyi*. Values are accurate to ±2 mm. (A) Median and quartiles for 8 trials during September 1995. Non-infested *M. leidyi* had significantly higher growth rates than infested individuals (sign test, $P < 0{\cdot}01$). (B) Pooled data for all trials were divided in 3 classes according to the initial length (< 20; 20–29 mm; > 30 mm). The data shown are medians and quartiles. Among non-infested *M. leidyi* small individuals had significantly higher growth rates than large non-infested individuals (Mann-Whitney-U test, $P < 0{\cdot}01$). For infested *M. leidyi* no size-dependent differences were observed (Mann-Whitney-U test, $P < 0{\cdot}5$).

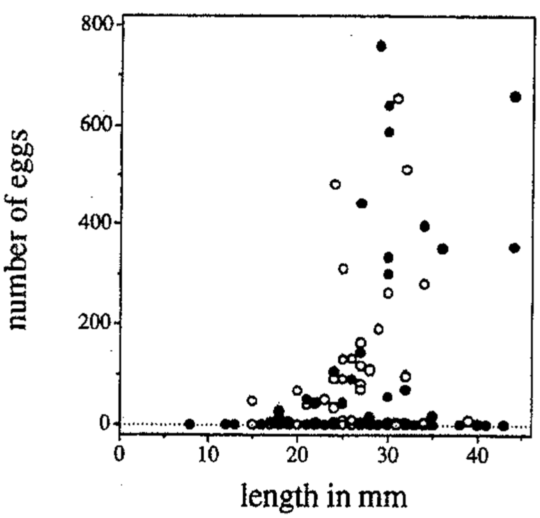

Fig. 3. Egg production of infested (●) and non-infested (○) *Mnemiopsis leidyi* during 20 h. Egg numbers are accurate to ±10. Length is accurate to ±1 mm.

oratory conditions which can lead to impaired feeding behaviour of ctenophores (Reeve, 1980; Sullivan & Reeve, 1982; Monteleone & Duguay, 1988; Gibbons & Painting, 1992). *M. leidyi* growth and egg production reflects its nutrition 2–4 days previously (Reeve *et al.* 1989). In the experiments reported here all individuals were kept for only 24 h in the laboratory, hence the results are likely to represent natural conditions. Long-term effects were predicted based on the short-term data shown in Figs 2 and 3. The simulations indicated a decrease of size for infested individuals while non-infested individuals grew to a more uniform size distribution (Fig. 4A). The infested population produced fewer and fewer eggs while the non-infested population produced increasing numbers of eggs (Fig. 4B).

DISCUSSION

Parasitic *E. lineata* larvae feed on food previously ingested by *M. leidyi*. In the aboral part of the pharynx the food is pre-digested but still almost complete and easy to swallow at once. This could explain why that region of the gastrovascular system of *M. leidyi* is the preferred position of *E. lineata*. Other parasites including sea anemone larvae, a nematode, and various arthropods have been found in the gastrovascular system of ctenophores (Stephenson, 1935; Harbison, Biggs & Madin, 1977; Harbison, Madin & Swanberg, 1978; Stunkard, 1980; Yip, 1984; Gaevskaya & Mordvinova, 1994) and medusae (Stephenson, 1935; Nyholm, 1949; Spaulding, 1972). Possibly, these parasites also feed on food previously ingested and pre-digested by their respective hosts.

As expected from the high efficiency with which *E. lineata* removes food, infested *M. leidyi* have insignificant or negative growth rates. Surprisingly, however, egg production is not different for infested and non-infested *M. leidyi* of similar size although starvation leads to a decrease in egg number under

