

Cockle emergence at the sediment surface: 'favourization' mechanism by digenean parasites?

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ABSTRACT: The aim of the present work was to assess the effect of digenean trematodes on indirect mortality of the cockle *Cerastoderma edule*, an infaunal bivalve. The tested hypothesis was that parasites altered the burrowing capacity of cockles and thus exposed them at the sediment surface, where they are more vulnerable to predators. If the predator is the final host, this mechanism, which drives the cockle out of the sediment, is considered as a 'favourization'. Cockle populations from 2 stations in Arcachon Bay (France)—Banc d'Arguin (oceanic situation) and La Canelette (lagoonal situation)—were sampled for 1 yr. At La Canelette, monitoring every 2 d showed that 50% of adult cockles regularly migrated to the sediment surface at a rate of 5 cockles m⁻² yr⁻¹ and disappeared in a few days. In the laboratory, 67% of these 'surface cockles' did not burrow again, suggesting that they would die in the field. Moreover, mortality measured after 7 d in the laboratory was 2 to 5 times higher than mortality of 'buried cockles', at both stations and particularly during summer. Species richness and abundance of digeneans from both stations were compared in 'buried' and 'surface' individuals to determine whether parasites played a role in cockle migration and mortality. Ten and 9 digeneans were found at Banc d'Arguin and La Canelette, respectively, with *Himasthla quissetensis* and *Labratrema minimus* being the most prevalent and abundant species at both stations. The abundance of *H. quissetensis* was slightly higher in surface cockles at Banc d'Arguin, but the difference fluctuated with station and cockle age (or size). *L. minimus* prevalence was only higher in surface cockles at La Canelette. In the latter station, we estimated that *L. minimus* and *H. quissetensis* were responsible for the emergence of 9 and 2%, respectively, of the buried cockles. Although this favourization mechanism may induce some mortality in cockles, it does not alone explain the magnitude of the observed mortalities (41 and 57% at La Canelette and Banc d'Arguin, respectively). A correspondence analysis did not show the presence of a particular parasite community in buried or surface cockles, which could explain these high surface cockle mortalities in association with the 2 dominant digeneans.

KEY WORDS: Digeneans · *Cerastoderma edule* · Favourization · Mortality · Population dynamics

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INTRODUCTION

Parasites are omnipresent, and every animal or vegetal species can undergo a more or less specific parasitic attack. They have attracted considerable attention of medical helminthologists but parasitism as a regulation process of marine invertebrate populations has yet received little attention from ecologists.

In marine invertebrates, digeneans are the most common metazoan parasites. Several debilitating effects have been reported at the host-individual level. The main effects are castration of the host (Feral et al. 1972, Mouritsen & Jensen 1994, Gorbushin 1997), alteration of growth (Huxham et al. 1993, Gorbushin 1997, Poulin et al. 1998, Gorbushin & Levakin 1999), locomotion deficiency or modification of burrowing behaviour (Bartoli 1976, Lauckner 1983, 1984, Bowers et al. 1996, Poulin et al. 1998, Jensen et al. 1999), a decrease in resistance to environmental stress (Micha-

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elis 1979, Lauckner 1983, 1987a, Brown & Pascoe 1989, Wegeberg 1998, Lafferty & Kuris 1999). In contrast, studies on the impact of parasitism at the host-population level remain rare (Sousa 1991, Jonsson & André 1992, Mouritsen & Jensen 1997, de Montaudouin et al. 2000) and are generally focused on exploited bivalves (Hancock & Urquhart 1965, Seed & Brown 1978, Lauckner 1983, 1984).

The common cockle *Cerastoderma edule* (L.) is a dominant, exploited bivalve mollusc in intertidal and shallow marine areas along the northwestern European coasts and estuaries, ranging in latitude from the Barents Sea to Morocco (Tebble 1966). Its population abundance and biomass fluctuate greatly in space and time (Ducrotoy et al. 1991) but the causes of this variability are not yet completely understood (Jensen 1992). Mortality of adult cockles has often been ascribed to predation by epifauna (Sanchez-Salazar et al. 1987a,b) or coastal birds (Hancock & Urquhart 1965, Seed & Brown 1975), sedimentary movements (Deltreil & His 1970, Dewarumez 1983, Desprez et al. 1987, de Montaudouin 1995) or dystrophic crisis (Rosenberg & Loo 1988, Desprez et al. 1992). Although frequent in intertidal bivalves, parasitism has rarely been identified as a source of mortality in cockles (Deltreil & His 1970, Jonsson & André 1992). Because most parasites do not leave any marks on the shells of their bivalve host, it is impossible to assess *a posteriori* their responsibility in bivalve mortalities.

Nevertheless, parasites can act directly on cockle mortality (Deltreil & His 1970, Jonsson & André 1992) or indirectly by modification of the host behaviour to increase the probability for larval stages to encounter their host-target (Combes 1980, 1991, Moore & Gotelli 1990, Poulin 1995). Few cases of massive direct mortalities have been reported for cockles (Michaelis 1979, Jonsson & André 1992), or for gastropods and corophid amphipods (Lauckner 1987a, Jensen & Mouritsen 1992). According to Combes (1995), such direct mortalities can be considered as 'additive' mortalities, i.e. mortalities added to other causes (predation, diseases, etc.), while indirect mortalities are considered as 'compensatory' mortalities, where parasitism induces mortality in weakened individuals and indirectly influences the predation of individuals which would probably die for other reasons. In the latter case, parasites increase the chances of infesting the final host by trophic transmission. Combes (1980) used the French term 'favorisation' to define the whole process that enhances a host encounter. Many authors described these mechanisms of 'favourization' as an alteration of host behaviour (Holmes & Bethel 1972, Bartoli 1976, Helluy 1983, Lauckner 1983, Dobson 1988, Moore & Gotelli 1990, Curtis 1993, Kuris 1997, Poulin et al. 1998, Thomas & Poulin 1998, Jensen et al. 1999). Neverthe-

less, recent studies were at variance with this favourization hypothesis. For instance, after Swennen (1969) and Swennen & Ching (1974) correlated crawling tracks of *Macoma balthica* with trematode infection, Mouritsen (1997) showed that this infaunal bivalve could crawl at the sediment surface (thus becoming more vulnerable to predation) without being parasitized.

In this study, we focused on cockles and digeneans. Digeneans are parasites with a complex life cycle. Cockles are their primary or intermediate hosts (according to the parasite species) and cockle predators (shorebirds) are the final hosts.

The aim of the present investigation was to determine whether digenean parasites could affect cockle populations through the mechanism of favourization, i.e. by increasing the chance for cockles to be accessible to their predators. Three aspects were developed in the following study. The first was to quantify the movement of cockles from within the sediment to the sediment surface. The second consisted in the comparison of cockle health among individuals found at the sediment surface and cockles found in their normal position, i.e. buried in the sediment. Thirdly, the relation between parasite infection (abundance and prevalence) and cockle position (surface or buried) was investigated.

MATERIALS AND METHODS

Study areas. Two cockle populations were studied in Arcachon Bay (44° 40' N, 1° 10' W), a 156 km² macrotidal shallow embayment on the southwestern Atlantic coast of France (Fig. 1).

The first site, 'Banc d'Arguin', was situated in the most oceanic part of the bay with a constant salinity (34 to 35 psu) and a water temperature which varies seasonally between 9.5 and 21°C. The second site, 'La Canelette', was in a more lagoonal situation, in the eastern part of the bay; this station is characterized by a salinity range of 22 to 32 psu and a water temperature that fluctuates seasonally between 1 and 25°C (Auby et al. 1999).

Banc d'Arguin sediment consists of medium sand (median grain size = 360 µm) with 3.5% silt and clay and 1.0% organic matter (de Montaudouin 1996). A cockle population is located at 1.9 m above chart datum (CD). This site is a nature reserve with the largest European population of Sandwich tern and many wintering birds such as gulls, oystercatchers, and dunlins (Campredon 1976). La Canelette is a medium sandflat (median grain size = 225 µm) with 5.5% silt and clay and 0.7% organic matter in the sediment. The sampling area is situated at 2.7 m above

CD. The lower part of the flat is colonized by a *Zostera noltii* bed. This site is localized near Arcachon harbour and its petrol station. As a consequence, heavy metals and TBT may be encountered (Carruesco et al. 1986).

