

## Parasitic anemone infects the invasive ctenophore *Mnemiopsis leidyi* in the North East Atlantic

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Received: 3 January 2008 / Accepted: 27 July 2009 / Published online: 4 September 2009  
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**Abstract** We report of the first finding of parasitic sea anemone larvae infecting the invasive ctenophore *Mnemiopsis leidyi* in the North East Atlantic. Parasitic anemone larvae are common in the native habitat of *Mnemiopsis*, but have not previously been reported from any of the locations where *Mnemiopsis* has been introduced. General morphology and 18S rRNA sequences support the identification of the larvae as *Edwardsiella* sp. Excised anemone larvae were reared through metamorphosis and confirmed the identification of the parasite. Both *Mnemiopsis* and *Edwardsiella* larvae were monitored weekly during 2007 and 2008 and parasitic larvae were recorded from September to November both years. The highest density was observed in September 2008 when *Edwardsiidae* larvae reached  $2.3 \text{ ind m}^{-3}$ . In 2008 total density of the parasite occasionally exceeded 40% of the host density and the potential consequences for *Mnemiopsis* population dynamics are discussed.

**Keywords** *Mnemiopsis leidyi* · *Edwardsiella lineata* · *Edwardsiella carnea* · Enemy release hypothesis · DNA barcoding · Invasive species

### Introduction

The ctenophore *Mnemiopsis leidyi* (Agassiz) was originally described from the North American east coast but was accidentally introduced to the Black Sea in the 1980s, and subsequently spread to adjacent waters in the Mediterranean (Shiganova et al. 2001b). In the Baltic Sea, *Mnemiopsis* was first recorded in 2006 near Kiel (Javidpour et al. 2006) and shortly thereafter in the North Sea (Boersma et al. 2007; Faasse and Bayha 2006) and the Skagerrak (Hansson 2006). Upon introduction, *M. leidyi* often demonstrates rapid population growth, e.g., in the Black Sea (Vinogradov et al. 1989), and has been associated with negative effects on e.g., the recruitment of commercial fish stocks due to extensive predation on the zooplankton community (Purcell et al. 2001). The successful establishment of *M. leidyi* in new habitats has been attributed to the lack of natural enemies in exotic habitats (Purcell et al. 2001). In the Black Sea, this was further supported when *M. leidyi* decreased upon the introduction of yet another ctenophore, *Beroe ovata*, that feeds on *M. leidyi* (Shiganova et al. 2001a).

Similar to in the Black Sea, *M. leidyi* reached high densities in the Skagerrak after it had been discovered

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(Hansson 2006). There are some potential predators in the area e.g., the Scyphozoan jellyfishes *Cyanea capillata* and two of the native ctenophore species; *Beroe cucumis* and *B. gracilis*. *Cyanea capillata* was commonly found together with *M. leidy* during the *M. leidy* population peak in 2007, but was not observed to catch or consume visible specimen of *M. leidy* (personal observation E.S.). *Beroe* sp. occurred during 2006 (Hansson 2006) but was rarely recorded together with *Mnemiopsis* in 2007 and 2008. Thus, it is possible that the enemy release phenomenon contributed to the successful invasion of *M. leidy* in the Skagerrak area. During the peak abundance of the *M. leidy* population in 2007, however, endoparasitic sea anemone larvae, was for the first time observed inside live *M. leidy*. In the native habitat of the ctenophore, parasitic infections from the sea anemone *Edwardsiella lineata* are common and parasitized *Mnemiopsis* have significantly lower, sometimes negative growth rates. Prevalence can be higher than 50% (Crowell 1976; Reitzel et al. 2007) and as a consequence parasite infection may be one of the factors that contribute to population control (Bumann and Puls 1996). Here we report of the first occurrence of parasitic sea anemone larvae in *M. leidy* from the NE Atlantic, together with densities of the parasite and the host ctenophore during 2007 and 2008.

