

Inertia of parasite infection versus host biomass fluctuation

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ABSTRACT

Infection by parasites with complex life cycles such as trematodes depends on many environmental factors which may result in a time-lag between host biomass fluctuations and parasite density in hosts. A cockle (marine bivalve, second intermediate host) population and its associated parasite community were monitored over 15 years. A time-shift correlation analysis suggests that trematode abundance in cockles responds to cockle biomass after a long delay (8 year time-lag). Thus, these parasites can sustainably support a deficit of their intermediate host.

Keywords: Trematode; Life cycle; *Cerastoderma edule*; Biomass

Interspecific biotic interactions need at least the sympatric occurrence of two species. However, the presence of species is not sufficient to guarantee the sustainability of the interaction and we know that the characteristics of the habitat are also a key point. Pilot experiments by Huffaker (Begon et al., 1990) with mites demonstrated that a predator/prey system can be sustainable only if the substrate where they live displays a certain heterogeneity. This is a fragile equilibrium since too much heterogeneity provides too many refuges for prey, leading to predators finally starving and disappearing, while too little heterogeneity facilitates predation with the risk of prey extinction. This also raises the question of how many preys (and predators) are necessary to keep the system running, which is one of the main points analyzed in the Lotka-Volterra model that can also be adapted to other biotic interactions such as competition (Wangersky, 1978). Furthermore, a population's long-term persistence is linked to the Allee effect which describes how per capita growth in a population can reach zero and even become negative (i.e. risk of extinction) when the density of that population reaches a critical value (Courchamp et al., 1999). Here, we proposed extrapolating these concepts to parasite/host systems, by questioning whether a correlation exists between host biomass and associated parasite abundance.

Some parasites display complex life cycles, meaning that they need several host species in order to complete it. For example, trematodes typically need three species (Cribb, 2005). Adult parasites live and reproduce in the definitive host, a vertebrate (generally a shorebird or a fish). The parasites' eggs are emitted in the environment through host faeces and hatch into miracidium larvae that infect the first intermediate host (usually a mollusc). Each larva develops into a sac-like sporocyst which asexually produces cercariae larvae. These cercariae emerge from the first intermediate host and swim to penetrate the second intermediate host (an invertebrate or a vertebrate) and settle as metacercariae. The cycle is completed when the second intermediate host is predated by the definitive host, with metacercariae transforming into the adult stage in the final host. That life cycle considerably multiplies the number of possible biotic interactions. Some are pure

parasite/host interactions: a parasite can alter population dynamics of its first intermediate host (Jonsson and André, 1992), and/or its second intermediate host (Gunn et al., 2021). But more complex interactions also have been demonstrated. For example, for a given abundance of available parasites in the environment, hosts can “compete” for parasites with, eventually, less parasites per capita when the host density becomes higher (dilution effect) (Magalhães et al., 2017). Also, trematode parasites can compete inside their host (Keeney et al., 2008) or can be parasitized themselves (hyperparasitism) (Fermer et al., 2009). Some models also predict that parasites could modify the ecosystem by altering the grazing, predating, or competing pressure on their host (Mouritsen and Poulin, 2002). Finally, it becomes tricky to predict how a parasite/host interaction can sustain itself when one host species in the life cycle becomes rare.

The cockle *Cerastoderma edule*, a marine bivalve, is the second intermediate host of at least 14 trematode species (de Montaudouin et al., 2021a). Depending on the trematode species, the metacercariae abundance can remain low (i.e. less than 10 individuals per cockle) as is generally the case for species such as *Psilostomum brevicolle* or *Diphterostomum brusinae*, or it can reach high values (> 100 metacercariae per cockle) as is the case for *Gymnophallus minutus*, or it is highly fluctuating as for species of the family Echinostomatid. On the one hand, cockle biomass (or density) can display high spatial variability, with a negative correlation between cockle biomass and metacercariae abundance per individual host attributed to a dilution effect (see above) (Thieltges and Reise, 2007; Lagrue and Poulin, 2015). This negative correlation was found in other studies with other biological models (Mouritsen et al., 2003), but still is not the rule as no effect of cockle density on metacercariae abundance was found by Studer et al. (2013). On the other hand, cockle biomass can also display dramatic temporal fluctuations, with years when cockles are close to extinction (Beukema et al., 2010; Magalhães et al., 2016). Hypothesizing that other hosts in the life cycle remain at a constant density, we addressed the question whether fluctuations in a cockle biomass could affect the abundance of its associated trematode parasite species, and with what time-lag. Our

hypothesis was that when cockle biomass drops, the parasites have greater difficulty in completing their life cycle and their abundance decreases in all hosts including in their second intermediate host (herein the cockle).