Sampling procedures. Estimation of cockle emergence at the sediment surface: Whereas cockles normally live within the sediment, living individuals are sometimes observed at the sediment surface of intertidal sandflats. To quantify the emergence of cockles at the sediment surface, the cockle population at La Canelette was surveyed every 2 d between January 1999 and January 2000.

The cockles present at the surface of the sediment ('surface cockles') were always collected inside the same 1920 m² area. Sampling was performed with 4 different sampling steps. The total area was divided into 4 similar adjacent subareas (12 × 40 m each), each with a different sampling interval, namely 2, 7, 14, and 28 d. Every 4 wk, the sampling steps in each zone were changed to maintain the stability of the whole cockle population in both space and time.

Capability of 'surface cockles' to burrow again: In the laboratory, 8 transparent plastic aquaria (23 × 17 × 9 cm) with a 4.5 cm layer of defaunated sediment were immersed together in a large aquarium under a constant current of seawater, saturated in oxygen and under natural photoperiod (14:10 h light:dark at this time of the year [27 April 1999]), at room temperature (14.7 ± 0.2°C). In 4 aquaria, 10 surface cockles (shell length: 24 ± 3 mm [±SD]) from La Canelette were placed at the sediment surface of each aquarium. In the other 4 aquaria, the same treatment was applied to 'buried cockles' (shell length: 22 ± 3 mm) collected at the same site. Twelve hours later (a tidal cycle), cockles found at the surface of the sediment were counted and all cockles (80) were dissected.

The abundance of *Himasthla quissetensis* (= the dominant digenean) in buried cockles which buried again during the experiment and in surface cockles which remained at the sediment surface was compared using a 1-way ANOVA (Sokal & Rohlf 1981). Previously, normality was assumed and homogeneity of variance was verified with Cochran's test (Winer 1971).

Cockle mortality and intensity of parasite infection: Cockle populations at Banc d'Arguin and La Canelette were sampled at monthly intervals from January 1999 to December 2000. The health of surface and buried cockles at the 2 sampling sites was assessed by comparing their mortality rate and parasite load. Freshly collected surface and buried cockles, of similar size and in equal numbers, were maintained separately in the laboratory, in running seawater for 7 d at ambient temperature. During this period, all dead cockles (with valves gaping) were immediately dissected and counted. At the end, the surviving individuals were all

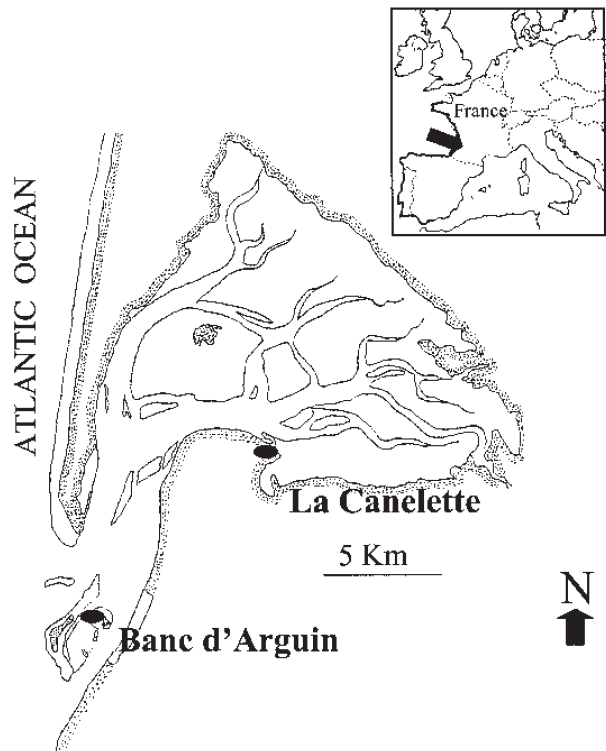


Fig. 1. Location of the 2 sampling stations in Arcachon Bay

dissected. A 2-way ANOVA was performed (Sokal & Rohlf 1981) to compare cockle mortalities at each station and in each sediment position (surface or buried).

Among cockles of each population, individuals belonging to the most represented cohorts were selected for further analysis: 1996 cohort at La Canelette, and 1998 cohort at Banc d'Arguin. Parasites of these cockles were identified and counted. Then the prevalence and the abundance of infection of parasites for surface and buried cockles were calculated. According to Margolis et al. (1982), prevalence of infection is defined as 'the number of individuals of a host species infected with a particular parasite species divided by the number of hosts examined' and the abundance of infection is 'the mean number of individuals of a particular parasite species per host examined (infected + uninfected)'. Here, the median number was used instead of the mean number, because of the aggregated distribution of parasites in host populations.

Cockle parasite infection between surface and buried individuals were compared using a Kolmogorov-Smirnov non-parametric test because homogeneity of variance was not achieved (Sokal & Rohlf 1981).

Study of parasite communities by correspondence analysis. The parasite communities in cockles were analyzed in order to determine whether the digenean

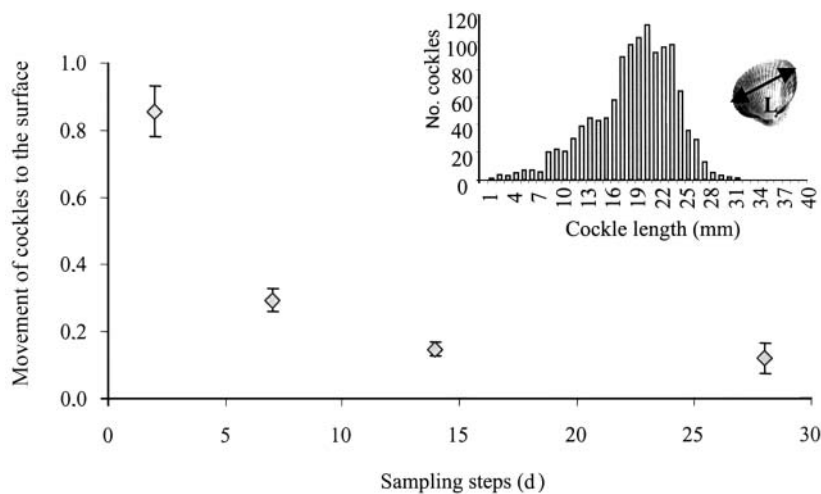


Fig. 2. *Cerastoderma edule*. Movement to sediment surface (ind. d⁻¹ per 100 m² ± SE) in relation with sampling intervals (every 2, 7, 14, or 28 d) from January 1999 to January 2000 at La Canelette. Insert: length frequency distribution of surface cockles collected during the study

species assemblage was similar at both stations (La Canelette and Banc d'Arguin), in both positions (surface and buried) and throughout the year (12 mo in 1999). A correspondence analysis was performed with Statistica software as recommended by Chardy et al. (1976). The prevalence of the 8 identified digeneans was considered: *Himasthla* sp., *H. quissetensis*, *H. interrupta*, *Meiogymnophallus minutus*, *Psilostomum brevicolle*, *Labratrema minimus*, *Diphtherostomum brusinae* and *Renicola roscovita*.

RESULTS

Vertical migration of cockles towards the surface of the sediment

In situ survey

The movement of cockles sampled at La Canelette from January 1999 to January 2000 is represented in Fig. 2 with the number of cockles found on the sediment, in relation to the 4 sample steps: 2 d (N = 159 samples), 7 d (N = 54), 14 d (N = 28) and 28 d (N = 15), and extrapolated to 1 d. The curve fits with the following relation:

$$y = 1.3803x^{-0.781} \quad (R^2 = 0.98) \quad (1)$$

where y = number of emerging cockles per day and per 100 m² and x = number of days.

This monitoring showed that cockles appeared and disappeared rapidly at the surface of sediment. From Eq. (1), it can be assumed that 1.4 cockles per 100 m² emerged every day. This is equivalent to a vertical migration of 5 cockles m⁻² yr⁻¹. Therefore, in 1 yr, 9600 cockles reach the sediment surface of the total sampled area, which represents 50% of the buried cockles (of similar length, i.e. 9 to 33 mm, mean = 19 ± 4 mm, Fig. 2) in this area. With the same relation (Eq. 1), it appears that 50% of surface cockles disappeared within 2 to 3 d, and 90% within 19 d.

Laboratory experiment

After 12 h in aquaria, only 33% of surface cockles burrowed in the sediment versus 95% for initially buried cockles (Fig. 3A). Mean abundance of infection by the dominant parasite, *Himasthla quissetensis*, was low (<11 cysts per cockle) and did not significantly differ between surface cockles which remained at the surface and buried cockles which buried again ($F = 3.005$; $df = 1$; $p > 0.05$) (Fig. 3B).