## Materials and methods

### Collection and observations

*Edwardsiidae* larvae was first observed in situ inside *M. leidy* by SCUBA divers and subsequently included in the weekly *M. leidy* monitoring program on the Swedish west coast (N 58° 24' E 11° 24', Møller & Tiselius unpublished data). The sampling location (Fig. 1) is typically stratified due to the brackish water influence of the Baltic surface current, and salinity in the surface water is variable but averages  $23 \pm 4$  psu 95 (annual mean  $\pm$  SD; aug 2007–aug 2008 <http://www.weather.loven.gu.se>). The halocline is typically situated between 10 and 20 m depth and below 20 m the salinity is normally stable around 33 psu. Quantitative sampling of ctenophores and parasites were conducted once a week with duplicate oblique tows using a 450  $\mu$ m WP-3 net



**Fig. 1** Map showing the sample site. Monitoring station indicated by black arrow

from 20 m to the surface. Specimens of *M. leidy* and *E. lineata* were counted live.

### Metamorphosis of larvae

Approximately ten of the larger *Edwardsiidae* parasites ( $\sim 10$  mm length) were excised from the ctenophore host and placed in filtered autoclaved seawater. Most of the water was replaced every second day. A small amount of newly hatched *Artemia* naupli was added as the larvae approached metamorphosis. Juvenile anemones were fed *Artemia* naupli two to three times a week. Pictures were taken during the course of development (Nikon D80 fitted with a 55 mm micro nikkor and bellows) to document the different life stages.

### Genetic analysis

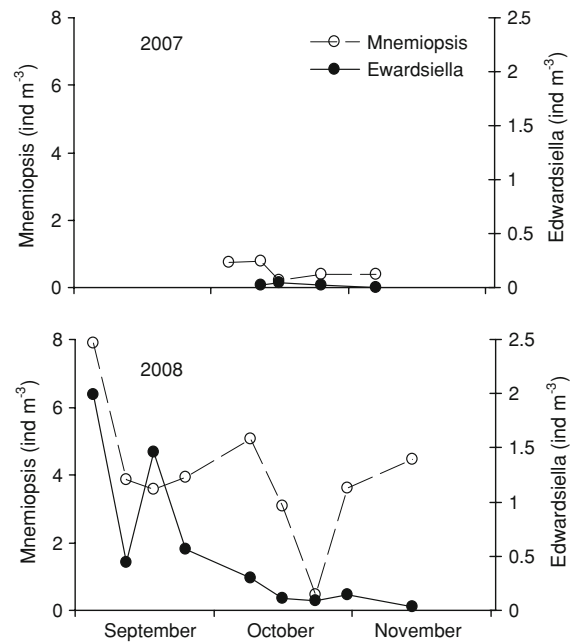
General morphology of larvae and adult anemone was complemented with genetic sequences. The 18S gene was sequenced from larvae obtained from *Mnemiopsis leidy* collected on the Swedish west coast (Genbank accession number FJ913836, voucher SMNH 105141 (Stockholm Museum of Natural History, Sweden))

and the east coast of USA (Genbank accession number FJ899707, voucher SMNH 105142), and compared with published sequences from various *Edwardsia* and *Edwardsiella* species published on GenBank. Amplification of the 18S rRNA gene was carried out by PCR using a thermal cycler (MJ Research Inc. PTC-100 Programmable Thermal Controller) and eukaryotic specific primers (Medlin et al. 1988; Turbeville et al. 1992; Nygren and Sundberg 2003). The gene was either amplified in one region of approximately 1,850 bp or in two shorter regions of approximately 1,000 bp each. PCR was performed with illustra PuRe taq Ready-To-Go pcr beds (GE Healthcare). Thermal cycling was initiated with 1–2 min of denaturation at 94–95°C followed by 35–60 cycles of 30 s at 94°C, 1 min at 44–50°C, 2 min at 72°C. After cycling the reaction was ended with an extension phase at 72° for 7 min. PCR products were purified with EZNA Cycle-Pure Kit PCR Clean-up (VWR International). Sequencing was performed by the genetic service facilities of Macrogen (Korea).