Between 1999 and 2013 ($n=15$ years), cockles were collected every month on Banc d'Arguin, France ($44^{\circ}40'N$; $1^{\circ}10'W$) using six 0.25-m^2 quadrates sieved with a 1 mm mesh. The quadrates were aligned along a 100 m transect parallel to the water border, between 0.5 and 2.0 m above low tide level. Cockles were counted and sized. Their biomass was computed based on a weight/length relationship (Gam et al., 2010), and the mean annual biomass was calculated. Concomitantly, 10 cockles per cohort and per month were dissected in order to identify and count their trematode parasites. Then, the mean number of parasites (metacercariae) per cockle and per year were also calculated. Finally, the correlation between the mean annual cockle biomass and the mean trematode abundance (per species and total) was estimated by a "shift analysis" (Spearman test): correlation of cockle biomass of year 0 compared with parasite abundance of year 0, then with parasite abundance of year +1, +2, etc.

A total of seven parasite species were identified as metacercariae, but four of them (Table 1) represented 88 - 100% of the total abundance, depending on the year. The mean cockle biomass fluctuated between $1.3\text{ g Dry Weight (DW)/m}^2$ (2013) and 36.9 gDW/m^2 (2010) and the mean number of trematodes between 17 metacercariae/cockle (2010) and 346 metacercariae/cockle (2005). The time shift analysis showed that the first positive and significant correlation ($Rho=0.89$, $P<0.05$, $n=7$) between the number of metacercariae and the cockle biomass is reached when an 8 year time-lag is applied (Fig. 1). This suggests that a modification of the second intermediate host biomass (cockles) would alter trematode dynamics after a time period of 8 years. For example, cockle biomass was particularly low in 2002, but trematode abundance remained high until 2010. In the present case, this positive correlation is mainly due to two dominant trematode species, *Curtuteria*

arguinae which represents 37% of metacercariae ($Rho=0.86$, $P<0.05$, $n=7$) and *Himasthla interrupta* which represents 32% of metacercariae ($Rho=0.79$, $P<0.05$, $n=7$) (Fig. 1).

We believe our study was the first attempt to investigate the relationship between host biomass and the abundance of associated trematode parasites at a temporal scale. This time-lag of 8 years suggests a strong inertia in the parasite-host system. It is much longer than the cockle's lifespan which in theory can reach up to 6 years but is rather < 2 years on Banc d'Arguin (de Montaudouin et al., 2021b). The maximum lifespan of metacercariae in the wild, however, remains unknown but cannot exceed its host's lifespan. Under in vitro conditions at least, metacercariae of *Fasciola hepatica* survive ca. 6 months (Luzón-Peña et al., 1992). This long 8 year time-lag between host biomass and abundance of metacercariae per cockle also represents an important advantage for trematode parasites, balancing the negative effect of their host specificity. Indeed, the sudden scarcity of the second intermediate host represents a danger for parasites if there is no alternative host. But these effects could be counterbalanced by (i) the longevity of the parasites in the definitive host which could be of several years (Cribb, 2005), or (ii) even in the first intermediate host whose infection has been maintained for 2 years under our laboratory conditions (unpublished data). We could also expect that the parasite/second intermediate host system would last even longer if parasites are introduced in the studied ecosystem from infected definitive or first intermediate hosts coming from other areas. However, our study suggests that if the second intermediate host population collapses, the local associated parasite community is eventually exhausted. In comparison, predator-prey dynamics seem much more reactive, i.e. with a lower inertia, at least when no alternative prey presents itself to a given predator. Under experimental conditions, the time between prey extinction and predator collapse was a few days in mites (Begon et al., 1990). In the field, the delay between snowshoe hare (prey) and lynx (predator) extinction was 1-2 years (Begon et al., 1990). Our results suggest an effect on the parasite population appearing with a time-lag of 8 years. Our demonstration was only based on the correlation between cockle biomass and

metacercariae number in cockles, yet other confounding factors than the second intermediate host biomass could explain this significant correlation. In particular, the abundance of the bird definitive host can promote not only first intermediate host infection (Skirnisson et al., 2004; Fredensborg et al., 2006), but also second intermediate host infection as was demonstrated in *Mytilus edulis* (Wilson et al., 2013). On Banc d'Arguin, reliable bird counting data were not available during the study period (1999-2013), except for the European oystercatcher *Haematopus ostralegus*. However, yearly fluctuations were too small (mean = 299 birds, minimum = 254 and maximum = 331, (unpublished data) to explain infection variation by the associated trematode, *G. minutus*. Concerning the two main parasite species involved, on the one hand it is impossible to explore whether other hosts of *C. arguinae* could be involved since its life cycle remains unknown. On the other hand, for *H. interrupta*, *Peringia ulvae* (first intermediate host) and *Larus* spp. (definitive host) were ruled out as they are always abundant in this national nature reserve (personal observations). Finally, it is highly improbable that abiotic factors (temperature, salinity) impact parasite infection with an 8 year time-lag.

Thus, we can assume that the second intermediate host biomass is negatively correlated to parasite abundance on a short time-scale (ca. 1 year) due to the dilution effect (Magalhães et al., 2017): cercariae are distributed in many cockles, reducing parasite abundance per cockle. But the present study suggests that the biomass of the second intermediate host fuels the dynamics of the parasite life cycle as well, with effect after a longer period of time (ca. 8 years).