Health of surface cockles

During the monthly survey at both stations, only cockles >1 yr old were considered for mortality estimation. During the 7 d periods following sampling, surface cockles died throughout the year in greater proportion (ANOVA, $p < 0.001$) than buried cockles at both stations (Fig. 4). At La Canelette, mean mortality

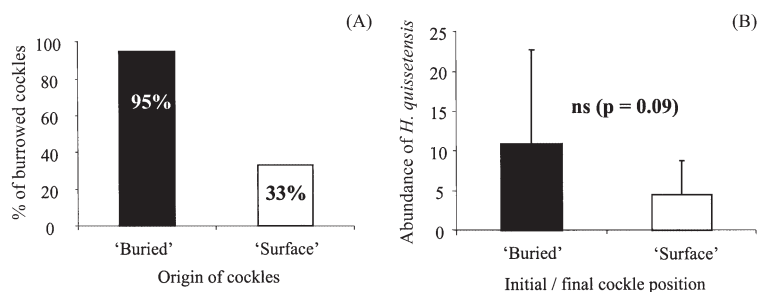


Fig. 3. *Cerastoderma edule*. Percentage of surface and buried cockles remaining at the sediment surface after 12 h in aquaria (A). Mean abundance of infestation by *Himasthla quissetensis* (±SD) for buried cockles burying again and surface cockles remaining at the surface (B). ns = not significant ($p > 0.05$)

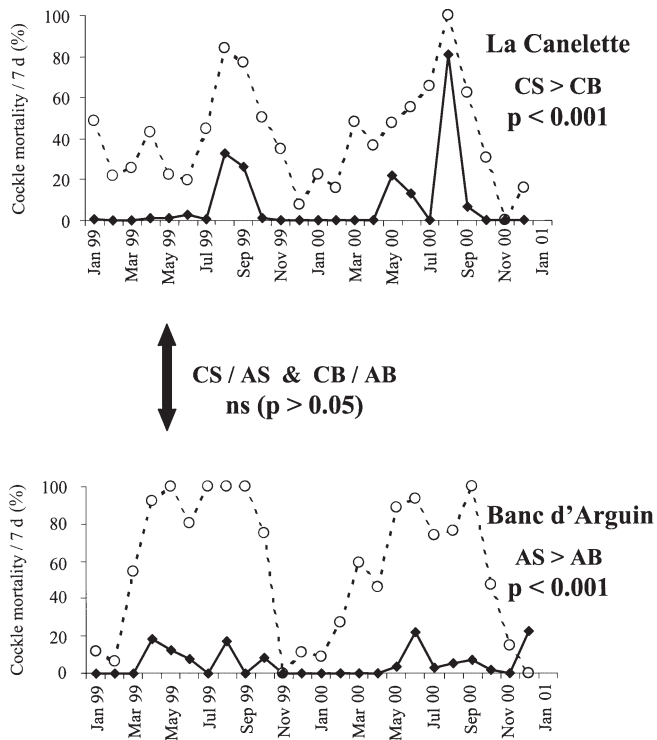


Fig. 4. *Cerastoderma edule*. Mortality of surface and buried cockles from La Canelette and Banc d'Arguin after 7 d in running water in the laboratory. Results of a 2-way ANOVA comparing the cockle mortality between position (surface [S, -O-] or buried [B, -●-]) for both stations (La Canelette [C] or Banc d'Arguin [A]), and cockle mortality between both stations for each position

per 7 d was 41 ± 5 and 8 ± 4 % for surface and buried cockles, respectively; at Banc d'Arguin, these values were 57 ± 8 and 5 ± 2 %, respectively (Table 1). Mortality rate was higher in warm months, particularly in August 1999 and August 2000, with 84 and 100 %, respectively, for surface cockles versus 33 and 80 % for buried cockles. Mortalities of surface cockles were not significantly different (ANOVA, $p > 0.05$) at Banc d'Arguin or at La Canelette.

Parasite load of surface and buried cockles

Diversity of digenean parasites

At La Canelette, surface cockles were parasitized by 9 trematode species versus 8 in the buried cockles (absence of *Monorchis parvus*) (Fig. 5). At this site, 3 species were present in high proportion: *Himasthla quissetensis* (100% for buried cockles vs 99% for surface cockles), *Himasthla sp.* (82 vs 91 %) and *Renicola roscovita* (89 vs 84 %). These digeneans use cockles as

Table 1. *Cerastoderma edule*. Percent mortality (mean \pm SD, range in parentheses) per 7 d in surface and buried cockles at La Canelette and Banc d'Arguin

	— Surface —	— Buried —
La Canelette	41 ± 5 (0–100)	8 ± 4 (0–81)
Banc d'Arguin	57 ± 8 (0–100)	5 ± 2 (0–23)

an intermediate host in their life cycle. Two trematodes using cockles as a primary host were found at La Canelette: *Labratrema minimus*, which dominated with up to 17.2 % prevalence in surface cockles, and *Monorchis parvus*. These parasites are highly deleterious and have been involved in massive mortalities in bivalve populations (Sannia & James 1978, Lauckner 1987a).

At Banc d'Arguin, surface and buried cockles hosted 10 and 9 trematodes, respectively. The species composition was similar to that found at La Canelette, with only one more species, *Himasthla elongata*. In terms of prevalence the dominant parasites were *Himasthla sp.*, *Meiogymnophallus minutus*, *H. quissetensis* and *Renicola roscovita* with a minimum of 58 % prevalence. For

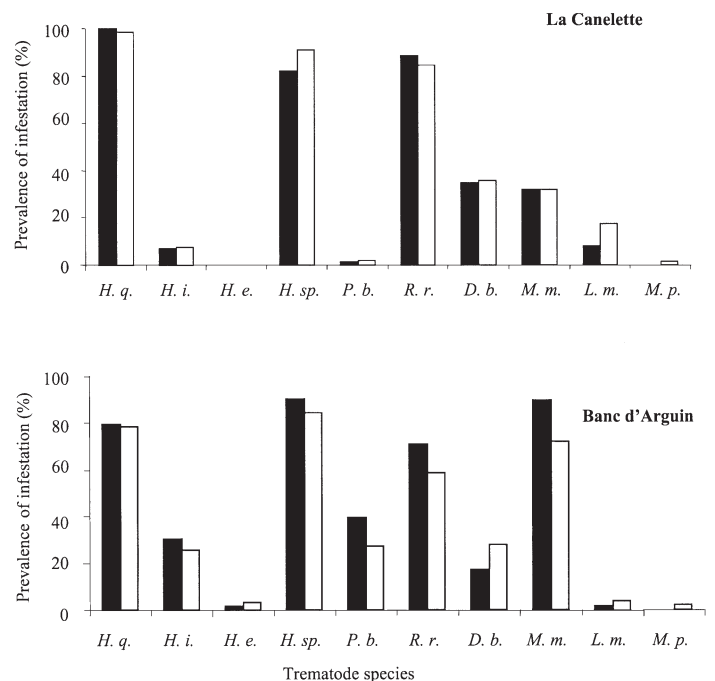


Fig. 5. *Cerastoderma edule*. Prevalence (%) of parasites for surface (□) and buried (■) cockles at La Canelette and Banc d'Arguin. The digenean species are: *H. q.*, *Himasthla quissetensis*; *H. i.*, *H. interrupta*; *H. e.*, *H. elongata*; *H. sp.*, *Himasthla sp.*; *P. b.*, *Psilostomum brevicolle*; *R. r.*, *Renicola roscovita*; *D. b.*, *Diptherostomum brusinae*; *M. m.*, *M. minutus*; *L. m.*, *Labratrema minimus*; *M. p.*, *Monorchis parvus*

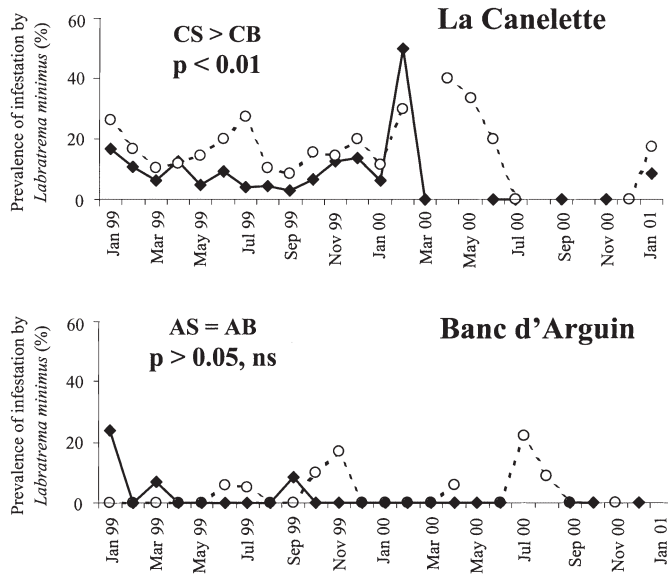


Fig. 6. *Cerastoderma edule*. Prevalence (%) of infestation by *Labratrema minimus* in surface (S, --○--○) and buried cockles (B, —●—●), at La Canelette (C) and Banc d'Arguin (A). Results of non-parametric Kolmogorov-Smirnov test showing the *L. minimus* prevalence differences between cockle positions (CS vs CB and AS vs AB)

digeneans using cockles as a primary host, the prevalence of *Labratrema minimus* was the most important with 3.6% for surface cockles.