We carried a phylogenetic analysis based on maximum likelihood (in PAUP\* 4.0b10 (Swofford 2000), GTR model, unequal base frequencies (A = 0.261, C = 0.203, G = 0.268, T = 0.268). The phylogeny is based on an alignment (trimmed ends) of 1,666 bp (19 parsimony informative) of the sequenced (supposedly) *Edwardsiella lineata* (above) larvae and *Edwardsia/iella* spp. 18S sequences available in Genbank to check for relatedness.

## Results

*Edwardsiidae* larvae were first observed inside free swimming *Mnemiopsis* in September 2007 (data not shown). Subsequently they were found in monitoring samples at low densities throughout October and November. The following year, 2008, *Edwardsiidae* larvae were again present from September through November and the highest density was reached in September 2008, when *Edwardsiidae* larvae densities of 2.3 individuals  $m^{-3}$  was observed (Fig. 2). Most larvae were found outside the host ctenophores in the samples, probably as a result of mechanical stress during sampling. Number of parasites per host that still had internal parasites was counted in 2008 and averaged  $2.2 \pm 2.3$  parasites  $ind^{-1}$  (mean  $\pm$  SD). The highest number of parasites observed in a single



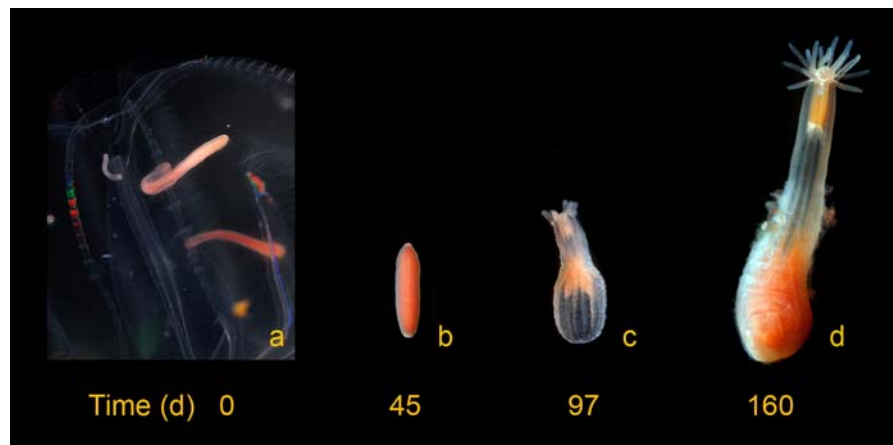
**Fig. 2** Density ( $ind\ m^{-3}$ ) of *Mnemiopsis* (open symbols) and *Edwardsiella* larvae (closed symbols) in 2007 and 2008. Data show samples where both species were found. Note the different scales on the double Y axis

*Mnemiopsis* was 11. Multiple infections may have resulted from the sampling methodology, but were also observed in the field and is well documented in the literature (Crowell 1976; Reitzel et al. 2007). During 2008, the percentage of *Mnemiopsis* with internal parasites ranged from 0 to 6.3%, and the percentage of parasites found outside hosts averaged  $50 \pm 43\%$  (mean  $\pm$  SD). As a consequence it was not possible to calculate the prevalence of the parasite accurately. Total density of the parasite, however, varied between 0 and 41.2% of the host density (Fig. 2).

Parasitized *Mnemiopsis* were also observed 100 km north from the monitoring station both in both 2007 and 2008, outside Sven Ioven center for marine sciences, Tjärnö. No quantitative samples were taken at this location.

## General morphology

Similar to *E. lineata* from the North American east coast (Reitzel et al. 2007), the larvae were most commonly found attached to the pharynx region of the *Mnemiopsis* (Fig. 3a). Figure 3b shows the free planula larva which typically becomes shorter and



**Fig. 3** Developmental stages of the parasite: Endoparasitic *Edwardsiella* larvae inside a *Mnemiopsis leidy* retrieved from the Skagerrak (a). Free *Edwardsiella* larva (b). Newly metamorphosed *Edwardsiella* sp. (c) finally the juvenile

anemone (d). Column of adult *E. lineata* is typically 10 to 30 mm long (Daly 2002). Time scale in days denote days after excision from host

thicker after leaving the host (Daly 2002). After approximately 2–3 months larvae maintained in filtered seawater settled and metamorphosed into juvenile anemones (Fig. 3c). The juveniles differentiated gradually to the 16 tentacle stage seen in Fig. 3d which was reached 5–6 months after excision. The morphology closely resemble the species *Edwardsiella lineata* and *E. carnea* as described by Daly (2002) and morphological characters alone did not lead us to a certain distinction between these two species.