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Figure legend

Fig. 1. Rho coefficient values (Spearman test) of correlation between cockle *Cerastoderma edule* biomass and mean parasite abundance per cockle, for applied time shifts (years) ranging between 0 ($n=15$) and 9 years ($n=6$). The number of parasites was pooled (Total) and there was a particular focus on the two species displaying significant correlations with their host's biomass, *Curtuteria arguinae* (*Ca*) and *Himasthla interrupta* (*Hi*).

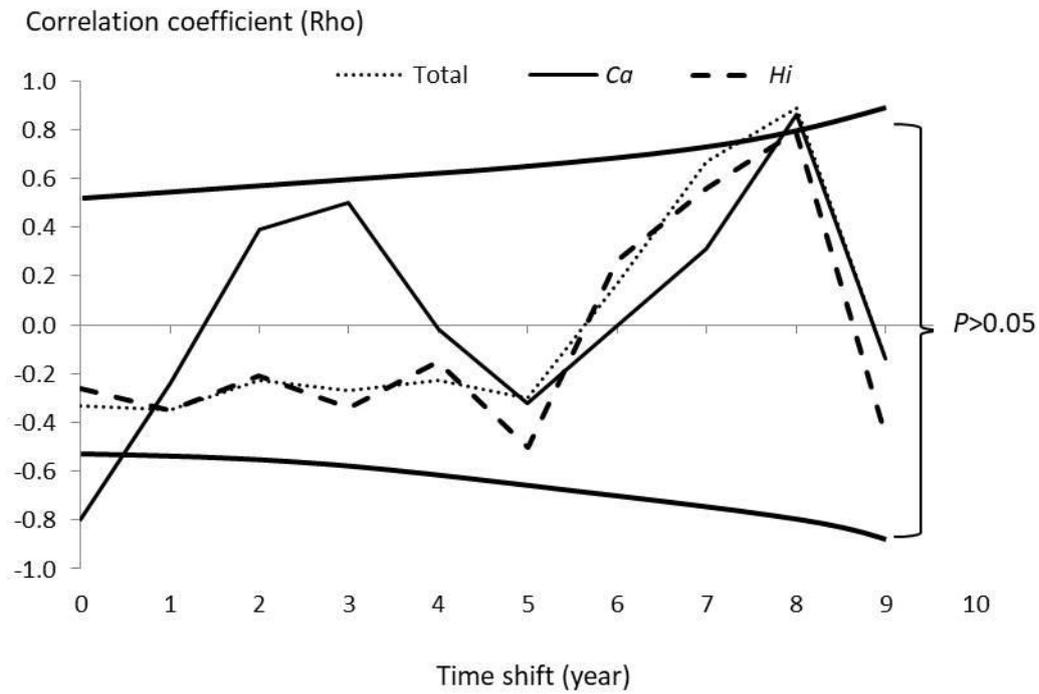


Table 1

Mean biomass of cockles (*Cerastoderma edule*; g dry weight.m⁻²) and mean abundance of trematode parasites (metacercariae.cockle⁻¹).

| Year | Biomass | <i>Gm</i> | <i>Ca</i> | <i>Hi</i> | <i>Hq</i> | Others | Total |
|------|---------|-----------|-----------|-----------|-----------|--------|-------|
| 1999 | 17.2 | 40 | 11 | 0 | 10 | 2 | 64 |
| 2000 | 9.4 | 10 | 6 | 2 | 24 | 2 | 45 |
| 2001 | 15.0 | 8 | 1 | 2 | 32 | 3 | 44 |
| 2002 | 5.0 | 7 | 28 | 12 | 27 | 3 | 78 |
| 2003 | 5.1 | 4 | 35 | 126 | 9 | 2 | 177 |
| 2004 | 12.6 | 41 | 9 | 92 | 9 | 1 | 152 |
| 2005 | 25.8 | 285 | 1 | 50 | 9 | 1 | 346 |
| 2006 | 21.2 | 38 | 4 | 22 | 4 | 2 | 69 |
| 2007 | 14.0 | 18 | 16 | 16 | 3 | 2 | 55 |
| 2008 | 11.4 | 12 | 10 | 5 | 2 | 1 | 30 |
| 2009 | 7.0 | 0 | 23 | 19 | 3 | 1 | 47 |
| 2010 | 36.9 | 0 | 7 | 5 | 3 | 2 | 17 |
| 2011 | 19.0 | 2 | 7 | 10 | 5 | 2 | 26 |
| 2012 | 6.8 | 7 | 25 | 20 | 9 | 4 | 65 |
| 2013 | 1.3 | 9 | 43 | 37 | 13 | 4 | 106 |

Gm, *Gymnophallus minutus*; *Ca*, *Curtuteria arguinae*; *Hi*, *Himasthla interrupta*; *Hq*, *Himasthla*