Effects of the 2 dominant trematode species

Prevalence of Labratrema minimus: Using cockles as a primary host, *Labratrema minimus* invades all tissues

Table 2. *Cerastoderma edule*. Comparison of mean parasite prevalence (%) and median parasite abundance between cockles infected by *Labratrema minimus* and non-infected cockles, at La Canelette. N: number of dissected cockles

Parasites	With <i>L. minimus</i> (N = 56)		Without <i>L. minimus</i> (N = 288)	
	Prevalence	Abundance	Prevalence	Abundance
Primary host				
<i>Monorchis parvus</i>	0	—	3	—
Intermediate host				
<i>Himasthla quissetensis</i>	98	40	99	41
<i>Himasthla interrupta</i>	0	0	3	0
<i>Himasthla</i> sp.	88	4	90	4
<i>Meiogymnophallus minutus</i>	21	—	22	—
<i>Psilostomum brevicolle</i>	2	0	2	0
<i>Renicola roscovita</i>	77	5.5	87	7
<i>Diphtherostomum brusinae</i>	29	—	38	—
Species richness	6		8	

with thousands of sporocysts and cercariae. Therefore, the prevalence is a good estimate of population infection. At La Canelette, the prevalence of *L. minimus* was significantly higher ($p < 0.01$) for surface cockles (mean prevalence = $17 \pm 2\%$) than for buried cockles (mean = $8 \pm 3\%$) but with the same trend during the year for both positions of cockles (Fig. 6). Moreover, it appeared that cockles with lower global infection tended to be more infested by *L. minimus* (Table 2). At Banc d'Arguin, the prevalence of *L. minimus* was much lower than at La Canelette, with no difference ($p > 0.05$) between surface (mean = $4 \pm 1\%$) and buried (mean = $2 \pm 1\%$) cockles (Fig. 6).

Abundance of Himasthla quissetensis: *Himasthla quissetensis* uses cockles as an intermediate host where it lives as cyst(s), mainly in the foot. Therefore, parasite abundance (= median number of cysts per cockle) is a better estimate than prevalence for characterizing cockle infection.

At La Canelette, from January to May 1999, the abundance of infection of surface cockles decreased from 63 to 23 metacercariae per cockle and from 49 to 12 metacercariae for buried cockles (Fig. 7). The infection then increased during the summer period, with 89 metacercariae for buried cockles versus 73 for surface cockles. For both positions, median parasite abundance decreased to 40 cysts during the following winter. The next summer (2000), the number of cockles was too low to obtain a clear pattern, but median infection reached about 200 cysts. When pooling all cockles ($n = 782$) and performing a Kolmogorov-Smirnov test, no difference in parasite abundance appeared between surface and buried cockles ($p > 0.05$). However, amongst cockles hosting more than 150 metacercariae (4% of the cockle population), 74% were at the sediment surface (Fig. 8).

At Banc d'Arguin, the parasite abundance was 2 to 3 times lower than at La Canelette, but the seasonal trend was similar. However, for both years, surface cockles ($n = 246$) were significantly more infested in *Himasthla quissetensis* (Kolmogorov-Smirnov, $p < 0.001$) than buried cockles ($n = 250$). Even if the parasite burden was moderate (median abundance: 15 ± 2), with surface cockles being only 1.1 times more infested than buried cockles ($p < 0.001$), this difference was mainly due to the September 1999 period ($p < 0.001$) when surface cockles were 10 times more infested. Moreover, for cockles hosting less than 10 metacercariae (78% of dissected cockles), the percentage of buried cockles (56%) was similar to sur-

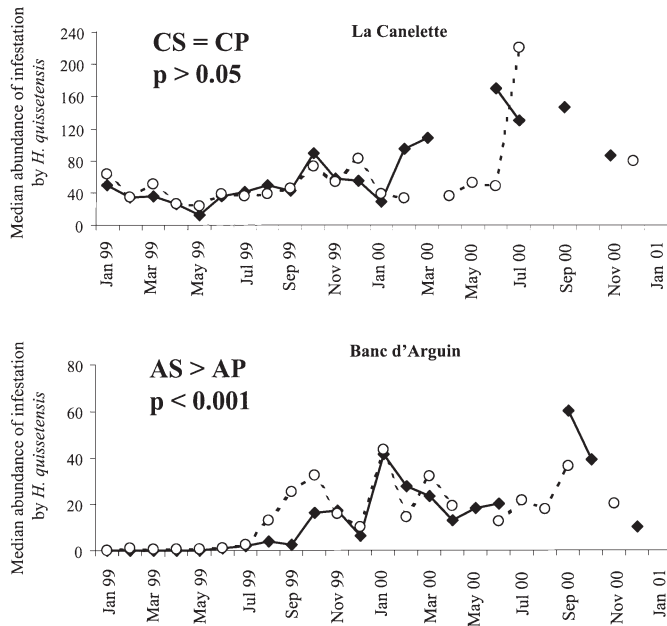


Fig. 7. *Cerastoderma edule*. Abundance of infestation by *Himasthla quissetensis* in surface (S, -o-) and buried (B, -◆-) cockles, at La Canelette (C) and Banc d'Arguin (A). Results of a non parametric Kolmogorov-Smirnov test determining abundance differences in *H. quissetensis* for surface and buried cockles at La Canelette (CS vs CB) and Banc d'Arguin (AS vs AB)

face cockles. However, 69% of cockles harbouring more than 10 metacercariae (i.e. 22% of dissected cockles) were in the surface population (Fig. 8).

Comparison of parasite communities by correspondence analysis

The above results showed a dominance of infection by *Himasthla quissetensis* and *Labratrema minimus* for surface cockles at Banc d'Arguin and La Canelette, respectively. Even if *L. minimus* is debilitating for cockles (Bowers 1969, Deltreil & His 1970), it cannot solely explain 84 to 100% mortality when its maximum prevalence is 50%. A correspondence analysis was performed to take into account the whole community of parasites. The prevalence of infection for each parasite species on cockles at both stations (La Canelette and Banc d'Arguin), in both positions (surface and buried) and throughout the year (12 mo in 1999) were compared. The first 2 axes of the correspondence analysis accounted for 65% of the total inertia (Fig. 9). Discrimination was low (points around the origin) but the analysis showed some tendencies. Axis 1 (45%) separated cockles of Banc d'Arguin from cockles of La Canelette, without any seasonal trend. Axis 2 (20%) was more discriminant for parasite species than for

stations. La Canelette was represented by characteristic digenean parasites such as *Labratrema minimus*, *Diptherostomum brusinae* and *Himasthla interrupta*. Banc d'Arguin was characterized by 2 parasites: *Psilostomum brevicolle* and *Meiogymnophallus minutus*. Parasites such as *Himasthla quissetensis*, *Himasthla* sp. and *Renicola roscovita* were ubiquitous with a position very close to the origin of both axes: they were present at both stations, all year long. At La Canelette, there was no characteristic parasite community for buried cockles compared to surface cockles. At Banc d'Arguin, there was a moderate discrimination along Axis 1 with surface cockles mostly 'to the left' of buried cockles for each month. This slight trend is consistent with the results shown in Fig. 5, where specific prevalence at Banc d'Arguin was usually higher in buried cockles.