#### 18S rRNA sequencing

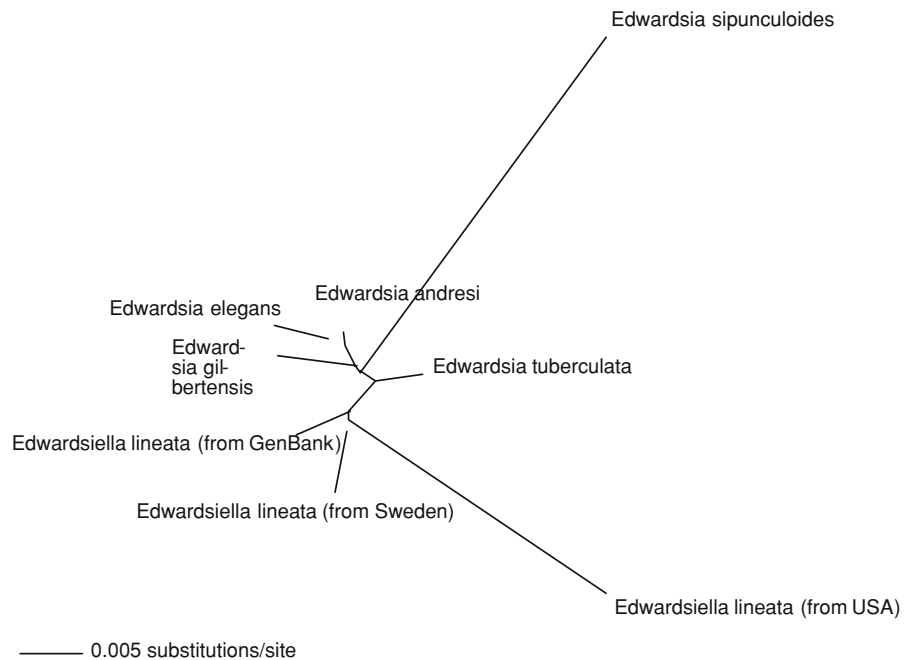
We sequenced a 1,727 bp stretch of the 18S gene. A blast search of the GenBank nucleotide database returned the highest match, 99%, with *Edwardsiella lineata*. We also sequenced a specimen of *lineata* (1,728 bp) collected in *Mnemiopsis leidy* from the USA east coast with a resemblance of 97.5 and 97.7% with the Swedish specimens (not counting insertions). The phylogeny analysis of the *Edwardsiella* and *Edwardsiella* spp. where there are 18S sequences available (Fig. 4) shows that parasite from the Swedish sample forms a clade with other *E. lineata* specimens. This supports that the larvae is of the species *Edwardsiella lineata*, although not totally conclusive evidence.

#### Discussion

This is, to our knowledge, the first report of *Edwardsiidae* endoparasites in *Mnemiopsis leidy* from a location where *Mnemiopsis* has been introduced. The successful establishment of *Mnemiopsis* in new habitats has been attributed to the lack of natural enemies (Purcell et al. 2001) and the discovery of the parasite in an exotic habitat is therefore especially interesting. Parasitic anemone larvae are common in the native habitat of the ctenophore and sometimes more than 50% of the ctenophores are parasitized by larvae from the anemone *Edwardsiella lineata* (Reitzel et al. 2007). General morphology and 18S rRNA sequences both supports the identification of the parasites found in this study as belonging to the genus *Edwardsiella*, and it is possible that *E. lineata* has followed the host across the Atlantic and established in its new habitat. The parasitic life-stage survives for extended time periods outside the host (>3 months in this study) and is able to re-infect *Mnemiopsis* upon encounter (Reitzel et al. 2007). Thus, *E. lineata* larvae may easily have survived transatlantic transport with e.g., ship ballast water, and arguably also by passive transport with the Gulf Stream.

