Journal of Experimental Marine Biology and Ecology 446 (2013) 209–215

Contents lists available at SciVerse ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Influence of infection by *Sacculina carcini* (Cirripedia, Rhizocephala) on consumption rate and prey size selection in the shore crab *Carcinus maenas*

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ARTICLE INFO

Article history:
Received 26 March 2013
Received in revised form 30 May 2013
Accepted 31 May 2013
Available online 20 June 2013

Keywords:
Community structure
Feeding behavior
Feminization
Host–parasite interaction
Mytilus edulis
Parasitism

ABSTRACT

Parasites generally influence the feeding behavior of their host and may therefore indirectly impact ecosystem structure and functioning if the host plays an ecological key role. The ecologically important shore crab (*Carcinus maenas*) is commonly infected by the rhizocephalan parasite *Sacculina carcini* that aside from inflicting behavioral change, castration and ceased molting, also feminizes its male host morphologically. The latter results in reduced cheliped size, and, together with the other parasite-induced effects, this may potentially impact host feeding behavior. In two separate laboratory experiments, we offered infected and uninfected adult male crabs respectively ad libitum small, easy-to-handle blue mussels (*Mytilus edulis*) (10–15 mm in shell-length), and a limited, size-structured prey population (15–45 mm in shell-length; seven size-classes, ten mussels per class) during 10–15 days. Corrected for carapace width, the per capita consumption rate of the infected and uninfected crabs was similar in either experiment, both regarding number of mussels and amount of tissue dry-weight consumed. Also, the median mussel size preyed upon when exposed to the size-structure prey population was unaffected by infection. However, infected crabs preyed less frequently (26%) on intermediate mussel sizes (25–30 mm) than uninfected crabs. For both infected and uninfected crabs the median prey size increased linearly with maximum claw height. Host dry weight was significantly reduced by infection, assumed to be the result of the morphological feminization (reduced appendage size) rather than reflecting poorer general condition of infected individuals. Infected crabs were nonetheless subjected to a higher mortality rate than uninfected crabs during the experimental period. We conclude that *Sacculina* infection has a very limited effect on its host crabs' feeding biology and that any measurable ecosystem ramifications of the host–parasite association must originate from other processes; for instance reduced mean size (infection inhibits molting) and density (infection increases mortality) of the crab population where parasitism is high.

1. Introduction

Parasites are ubiquitous components of marine environments with the potential to affect the behavior, energetic requirement, condition, reproduction and survival of their hosts (Lafferty and Kuris, 2009; Moore, 2002; Mouritsen and Poulin, 2002; Sousa, 1991). If the host is a keystone species or otherwise ecologically dominant, such host–parasite interactions may ultimately influence the organization and functioning of coastal communities (Mouritsen and Haun, 2008; Mouritsen and Poulin, 2002, 2010; Wood et al., 2007).

The shore crab, *Carcinus maenas* (Linné, 1758), is a widely distributed and often abundant epibenthic predator that inhabits intertidal soft and hard bottom habitats of European coasts and estuaries. It was inadvertently introduced to the Atlantic coast of North America in the early 19th century and has since then colonized some regions of Japan, Australia, Argentina, South Africa, Tasmania and western North America (see Darling et al., 2008). Throughout its distributional range, the shore crab is an ecologically influential species in benthic communities, particularly as a consequence of its feeding ecology (Grosholz and Ruiz, 1995; Grosholz et al., 2000; Reise, 1985). The diet of the shore crab consists of a variety of invertebrate species as well as teleosts and macroalgae, but it often exhibits a preference for bivalves, particularly thin-shelled species such as the blue mussel (*Mytilus edulis*) (Baeta et al., 2006; Lee and Seed, 1992; Mascaró and Seed, 2001; Raffaelli et al., 1989; Reid et al., 1997). Because the crab also prefers certain bivalve size classes, it may impact not only the abundance but also the size distribution of bivalves (Burch and Seed, 2000; Elner and Hughes, 1978; Mascaró and Seed, 2001).

The shore crab serves as host for the rhizocephalan barnacle *Sacculina carcini* Thompson, 1836. Cyprids of *S. carcini* settle on the crab cuticle, penetrate into the hemocoel and develop an internal

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http://dx.doi.org/10.1016/j.jembe.2013.05.029

root-like network (interna) throughout the tissue of the crab. On maturation, a part of the interna ruptures the crab's abdominal exoskeleton and forms a saclike structure (externa) containing the reproductive organs of the parasite (Høeg and Lützen, 1995). The infection prevalence of *S. carcini* in the shore crab population show great spatio-temporal variation usually ranging between a few to 20%, and can locally even reach 40–90% (Lützen, 1984; Mathieson et al., 1998; Rasmussen, 1973; Torchin et al., 2001; Werner, 2001; Zetlmeisl et al., 2011; unpublished data).

S. carcini infects and castrates both sexes of *C. maenas* and inhibits molting (Høeg, 1995), reduces general condition (Mouritsen and Jensen, 2006) and increases the mortality rate of infected crabs (Goddard et al., 2005). In addition, male shore crabs generally become behaviorally and morphologically feminized, the latter involving also a reduction in cheliped size (Høeg, 1995; Kristensen et al., 2012; Lafferty and Kuris, 2009; Mouritsen and Jensen, 2006).