DISCUSSION

Emergence and disappearance of surface cockles

Although the presence of infaunal bivalves at the sediment surface has already been described (Hancock & Urquhart 1965, Deltreil & His 1970, Richardson et al. 1993, Thomas & Poulin 1998), quantitative results

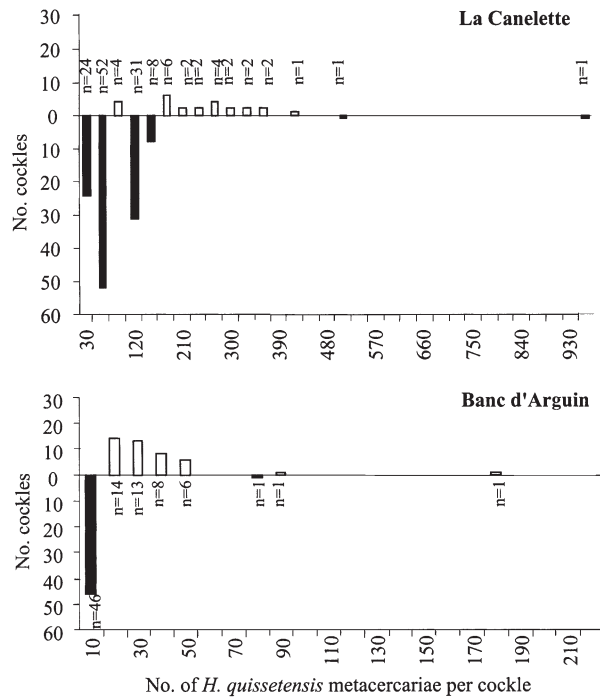


Fig. 8. *Cerastoderma edule*. Frequency distribution of the numbers of *Himasthla quissetensis* metacercariae per cockle, at La Canelette and Banc d'Arguin. n: number of dissected cockles. (■) Dominance of 'buried cockles', (□) dominance of 'surface cockles'

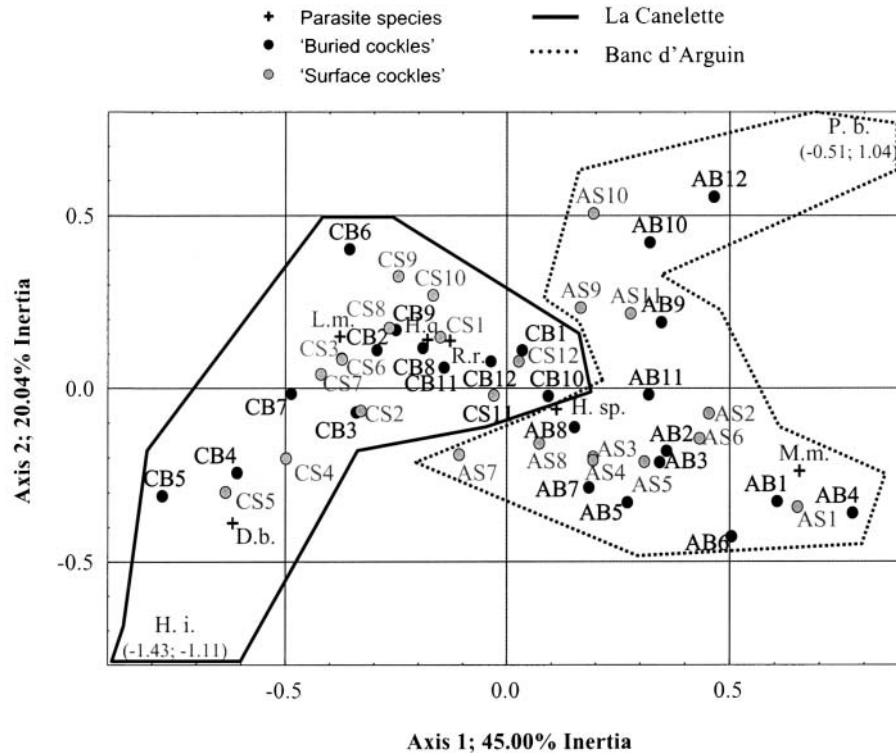


Fig. 9. *Cerastoderma edule*. Site plots (by month) and parasite species plots of the correspondence analysis on Axes 1 and 2, for surface (S) and buried (B) cockles at La Canelette (C) and Banc d'Arguin (A). Crosses represent the digenean species: L. m., *Labratrema minimus*; H. q., *Himasthla quissetensis*; H. sp., *Himasthla* sp.; H. i., *H. interrupta*; R. r., *Renicola roscovita*; P. b., *Psilostomum brevicolle*; M. m., *Meiogygnophallus minutus*; D. b., *Diptherostomum brusinae*. Months when cockles were collected are numbered from 1 = January 1999 to 12 = December 1999

on this vertical migration were still missing. The intensive sampling strategy applied during the present study (every 2 d for 13 mo) allowed us to estimate this in cockle populations. The migration mainly concerned cockles with a shell length between 9 and 33 mm (Fig. 2). We showed that, for 1 yr, 50% of the cockles at La Canelette came to the surface.

Several hypotheses can be formulated to explain the rapid and steady movement of cockles towards the sediment surface: (1) Cockles can emerge actively in response to physical factors such as high temperature variations (Lauckner 1987b), tidal and/or daily rhythms (nycthemeral cycle). This latter natural emergence of cockles generally occurs in the dark and in storm events (Richardson et al. 1993). However, in the present study, cockles were found at low tide, during daytime and in calm conditions. (2) Cockles may emerge at the surface when abundance is high, and when individuals crowd against one another (Richardson et al. 1993). Such a competitive interaction for space did not occur at La Canelette, where cockle abundance was about 10 ind. m⁻². (3) Cockles could be weakened by some physiological stress induced by anoxia or oxygen deficiency (Brafeld 1963, Rosenberg

& Loo 1988, Modig & Olafsson 1998), especially under persistent macroalgal mats (Desprez et al. 1992, de Montaudouin 1995). None of these factors could have affected cockles for 13 mo in this area. The green alga *Monostroma obscurum* and other macrophytes were observed at La Canelette in high proportion in March and April 1999 only. (4) Cockles could suffer from pathogenic agents such as bacteria (Babarro & Zwaan 2001, Zwaan & Babarro 2001) and parasites (Swennen 1969, Swennen & Ching 1974, Bartoli 1976, Lauckner 1983, 1984, Poulin et al. 1998, Jensen et al. 1999), certainly in interaction with environmental stress (Michaelis 1979, Lauckner 1983, Brown & Pascoe 1989, Sousa & Gleason 1989, Wegeberg 1998, Lafferty & Kuris 1999).

While cockles emerged at the surface of the sediment at a mean rate of 1.4 cockle d⁻¹ per 100 m², our results showed that surface cockles also disappeared rapidly (50% within 2 to 3 d). An explanation of this disappearance is the emigration of cockles from the sediment surface. This migration could be horizontal, cockles being passively washed away during high tide; such an advective transport is unlikely at La Canelette because the site is sheltered and surrounded by a sea-

grass bed, which acts as a physical barrier preventing cockle migration. The migration could also be vertical, with individuals burrowing again (Richardson et al. 1993). However, our laboratory experiments showed that 67% of surface cockles remained on the sediment surface. An alternative hypothesis is that the rapid disappearance of surface cockles was due to mortality by desiccation (Lauckner 1983, 1987b) or predation (Hancock & Urquhart 1965, Seed & Brown 1975, Sanchez-Salazar et al. 1987a,b, Desprez et al. 1992).

In summary, the most relevant factor to explain the emergence of cockles would be some pathology preventing them from burrowing again. This hypothesis is consistent with our mortality experiments, which clearly demonstrated that surface cockles from both stations were not healthy but died rapidly all year long, even in optimal laboratory conditions.

Does favourization by digeneans apply to cockles?

Effect of *Labratrema minimus* on cockles

Amongst the digeneans using cockle as a primary host, *Labratrema minimus* dominated at both stations (La Canelette and Banc d'Arguin), with a mean prevalence of 12.5 and 2.7%, respectively (Fig. 6). Surface cockles were always more infected (2×) than buried cockles, and more significantly so at La Canelette than at Banc d'Arguin. *L. minimus* infection occurred all year long, especially during the warm season. Prevalence attained 25 to 50%. These values are higher than those observed by Maillard (1976) in the Prévost lagoon (up to 11%), Cole (1956) in North Wales (~2%), and de Montaudouin et al. (2000) at Banc d'Arguin (6%). They are similar to the prevalence values found at Burry Inlet, South Wales (40%), by Hancock & Urquhart (1965) or at Banc d'Arguin in summer 1969 (40.7%) by Deltreil & His (1970). However, comparisons are biased by the fact that prevalence has been calculated from different data sets (cohorts, whole population, cockles of selected length, etc.). Out of the 92 cockles hosting *L. minimus* at La Canelette, the majority (61%) were found at the surface, i.e. in a 'pre-mortality' situation.