It is, however, not possible to exclude the closely related anemone *Edwardsiella carnea*, which is naturally occurring in the study area Skagerrak. There

**Fig. 4** Unrooted phylogeny of six *Edwardsiella* species based on 18S gene sequences, and estimated by maximum likelihood (see “Material and methods”). The parasite obtained from *Mnemiopsis leidy* in Sweden forms a clade with *Edwardsiella lineata* (sequence from GenBank (AF 254378)), and identified *E. lineata* from east coast USA (collector Adam Reitzel)



is a single record in the literature (Stephenson 1935) of a similar parasite found in the ctenophore “*Bolina*” (probably *Bolinopsis infundibulum*) that was identified as “probably belonging to *Milne-edwardsia carnea*” (now *Edwardsiella carnea*). *Bolinopsis infundibulum* is a native lobate ctenophore that resembles *M. leidy* closely (see Faasse and Bayha 2006 for comparison). This observation should, however, be viewed with some caution; if you are not aware of *E. lineata* and *M. leidy*, they can easily be mistaken for *E. carnea* and *B. infundibulum*. The morphological differences between especially *E. carnea* and *E. lineata* are deceitfully small. In a systematic revision of the *Edwardsiidae*, Daly (2002) report of two out of 60 characters examined to be different: the number of tentacles in the second cycle is fewer (6) in *E. carnea* than in *E. lineata* (12), and the mesentery microanatomy is slightly different as the retractor muscle branch arrangement is graduated towards the coelenteron in *E. lineata* and graduated on both sides in *E. carnea* (Daly 2002). Based on the material we were able to compare, with individuals that had not developed their final number of tentacles, we were not able to distinguish between *E. carnea* and *E. lineata*. We managed to get a shorter stretch of the 18S gene for an adult which had been identified as *E. carnea*. Since it was around 500 bp shorter we did not include it in the phylogenetic analysis above.

However, aligning it with the other sequences and carrying out a provisional analysis shows a close relationship with *lineata*. Together, these results raise the question whether *E. carnea* and *E. lineata* really are separate species or not.

The lack of good characters and the rapidly changing morphology of early developmental stages of marine larvae often make it exceedingly difficult to identify them to species level. It is sometimes necessary to rear larvae through metamorphosis to allow morphological characters to develop. DNA barcoding based on mtDNA COI could offer a convenient alternative to the identification of larvae and cryptic species, but it requires a suitable sequence is widely available for the group of interest. However, COI typically evolves an order of magnitude slower in Anthozoans compared to most other metazoan taxa and is probably not a suitable general marker for Anthozoans (Neigel et al. 2007 and references therein). Furthermore, we have not been able to obtain good COI sequences from the material despite several attempts using various protocols but it is clear that sequencing more genetic markers from *E. lineata* and local species of closely related sea anemone will resolve the taxonomic relationship between *E. lineata*, *E. carnea* and the *Edwardsiella* sp. found here.

The phylogeny in Fig. 4 shows a close relationship between *Edwardsia tuberculata* and *E. lineata*. This

species is also present in the Skagerrak area but does to our knowledge not have parasitic larvae and is morphologically distinct from *E. lineata* and *E. carnea* (Daly 2002).

*Edwardsiidae* endoparasites have not been reported from other locations where *Mnemiopsis leidyi* has been introduced. For example the Black Sea, where *M. leidyi* established in the early eighties, no *E. lineata* seems to exist and it is believed that the absence of both predators and parasites could have contributed to the development of *M. leidyi* in the Black Sea (Anninsky and Abolmasova 2000). The Black Sea has got low salinities <23 psu, and lower in the surface, and it is possible that this is too low to support the adult stage of *E. lineata*. It is, however, likely that the parasite will be spread be found in adjacent seas where *Mnemiopsis* has established, e.g., the duch part of the North Sea, which has hydrographical conditions resembling the native habitat of the parasite and the Skagerrak more closely.