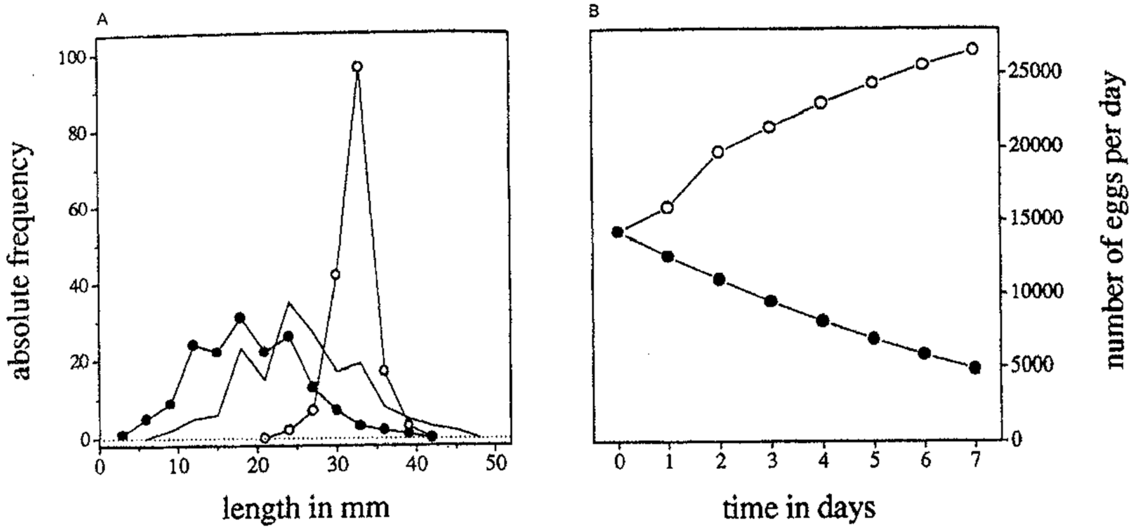

Fig. 4. Simulation of size distribution and egg production of infested and non-infested *Mnemiopsis leidyi* populations (192 individuals each). (A) Size distribution after 7 days for infested (●) and noninfested (○) individuals with the same initial size distribution (straight line). (B) Total egg production of infested (●) and non-infested (○) populations.

laboratory conditions (Reeve *et al.* 1989). Egg production accounts only for a minor fraction of the carbon budget of *M. leidyi* (Reeve *et al.* 1989), which might be available even to infested individuals.

Since egg production depends on the size, growing non-infested *M. leidyi* are expected to produce an increasing number of eggs while shrinking infested individuals are expected to have a decreasing egg production. Indeed, simulations showed that a considerable difference in egg production between infested and non-infested populations could appear in the course of a week. Data for mortality and infestation rate of juvenile *M. leidyi* would be necessary to obtain population size estimates on a longer time-scale. The high infestation of small individuals in September could indicate that few new-born individuals grow to the size where mass reproduction begins. Then infestation would be likely to lead to a sharp decline of the *M. leidyi* population.

Interestingly, field data indicate that in the US coastal waters heavy infestation in early September (Crowell, 1976; Oviatt & Kremer, 1977) is followed by a sharp decline of the population of *M. leidyi* in late September or October (Kremer, 1976; Deason & Smayda, 1982) which would be consistent with the suspected long-term effect of *E. lineata* infestation. Other factors including food availability, temperature, salinity, or predation (Kremer, 1994) seem to be of minor importance for the annual population decline at least in certain areas (Deason & Smayda, 1982). Moreover, there is less seasonal variation in *M. leidyi* populations in the Black Sea (Khoroshilov, 1994), where *E. lineata* infestation does not occur. The relative importance of the various factors might differ for different regions and the available field data are insufficient to draw final conclusions (Kremer, 1994). Mesocosm experiments could be carried out to clarify this subject (Houde *et al.* 1994).

In 1989, a bloom of the accidentally introduced *M. leidyi* in the Black Sea led to a sharp reduction in local fisheries. Although the abundance of *M. leidyi* has declined since then (Lebedeva & Shushkina, 1994), biological control might be needed to allow for the recovery of fish stocks (Harbison & Volovik, 1994*a*, *b*; Niermann *et al.* 1994). Moreover *M. leidyi* has already entered the Mediterranean Sea with unpredictable consequences for this ecosystem (Kideys & Niermann, 1994).

E. lineata is the only parasite known to affect major fractions of *M. leidyi* populations (Crowell, 1976; Oviatt & Kremer, 1977; Cahoon, Tronzo & Howe, 1986; Gaevskaya & Mordvinova, 1994). Moreover, *E. lineata* larvae selectively infest *M. leidyi* in US coastal waters while other gelatinous plankton species (*Chrysaora quinquecirrha*, *Aurelia aurita*) are not infested. *E. lineata* larvae were occasionally found in the ctenophore *Beroe* sp. (A. Moss & S. Tamm, personal communication) but were likely to be derived from infested *M. leidyi* eaten by *Beroe*. sp. Therefore, *E. lineata* could be a suitable candidate for the selective control of the accidentally introduced *M. leidyi* population in the Black Sea. However, it is necessary to carefully evaluate potential effects of *E. lineata* introduction as infestation of other hosts by the planula larvae or the change of benthic communities due to the adult sea anemone. Since species introduced to the Black Sea might spread to the East Atlantic the whole region must be considered.

Free-swimming *E. lineata* larvae can cause seabather's eruption in swimmers, a dermatitis normally lasting for a few days (Freudenthal & Joseph, 1993), and this is an obvious drawback for such a strategy. However, despite the periodically high abundance of *E. lineata* from North Carolina to Cape Cod, very few cases of seabather's eruption occur in this region except when *E. lineata* larvae leave their hosts unusually early (August) in the season (Freudenthal & Joseph, 1993). Most cases of seabather's eruption in the United States occur in southern regions where this disease is caused by a different cnidarian species (*Linuche unguiculata*) (Black, Szmant & Tomchik, 1994; Wong *et al.* 1994). To estimate the risk of seabather's eruption upon introduction of *E. lineata* to the Black Sea further studies could determine the factors which trigger the *E. lineata* larvae to leave its host and to settle. This would also lead to a better understanding and prediction of the erratic occurrence of the northern variant of seabather's eruption in the United States (Freudenthal & Joseph, 1993).

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