Sporocysts of this trematode first invade all the haemolymph of the gonad, then the digestive gland, and finally destroy all the tissues of their host. The asexual multiplication of such a parasite using mollusc as a primary host leads to the formation of thousands of cercariae contained in up to several hundreds of sporocysts. Consequently, the parasite partially or completely castrates its host and certainly alters its ability to burrow (Bowers 1969, Deltreil & His 1970).

There is no agreement concerning the lethality of

Labratrema minimus. Some authors incriminated *L. minimus* in cockle mortality (Menzel & Hopkins 1955, Hopkins 1957). According to Thébault (2001), *L. minimus* weakens cockles but does not kill them, increasing their vulnerability to other factors.

Even though *Labratrema minimus* certainly participates in cockle migration towards the surface of sediment (and is thus involved in cockle mortality), it is less evident to be able to interpret this process as a favourization strategy. Indeed, the final host of *L. minimus* is a gobiid fish, and the infection from the cockle towards the fish is performed by free swimming cercariae. For the cockle, being at the surface of the sediment is not a real advantage (nor a disadvantage) for transmission, although Deltreil & His (1970) postulated that when a cockle dies at the surface of sediment, it optimizes the dispersion of cercariae. *L. minimus* could also play an indirect role in favourization. Other digenean species could 'hitch-hike' in infected cockles in order to take advantage of the vertical migration and to be preyed upon by their own final hosts (Thomas et al. 1998). This was not confirmed in the present study. In contrast, cockles with lower global infection tended to be more infected by *L. minimus* (Table 2). This result suits the theory that heavy infection stresses bivalves which consequently have a lower pumping rate and therefore less probability to inhale parasite larvae (de Montaudouin et al. 1998, 2000, Javanshir 1999). In the present study, *L. minimus* can account for a maximum of 50% of cockle migration towards the surface of sediment, but more generally less than 25%. When subtracting mean prevalence of *L. minimus* in surface and buried cockles, it can be assumed that 9% of cockles emerge due to this digenean species.

Effect of *Himasthla quissetensis* on cockles

For trematodes using cockle as an intermediate host, *Himasthla quissetensis* dominated in terms of both prevalence and abundance of infection (Figs. 5 & 7).

The final host of *Himasthla quissetensis* is a lariid bird. Consequently, all factors contributing to predation on cockles also enhance the probability of achieving this digenean cycle. Favourization occurs if the parasite itself induces migration of cockles towards the sediment surface. *H. quissetensis*, like other Himasthlinea trematodes, is essentially encysted in the cockle foot (Lauckner 1984). Even if this parasite is considered less debilitating to cockles than *Labratrema minimus*, the larval stages are not simple inert cysts waiting for transmission (Holmes & Bethel 1972, Dobson 1988, Moore & Gotelli 1990, Poulin 1994). According to several authors (Thomas & Poulin 1998, Jensen et al. 1999, Poulin 1999), cockles heavily infested by Himasthlinea

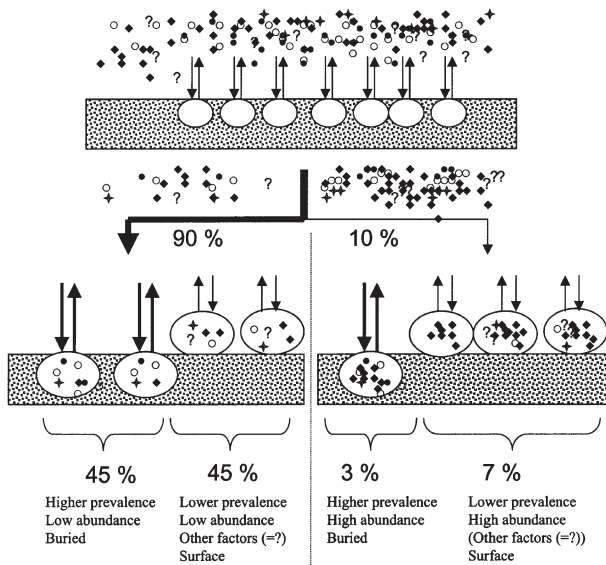


Fig. 10. *Cerastoderma edule*. Possible scenario of infestation by digenean cercariae and its effects on burrowing ability, based on results at station La Canelette. Cockles may be infected by several digenean species (●, ○, ◆, ★) through their pumping activity (arrows). Like in most settlement processes, infection follows an aggregative law with 90% cockles much less infected than the other 10% (see Fig. 8). At low infection level, the ratio buried:surface cockles is close to 1. Parasites are not responsible for the position of cockles, which can be attributed to other factors ('?'); this is the case of *Labratrema minimus* infection. Among the 10% highly infected cockles, the majority are at the sediment surface due to metacercariae (especially by a dominant species '◆' like *Himasthla quissetensis*) and/or other factors ('?'). When cockles are at the surface, their pumping rate is lower (finer arrows) and consequently the probability of being infected by non-dominant digeneans is lower (inducing lower prevalence). This scenario highlights the obvious role of factors other than parasites in explaining this important movement of cockles towards the sediment surface

are unable to burrow. Such inability is considered by Thomas & Poulin (1998) as an adaptive manipulation of host behaviour by the parasite. Poulin (1999) showed that this indirect effect of the parasite manipulation split the New Zealand cockle *Austrovenus stutchburyi* population into 2 distinct ecological categories, 'buried' and 'surface cockles', the latter existing solely because of the parasites.

Himasthla quissetensis dominance in surface cockles occurred only at Banc d'Arguin. Therefore, at both stations the trend was similar (Fig. 10), with a different threshold beyond which cockles were migrating towards the surface. An approximate calculation leads to the conclusion that at Banc d'Arguin 8% of cockles from the studied cohort emerged due to a favourization process by *H. quissetensis* (vs 2% at La Canelette).

Is there any effect of the digenean community on cockles?

The occurrence of such a diverse parasite community as that found in the cockle populations of Arca-chon Bay (Fig. 5) raises the question of its possible effects on host dynamics (Deltreil & His 1970, Lester 1984, Jensen & Mouritsen 1992, Mouritsen & Jensen 1997, de Montaudouin et al. 2000). Both parasite communities (Banc d'Arguin and La Canelette) were discriminated by correspondence analysis. However, the analysis did not discriminate a specific community for surface cockles at La Canelette. At Banc d'Arguin, for each month, the position of surface cockles compared to buried cockles on Axis 1 suggested a slight discrimination (confirmed in Fig. 5). Specific prevalence was moderately higher in buried cockles, which have higher fitness and a higher pumping rate (de Montaudouin et al. 1998, 2000, Javanshir 1999).

The use of prevalence as a dependent variable was motivated by the impossibility to use abundance when considering the parasites that infest cockles as primary hosts. But precision is lost concerning the abundance of infection of parasite species using cockles as intermediate hosts and explains why results concerning *Himasthla quissetensis* are not recovered here.