Reitzel and coworkers (Reitzel et al. 2007) have found a high prevalence of the parasite in *Beroe ovata*, another ctenophore species. The parasites present in *B. ovata* were probably transferred from infected prey as *B. ovata* was not infected by *E. lineata* in laboratory experiments. Furthermore, *B. ovata* had smaller *E. lineata* parasites that required longer time to metamorphose compared to parasites from *Mnemiopsis* (Reitzel et al. 2007). It is likely that the occurrence of *E. lineata* in *B. ovata* is a case of incidental transmission rather than true parasitism (Bumann and Puls 1996). Nevertheless, it can not be excluded that *E. lineata* may parasitize some of the native ctenophores in the Skagerrak, and it would be desirable to find out if the local species of ctenophores; *Bolinopsis infundibulum*, *Beroe cucumis*, *B. gracilis* and *Pleurobrachia pileus* are susceptible to parasitism. Although none of the more than 600 *P. pileus* investigated in Great Harbor in Woods Hole, Massachusetts, USA, by Reitzel et al. (2007), harboured parasites.

It is hard to predict what effect this new parasite will have on the population dynamics of the host *M. leidyi*. On one hand, Bumann & Puls (Bumann and Puls 1996) found that the growth rate decrease, often to negative values in infected *Mnemiopsis*. Parasite infection had no detectable direct effect on fecundity, but due to the relationship between size and fecundity in *Mnemiopsis*, Buman and Puls calculated ~50% decrease in fecundity of infected *Mnemiopsis* after

2 days of infection and ~80% decrease after 7 days of infection compared to uninfected individuals. It is not known to what extent fecundity controls the population development in *Mnemiopsis*, but Bumann and Puls (1996) suggested that high prevalence of *Edwardsiidae* parasites may contribute to the rapid decline of the *Mnemiopsis* population during fall in the US coastal waters. Native populations of marine invasive species typically have more than twice as high prevalence of parasites and three times higher parasite species richness compared to introduced populations (Torchin et al. 2002). Thus, it is likely that the *Edwardsiidae* parasite found here will reduce the enemy release effect on *M. leidyi* in the Skagerrak area. However, if the parasite infects the native ctenophores known to feed on *M. leidyi*, e.g., *Beroe* spp. the effect might be the opposite. *Edwardsiella lineata* has been suggested as one of the possible biological control organisms available to counteract the negative effects of *M. leidyi* in exotic habitats, but as pointed out by Reitzel and colleagues (Reitzel et al. 2007) as well as Daly (2002), risk assessment of such a measure is not an easy task. The occurrence of *Edwardsiella* larvae on the Swedish west coast may provide additional information on the impact of *Edwardsiella* on *Mnemiopsis* population dynamics as well as non-target organisms. Another important aspect of the occurrence of *Edwardsiella* sp. on the Swedish West Coast concerns the recreational value of the area. Planula larvae of *E. lineata* has been linked to “sea bathers eruption” a skin irritation that sometimes causes North American beaches unfit for swimming (Freudenthal and Joseph 1993).

In conclusion, endoparasitic anemone larvae infecting the invasive species *Mnemiopsis leidyi* has been found in the North East Atlantic. Further studies are, however, needed to sort out the taxonomic relationship between the observed *Edwardsiella*, *E. lineata* and *E. carnea*. It is is likely that the *Edwardsiidae* parasites will reduce the enemy release effect on *Mnemiopsis*, and it is also likely that the parasite will be found in adjacent seas hosting the *Mnemiopsis* in a near future.

**Acknowledgments** We thank Hans G Hansson, Dep. Marine Ecology, University of Gothenburg, for information on sea anemones in the Skagerrak, and Adam Reitzel for supplying specimens of *Edwardsiella lineata* from USA. Financial support was provided by FORMAS through contract number 223-2007-1809 and the BONUS+ project BAZOOCA

(FORMAS contract number 210-2008-1882) to PT and LFM, grant 272-06-0241 from the Danish Agency for Science, Technology and Innovation to LFM, EU Marie Curie “lidpop” to ES, and the Swedish Research Council (to PS).

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