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Assessing parasite community structure in cockles *Cerastoderma edule* at various spatio-temporal scales

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ABSTRACT

Cockles (*Cerastoderma edule*) are among the most exploited bivalves in Europe. They live in lagoons and estuaries where they undergo many stressors including parasites. Trematodes are the most prevalent macroparasites of cockles and can exert a significant impact on their host populations depending on parasite species and infection intensity. Monitoring these parasite–host systems in order to predict potential host mortalities require a correct knowledge of the spatio-temporal variation of infection.

A yearly monitoring of cockles from six stations around Ile aux Oiseaux, Arcachon Bay (France) was conducted between 1998 and 2005. Distance between two stations was ca. 1 km. Nine trematode species were identified. Despite a relative homogeneity of the parasite community structure in cockles, between three and six clusters were identified by Hierarchical Ascendant Classification showing that among-sites heterogeneity of trematode communities in cockles was higher than within-site heterogeneity. At the scale of 8 years, and for 2-year old cockles, these patterns remained stable in four out of six stations. Spatial aggregation disappeared with cockle age, since parasite communities in 3-year cockles did not reflect any particular station(s): with age, cockles eventually accumulated most trematode species and lost the site signature. On the other hand, we demonstrated that the commonly accepted theory stating that older/larger cockles accumulate more trematode larvae was not verified and that there could exist a vulnerable age/size that doesn't correspond to largest values. This study provided a new insight in the parasite community heterogeneity in their host, and in the significance of samples in relation with space and time.

1. Introduction

Knowledge of the distribution of organisms is important to understand the characteristics of ecological systems (Ysebaert et al., 2003). Aggregation is a common pattern of distribution of organisms and is often considered as the result of an active habitat choice by larvae during recruitment, and/or heterogeneity-dependent mortality after recruitment (Bourget et al., 1994). However, the notion of aggregation has a poor meaning when disconnected from scaling issues and the scale of an investigation may have great impact on the patterns of our findings (Wiens, 1989). What is true for free-living fauna is also true for parasite fauna which represent at least 40% of known species (Dobson et al., 2008) and can act as regulators for many host populations with knock-on effects on communities (Dobson and Hudson, 1986; Poulin, 1999; Thomas et al., 1999). In marine areas, molluscs are often dominant in terms of abundance and/or biomass and play a significant role in ecosystem functioning (Sousa et al., 2009). Consequently it is important to identify and understand factors that modulate their dynamics in a large set of ecosystems. For biotic factors, besides competition, predation and facilitation, parasitism can be a key factor (Thomas et al., 1997). The way parasites infect their host tissues can be compared to recruitment in free-living species, host and tissues being special habitats with intrinsic constraints like immune defences. Among macroparasites, digenean trematodes are particularly prevalent in mollusc communities (de Montaudouin et al., 2009). Adults live and reproduce in a vertebrate host (final host) which sheds parasite eggs with its faeces. The eggs develop in miracidium larvae (free-living stage) that will infect a molluscan 1st intermediate host. In the host tissues, the larva develops into sporocysts (or rediae) which in turn produce a new kind of larva, the cercariae. These cercariae are emitted into the water body and swim to infect the 2nd

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intermediate host and become a metacercariae (latent stage). The life cycle is complete when the 2nd intermediate host is predated by the final host. The cockle *Cerastoderma edule*, a common and exploited bivalve along European and Moroccan Atlantic estuaries, lagoons and wadis, and serves as 1st and/or 2nd intermediate host for at least sixteen trematode species (de Montaudouin et al., 2009). In the present study, we will focus on cockles as 2nd intermediate hosts. The role of second intermediate host as accumulator of genetic diversity in the trematode life cycle was recently clarified (Leung et al., 2009). Even though at this stage trematodes are supposed to be less deleterious than at the 1st intermediate stage, there are some cases of metacercariae-dependent mortality in cockles (Jensen et al., 1999; Desclaux et al., 2004; Thieltges and Rick, 2006; Gam et al., 2009).

A single cockle can harbour several trematode species, each species being represented by a variable number of its metacercariae. This parasite infra-community (i.e. parasite community within a single host individual) varies among cockles according to different factors, depending on the scale of observation. Very few studies have focused on the importance of scales in understanding parasite infection processes, particularly when considering intermediate hosts. In a two-scale study, Thieltges and Reise (2007) showed that at the km scale, the density of 1st intermediate upstream hosts was the strongest determinant of infection levels in cockles, the situation within sites being more complex with no single strong predictor variables. Recently, a five-scale study showed that climate and hydrodynamics conditions explain trematode heterogeneity at large scales (>×100 m), whereas the presence and the mobility capacity of other hosts species were the key factors at smaller scales (10 m–1 cm) (de Montaudouin and Lanceleur, 2011).