Given the ecological important role of shore crabs in benthic communities it is crucial to understand whether and to what extent parasitism alter the feeding biology of the crab, of which nothing is presently known. This is further underlined by the fact that *S. carcini* has never been introduced together with its hosts during shore crab invasions outside Europe (Thresher et al., 2000).

Parasitism generally affects the feeding behavior of hosts (Moore, 2002) and because infection by *S. carcini* results in reduced size in the claws of male crabs, a decisive part of the feeding apparatus, this parasite can potentially have a profound impact on its host's foraging behavior. Hence, the aim of the present investigation was to evaluate the impact of *S. carcini* infections on the consumption rate and prey size selection by male shore crabs, *C. maenas*, using blue mussels, *M. edulis*, as prey.

2. Materials and methods

During August–October 2011, two indoor mesocosm experiments were performed at Rønbjerg Marine Biological Station, Limfjorden, Denmark (56°53′27″N, 9°9′57″E). The first experiment, carried out between 28th August and 7th September (10 days), examined the consumption rate of uninfected and *Sacculina* infected male shore crabs *C. maenas* on blue mussels *M. edulis*. The second experiment, carried out between 4th and 19th October (15 days), was designed to determine the preferred mussel size classes eaten by uninfected and *Sacculina* infected male crabs, respectively. Solely male hosts were used in the experiments because only this gender becomes morphologically feminized by the infection. Female *C. maenas* do not develop super-feminization as a result of *S. carcini* infection (e.g., Kristensen et al., 2012).

2.1. Collection and storage of experimental animals

In *S. carcini* the time of development from larval infection to adult parasite lasts about a year, and it was therefore impractical to produce infested crabs experimentally (Høeg, 1995; Werner, 2001). Specimens of *C. maenas* were collected during June–September 2011 at several locations in the Limfjord using pots and eel traps. These were baited with frozen or fresh fish and typically deployed for 24 h at depths ranging from 1 to 7 m. In the laboratory, uninfected and *Sacculina* infected crabs were sorted out and stored separately until commencement of the experiments. Infection status was determined by the presence or absence of an *S. carcini* externa located on the ventral surface of the crab's abdomen. The externa contains the female reproductive system and two cryptic dwarf males (Høeg, 1995). The shore crabs were stored in containers submerged in large basins with continuously running seawater at ambient temperature and fed crushed blue mussels ad libitum. Crabs were held under these conditions for at least one week prior to experimentation. Only undamaged male crabs were used in the experiments (no missing limbs and no visual damage to the body cuticle). Only crabs hosting sexually mature *S. carcini* externae were selected for the experimental units with infected crabs (see below). The mature externa of *S. carcini* appears as a sac-like structure, pale yellow to orange/light brown in color and typically measuring between 13 and 18 mm in maximum width (Lützen, 1984) (Fig. 1).

Blue mussels, *M. edulis*, were sampled August–September 2011 from a long-line aquaculture situated in the Limfjord. This ensured homogenous shell characteristics and flesh content among the applied mussels. The mussels were maintained in large tanks with well-aerated running seawater at the same water temperature and light regime as the crabs. The mussels were stored in the tanks for a maximum of 3 weeks prior to the experiments.

2.2. Consumption rate

A 15 L rectangular plastic container (34 × 26 × 17 cm; length × width × height) served as the experimental unit in which shore crabs and blue mussels were established. Each unit was covered with a lid to prevent crabs from escaping during the experiment and supplied with 2 cm beach sand, rinsed and sieved through a 1 mm screen, and its own seawater supply (27–30‰) at a flow rate of 0.3 L min^{-1}. Three centimeters below the top of the container, a small hole (0.3 cm^2) served as water outflow. The outflow was placed at the opposite end of the influx of water to allow water flow through the container, thus yielding an effective exchange of water during the experiment. The setup had a water depth of 12 cm and a water retention time of ca. 35 min. The water temperature was measured every 30 min by submerged temperature loggers and the resulting mean temperature during the experiment was 17.0 °C (range: 16.1–18.2 °C).

Sixty experimental containers were arranged in five rows of twelve units. Thirty shore crabs of each infection status (i.e. *Sacculina* infected and uninfected) were individually added haphazardly to the containers, so that six infected and six uninfected crabs were placed in each of the five rows. The uninfected and infected crabs were matched according to carapace width (±1 mm), measured as the distance between the tips of the anterior carapace spines. The overall mean carapace width was 57.6 ± 0.4 (SE) mm (size range: 51.7–64.8 mm), and mean width did not differ between treatments (infected/non-infected crabs; Student's *t*-test, $t_{58} = 0.023$, $p = 0.982$). Crabs were starved for 24 h in the experimental containers prior to the addition of blue mussels to standardize hunger levels. In

Fig. 1. Ventral view of a shore crab (*Carcinus maenas*) infected by the rhizocephalan *Sacculina carcini*, showing an adult externa (containing the parasite ovary) below the abdomen of the host. Photo: Sissel N. S. Geyti.