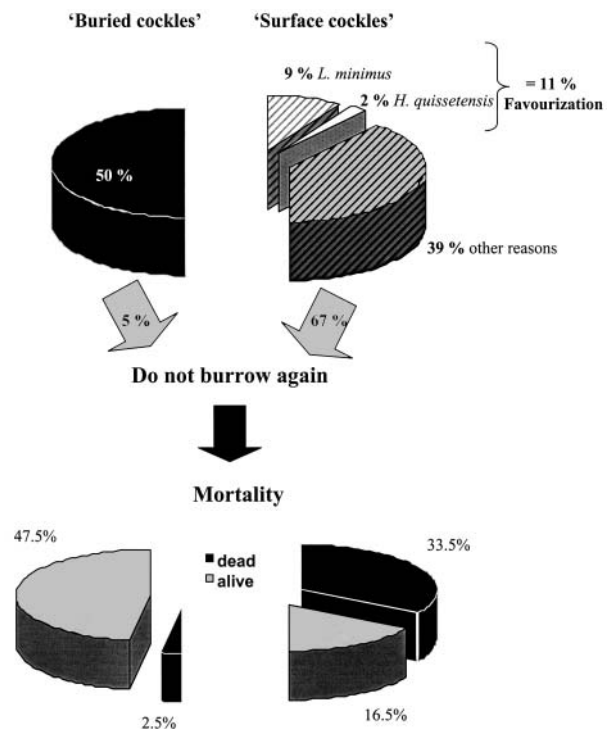


Fig. 11. *Cerastoderma edule*. Percentage of adults at La Canelette remaining in the sediment or emerging, in 1 yr, and mortality related to cockle position

At La Canelette we propose the following scenario regarding the effect of cockle infection on cockle burrowing ability. Concerning the 1996 cohort (adults ≈ 20 mm), 50% of the individuals come out at the surface of sediment in 1 yr (Fig. 11). The 2 dominant species *Labratrema minimus* and *Himasthla quissetensis* induce the emergence of 11% (9 + 2%, respectively) of cockles (Fig. 11). The other 39% emerge for unexplained reasons (tidal rhythm, bacteria, protozoans, etc.). Even if favourization plays a modest role ($\sim 11\%$ at La Canelette and $\sim 10\%$ at Banc d'Arguin) in cockle emergence, the total emergence rate, i.e. 50% of the adult population in 1 year, is high and puts cockles in an abnormal position (67% of surface cockles do not burrow again, causing the death of 33.5% of the emerged cockles; Fig. 11), which is much favourable for parasites.

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LITERATURE CITED

- Auby I, Trut G, d'Amico F, Beliaeff B (1999) Réseau hydrologique du Bassin d'Arcachon—synthèse des résultats 1988–1997. IFREMER Rep DEL/AR/RST/99-09, Arcachon
- Babarro JMF, Zwaan AD (2001) Factors involved in the (near) anoxic survival time of *Cerastoderma edule*: associated bacteria vs. endogenous fuel. *Comp Biochem Physiol* 128: 325–337
- Bartoli P (1976) Modification de la croissance et du comportement de *Venerupis aurea* parasité par *Gymnophallus fossarum* P. Bartoli, 1965 (Trematoda, Digenea). *Halictis* 7: 23–28
- Bowers EA (1969) *Cercaria bucephalopsis haimeana* (Lacaze-Duthiers, 1854) (Digenea: Bucephalidae) in the cockle, *Cardium edule* L. in South Wales. *J Nat Hist* 3:409–422
- Bowers EA, Bartoli P, Russell-Pinto F, James BL (1996) The metacercariae of sibling species of *Meiogymnophallus*, including *M. rebecqui* comb. nov. (Digenea: Gymnophallidae), and their effects on closely related *Cerastoderma* host species (Mollusca: Bivalvia). *Parasitol Res* 82:505–510
- Brafield AE (1963) The effects of oxygen deficiency on the behaviour of *Macoma balthica* (L.). *Anim Behav* 11: 345–346
- Brown AF, Pascoe D (1989) Parasitism and host sensitivity to cadmium: an acanthocephalan infection of the freshwater amphipod *Gammarus pulex*. *J Appl Ecol* 26:473–487
- Campredon P (1976) Observations ornithologiques sur le Banc d'Arguin (Gironde). *Alauda* 44:441–455
- Carruesco C, Lapaquellerie Y, Labourg PJ, Prunier D (1986) Impact des métaux lourds sur un environnement lagunaire: le Bassin d'Arcachon. *Bull Inst Géol Bassin d'Aquitaine Bordeaux* 39:85–93
- Chardy P, Glémarec M, Laurec A (1976) Application of inertia methods to benthic marine ecology. Practical implications of the basic options. *Estuar Coast Mar Sci* 4:179–205
- Cole HA (1956) A preliminary study of growth-rate in cockles (*Cardium edule* L.) in relation to commercial exploitation. *J Cons Perm Int Explor Mer* 22:77–90
- Combes C (1980) Les mécanismes de recrutement chez les métazoaires parasites et leur interprétation en termes de stratégies démographiques. *Vie Milieu* 30:55–63
- Combes C (1991) Ethological aspects of parasite transmission. *Am Nat* 138:866–880
- Combes C (1995) Interactions durables—écologie et évolution du parasitisme. Masson, Paris
- Curtis LA (1993) Parasite transmission in the intertidal zone: vertical migrations, infective stages, and snail trails. *J Exp Mar Biol Ecol* 173:197–209
- Deltreil JP, His E (1970) Sur la présence d'une cercaire de trematode chez *Cardium edule* L. dans le Bassin d'Arcachon. *Rev Trav Inst Pêches Marit* 34:1225–232
- de Montaudouin X (1995) Etude expérimentale de l'impact de facteurs biotiques et abiotiques sur le recrutement, la croissance et la survie des coques *Cerastoderma edule* (Mollusque-Bivalve). Thesis, University of Bordeaux I
- de Montaudouin X (1996) Factors involved in growth plasticity of cockles *Cerastoderma edule* (L.) identified by field survey and transplant experiments. *J Sea Res* 36:251–265
- de Montaudouin X, Wegeberg AM, Jensen KT, Sauriau PG (1998) Infection characteristics of *Himasthla elongata* cercaria in cockles as a function of water current. *Dis Aquat Org* 34:63–70
- de Montaudouin X, Kisielewski I, Bachelet G, Desclaux C (2000) A census of macroparasites in an intertidal bivalve community, Arcachon Bay, France. *Oceanol Acta* 23: 453–468
- Desprez M, Ducrotoy JP, Elkaim B (1987) Crise de la production des coques (*Cerastoderma edule*) en Baie de Somme. I. Synthèse des connaissances biologiques. *Rev Trav Inst Pêches Marit* 49:215–230
- Desprez M, Rybarczyk H, Wilson JG, Ducrotoy JP, Sueur F, Olivési R, Elkaim B (1992) Biological impact of eutrophication in the bay of Somme and the induction and impact of anoxia. *Neth J Sea Res* 30:149–159
- Dewarumez JM (1983) Evolution de populations de mollusques intertidaux en relation avec des modifications sédimentologiques sur le littoral de la Mer du Nord. *Halictis* 13:3–12
- Dobson AP (1988) The population biology of parasite-induced changes in host behavior. *Q Rev Biol* 63:139–165
- Ducrotoy JP, Rybarczyk H, Souprayan J, Bachelet G and 10 others (1991) A comparison of the population dynamics of the cockle (*Cerastoderma edule*, L.) in North-Western Europe. In: Elliott M, Ducrotoy JP (eds) Estuaries and coasts: spatial and temporal intercomparisons. Olsen & Olsen, Fredensborg, p 173–184
- Feral C, Breton JL, Streiff W (1972) Données nouvelles sur l'action de la castration parasitaire chez quelques mollusques gastéropodes. *Ann Inst Michel Pacha* 5:28–40
- Gorbushin AM (1997) Field evidence of trematode-induced gigantism in *Hydrobia* spp. (Gastropoda: Prosobranchia). *J Mar Biol Assoc UK* 77:785–800
- Gorbushin AM, Levakin IA (1999) The effect of trematode parthenitae on the growth of *Onoba aculeus*, *Littorina saxatilis* and *L. obtusata* (Gastropoda: Prosobranchia). *J Mar Biol Assoc UK* 79:273–279
- Hancock DA, Urquhart AE (1965) The determination of natural mortality and its causes in an exploited population of cockles (*Cardium edule* L.). *Fish Invest* 24:1–40