The main contribution of the present work is to provide new insights to this poorly investigated field which is the spatial epidemiology of coastal ecology. To do so, six stations around an island in the middle of Arcachon Bay were selected. The landscape is very homogeneous with a sandy area harbouring a low-density cockle population surrounded by salted marshes at the upper level and a *Zostera noltii* seagrass bed on the lower intertidal site. We compared the similarity of parasite infra-communities within each site to the similarity between sites (two-scale analysis) to see if aggregation was still the rule in such an (apparently) homogeneous habitat. Beyond spatial heterogeneity, this study aimed to assess the stability of spatial patterns (in terms of parasite communities in cockles) over time. There are two main ways to study temporal heterogeneity of infection. First, the investigation can be performed at constant ‘length-class’ and sampling date to privilege the variability of the surrounding environment while cockles characteristics are more homogeneous (same age, same stage within the reproductive cycle). Consequently, we sampled the five stations, always in May and during eight consecutive years. Secondly, temporal variability can be estimated through the monitoring of a given cockle cohort through time. This approach emphasises the effect of cockles’ parameters (age and associated variables like size, maturity, etc). The general agreement is that old/larger the bivalves are, more infected they become because they had longer period to accumulate parasites (i.e. probability to encounter them is higher) and also because large bivalves filtrate larger volumes of water which is the vector of infection (i.e. cercariae enter their bivalve hosts predominantly via the filtration current) (Wegeberg et al., 1999; Mouritsen et al., 2003). However, in the field, most of the time it is impossible to assess the only effect of size (shell length). Hosts gain more infections during the summer every year (cercariae maturation in first intermediate hosts and their emission from these hosts necessity relatively warm sea temperatures). Since they also grow larger every year, it may be misleading to consider size as a strong predictor of infection levels. If two different cohorts are compared, the oldest cockles have already been accumulating parasites during the previous year(s). In October 2003, on exceptional autumnal cockle recruitment occurred in Banc d’Arguin, a sandflat at the entrance of Arcachon Bay. Considering that there is no cockle infection during winter, we obtained two cockle cohorts the next spring, both free of trematodes: the October 2003 cohort with relatively large individuals (22 mm in July 2004) and the newly settled cohort (May 2004) with 8-mm shell length cockles in July 2004. Infection success could then be compared between two length-classes with no *a priori* infection as confounding factor.

2. Materials and methods

2.1. Study site

Arcachon Bay (44°40′N; 1°10′W) is a macrotidal, 182-km^2 coastal embayment on the Atlantic coast of south-western France where tidal flats occupy 115 km^2. Tides are semidiurnal with a range from 1.10 to 4.95 m. The main monitoring campaign was conducted at Ile aux Oiseaux, while the assessment of trematode infection according to cockle length was performed at Banc d’Arguin. Ile aux Oiseaux is the only island of Arcachon Bay. At high tide, the surface is only 0.44 km^2, but at low tide a vast flat is exposed (17 km^2). The lower level of this flat is muddy and covered with a *Z. noltii* seagrass. Our six stations were localised on the upper levels (+2.6 m above chart datum, 50% immersion time) that are often covered by medium sands (median grain size = 370 μm) and colonised by lugworms (*Arenicola marina*) and cockles (*C. edule*).

A side-monitoring was performed at Banc d’Arguin. This nature reserve is situated at Arcachon Bay entrance, in oceanic position (Fig. 1). The sampling site is a moderately sheltered intertidal flat (medium sands) where many previous studies on cockle/trematodes interactions have recently been performed (Gam et al., 2009; de Montaudouin and Lanceleur, 2011).

2.2. Sampling strategy and data analysis

2.2.1. Spatio-temporal variability of cockle infection at Ile aux Oiseaux

Between 1998 and 2005, in May, six stations, regularly located around Ile aux Oiseaux (Fig. 1), were sampled for cockles. In this area, cockle abundance is low with usually less than 10 cockles/m^2 (preliminary survey). Individuals were collected by hand. Cockle age was estimated by comparing their shell length to growth curves provided by G. Bachelet (unpublished data). One-year cockles were small and hardly infected, and cockles over 3 years were rare and difficult to age. Then, we focused on the 2-years old cockles and, to a lesser extent, the 3-years old cohort. All cockles were dissected (between 5 and 20 individuals per occasion depending on availability in the given cohort, with a mean of 12.5 individuals per occasion), trematode metacercariae were identified and counted. References for identification are reported in a previous review (de Montaudouin et al., 2009). Parasite abundance was defined as the average number of a given parasite species (metacercariae) per cockle from a given cohort (Bush et al., 1997).

In 1998 and 1999, a concomitant sampling of mudsnails *Hydrobia ulvae* potential upstream first intermediate host of trematodes infecting cockles (*Himasthla interrupta*, *Himasthla continua*, *Psilostomum brevicolle*) was performed. At each station, mudsnails were sieved with a 2-mm mesh in order to capture the highest probable number of infected individuals (de Montaudouin et al., 2003). Sixty mudsnails per station were dissected for