- Helluy S (1983) Un mode de favorisation de la transmission parasitaire: la manipulation du comportement de l'hôte intermédiaire. *Rev Ecol (Terre Vie)* 38:211–223
- Holmes JC, Bethel WH (1972) Modification of intermediate host behaviour by parasites. *Zool J Linn Soc* 51:123–149
- Hopkins SH (1957) Our present knowledge of the oyster parasite '*Bucephalus*' (*Bucephalopsis*). *Proc Natl Shellfish Assoc* 47:38–61
- Huxham M, Raffaelli D, Pike A (1993) The influence of *Cryptocotyle lingua* (Digenea: Platyhelminthes) infections on the survival and fecundity of *Littorina littorea* (Gastropoda: Prosobranchia); an ecological approach. *J Exp Mar Biol Ecol* 168:223–238
- Javanshir A (1999) Effets de quelques parasites (Digenea) sur la dynamique des populations et la physiologie respiratoire de la coque *Cerastoderma edule* (Mollusque bivalve) dans le Bassin d'Arcachon. Thesis, University of Paris 6
- Jensen KT (1992) Dynamics and growth of the cockle, *Cerastoderma edule*, on an intertidal mud-flat in the Danish Wadden Sea: effects of submersion time and density. *Neth J Sea Res* 28:335–345
- Jensen KT, Mouritsen KN (1992) Mass mortality in 2 common soft-bottom invertebrates, *Hydrobia ulvae* and *Corophium volutator*—the possible role of trematodes. *Helgol Meeresunters* 46:329–339
- Jensen KT, Fernández Castro N, Bachelet G (1999) Infectivity of *Himasthla* spp. (Trematoda) in cockle (*Cerastoderma edule*) spat. *J Mar Biol Assoc UK* 79:265–271
- Jonsson PR, André C (1992) Mass mortality of the bivalve *Cerastoderma edule* on the Swedish west coast caused by infection with the digenean trematode *Cercaria cerastodermae*. I. *Ophelia* 36:151–157
- Kuris AM (1997) Host behavior modification: an evolutionary perspective. In: Beckage NE (ed) *Parasites and pathogens—effects on host hormones and behavior*. Chapman & Hall, New York, p 239–315
- Lafferty KD, Kuris AM (1999) How environmental stress affects the impacts of parasites. *Limnol Oceanogr* 44:925–931
- Lauckner G (1983) Diseases of mollusca: bivalvia. In: Kinne O (ed) *Diseases of marine animals*. Biologische Anstalt Helgoland, Hamburg, p 477–961
- Lauckner G (1984) Impact of trematode parasitism on the fauna of a North Sea tidal flat. *Helgol Meeresunters* 37:185–199
- Lauckner G (1987a) Ecological effects of larval trematode infection on littoral marine invertebrate populations. *Int J Parasitol* 17:391–398
- Lauckner G (1987b) Effects of parasites on juvenile Wadden Sea invertebrates. In: Tougaard S, Asbirk S (eds) *Proc 5th Int Wadden Sea Symp, National Forest and Nature Agency and Museum of Fisheries and Shipping, Esbjerg*, p 103–121
- Lester RJG (1984) A review of methods for estimating mortality due to parasites in wild fish populations. *Helgol Meeresunters* 37:53–64
- Maillard C (1976) *Distomatoses de poissons en milieu lagunaire*. Thesis, University of Sciences et Technology of Languedoc, Montpellier
- Margolis L, Esch GW, Holmes JC, Kuris AM, Schad GA (1982) The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). *J Parasitol* 68:131–133
- Menzel RW, Hopkins SH (1955) The growth of oysters parasitised by the fungus *Dermocystidium marinum* and by the trematode *Bucephalus cuculus*. *J Parasitol* 41:333–342
- Michaelis H (1979) Recent changes in the communities of the Wadden Sea—natural phenomena or effects of pollution? In: Tougaard S, Helweg Ovensen C (eds) *Environmental problems of the Wadden Sea Region*. *Proc Sci Symp Ribe, Fiskeri-og Søfartsmuseet, Saltvandsakvariets Biologiske Meddelelser*, p 87–95
- Modig H, Olafsson E (1998) Responses of Baltic benthic invertebrates to hypoxic events. *J Exp Mar Biol Ecol* 229:133–148
- Moore J, Gotelli NJ (1990) A phylogenetic perspective on the evolution of altered host behaviours: a critical look at the manipulation hypothesis. In: Barnard CJ, Behnke JM (eds) *Parasitism and host behaviours*, Taylor & Francis, London, p 193–233
- Mouritsen KN (1997) Crawling behaviour in the bivalve *Macoma balthica*: the parasite-manipulation hypothesis revisited. *Oikos* 79:513–520
- Mouritsen KN, Jensen KT (1994) The enigma of gigantism: effect of larval trematodes on growth, fecundity, egestion and locomotion in *Hydrobia ulvae* (Pennant) (Gastropoda: Prosobranchia). *J Exp Mar Biol Ecol* 181:53–66
- Mouritsen KN, Jensen KT (1997) Parasite transmission between soft-bottom invertebrates: temperature mediated infection rates and mortality in *Corophium volutator*. *Mar Ecol Prog Ser* 151:123–134
- Poulin R (1994) Meta-analysis of parasite-induced behavioural changes. *Anim Behav* 48:137–146
- Poulin R (1995) 'Adaptative' changes in the behaviour of parasitized animals: a critical review. *Int J Parasitol* 25:1371–1383
- Poulin R (1999) The functional importance of parasites in animal communities: many roles at many levels? *Int J Parasitol* 29:903–914
- Poulin R, Hecker K, Thomas F (1998) Hosts manipulated by one parasite incur additional costs from infection by another parasite. *J Parasitol* 84:1050–1052
- Richardson CA, Ibarrola I, Ingham RJ (1993) Emergence pattern and spatial distribution of the common cockle *Cerastoderma edule*. *Mar Ecol Prog Ser* 99:71–81
- Rosenberg R, Loo LO (1988) Marine eutrophication induced oxygen deficiency: effects on soft bottom fauna, western Sweden. *Ophelia* 29:213–225
- Sanchez-Salazar ME, Griffith CL, Seed R (1987a) The interactive roles of predation and tidal elevation in structuring populations of the edible cockle, *Cerastoderma edule*. *Estuar Coast Shelf Sci* 25:245–260
- Sanchez-Salazar ME, Griffith CL, Seed R (1987b) The effect of size and temperature on the predation of cockles *Cerastoderma edule* (L.) by the shore crab *Carcinus maenas* (L.). *J Exp Mar Biol Ecol* 111:181–193
- Sannia A, James BL (1978) The occurrence of *Cercaria cerastodermae* I Sannia, James, and Bowers, 1978 (Digenea: Monorchidae) in populations of *Cerastoderma edule* (L.) from the commercial beds of the Lower Thames Estuary. *Z Parasitenkd* 56:1–11
- Seed R, Brown RA (1975) The influence of reproductive cycle, growth, and mortality on population structure in *Modiolus modiolus* (L.), *Cerastoderma edule* (L.), and *Mytilus edulis* (L.) (Mollusca: Bivalvia). In: Barnes H (ed) *Proc 9th Eur Mar Biol Symp*. Aberdeen University Press, Aberdeen, p 257–274
- Seed R, Brown RA (1978) Growth as a strategy for survival in two marine bivalves, *Cerastoderma edule* and *Modiolus modiolus*. *J Anim Ecol* 47:283–292
- Sokal R, Rohlf F (1981) *Biometry*. WH Freeman, New York
- Sousa WP (1991) Can models of soft-sediment community structure be complete without parasites? *Am Zool* 31:821–830

- Sousa WP, Gleason M (1989) Does parasitic infection compromise host survival under extreme environmental conditions? The case for *Cerithidea californica* (Gastropoda: Prosobranchia). *Oecologia* 80:456–464
- Swennen C (1969) Crawling-tracks of trematode infected *Macoma balthica* (L.). *Neth J Sea Res* 4:376–379
- Swennen C, Ching HL (1974) Observations on the trematode *Parvatrema affinis*, causative agent of crawling tracks of *Macoma balthica*. *Neth J Sea Res* 8:108–115
- Tebble N (1966) British bivalve seashells. Trustees of the British Museum of Natural History, London
- Thébault A (2001) Epidémiologie dans le cas de mortalités anormales de coquillages: exemple des coques du Croisic. Thesis, University of Medicine of Créteil
- Thomas F, Poulin R (1998) Manipulation of a mollusc by a trophically transmitted parasite: convergent evolution or phylogenetic inheritance? *Parasitology* 116:431–436
- Thomas F, Poulin R, Renaud F (1998) Nonmanipulative parasites in manipulated hosts: 'hitch-hikers' or simply 'lucky passengers'. *J Parasitol* 84:1059–1061
- Wegeberg AM (1998) Digene trematodes (Echinostomidae) infektionsøkologi og effekt på *Cerastoderma edule*. MS thesis, University of Aarhus
- Winer BJ (1971) Statistical principles in experimental design. McGraw-Hill, New York
- Zwaan AD, Babarro JMF (2001) Studies on the causes of mortality of the estuarine bivalve *Macoma balthica* under conditions of (near) anoxia. *Mar Biol* 138:1021–1028

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