

A sea of change: Tracing parasitic dynamics through the past millennia in the northern Adriatic, Italy

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ABSTRACT

Our study uses data from Holocene core samples and modern death assemblages to understand how human-induced environmental change in the northern Adriatic Sea (Italy) may have affected parasite-host dynamics in the economically important bivalve *Chamelea gallina*. Thirty-one radiocarbon dates confirm temporal distinctness between the periods before and after the onset of significant human influence and confirm that trematode prevalence has decreased by an order of magnitude over the past ~2 k.y. The median number of parasite-induced pits per bivalve host and parasite aggregation has also decreased significantly, signaling a substantial decrease in the effective population size of digenean trematodes. Gaussian finite mixture modeling of pit size does not support the hypothesis of parasite extinction. Combined, these results indicate the (potentially ongoing) collapse of parasite-host interactions in *C. gallina* in concert with human influence on the Adriatic and its transition to an “urban sea.”

INTRODUCTION

Parasites play an important role in ecosystems and can have a significant impact on ecosystem stability (Hudson et al., 2006). Therefore, changes in the prevalence, distribution, or diversity of parasites could signal disruptions in ecological functions due to habitat degradation, pollution, or climate change (Wood et al., 2023). However, ecological monitoring, being restricted in time, suffers from the inability to discriminate short-term fluctuations from long-term regime shifts (i.e., large, persistent changes in ecosystem structure). In this respect, long-term geological data can provide key contexts to current population status and trends. Given their substantial ecological influence, it is useful to have similar long-term data for parasites. Although small, soft-bodied parasites have a low preservation potential, some parasite-host interactions are recorded on the skeleton of their hosts (Huntley et al., 2021), enabling a temporal scale of observation well beyond that of even the longest-term ecological studies (De Baets et al., 2021a). Our goal is to leverage this underexploited fossil record to reconstruct recent par-

asite-host dynamics and to place those dynamics in a broader historical context of increasing human influence on ecosystems (e.g., Huntley and Scarponi, 2021).

Trematode flatworms (Platyhelminthes) are complex life cycle parasites (i.e., with multiple hosts) that induce a characteristic, preservable growth response (pitting) on their bivalve host's shell interior (Ruiz and Lindberg, 1989; Huntley et al., 2021). We use the Holocene sedimentary record to assess parasitic infestation in *Chamelea gallina*—an ecologically and economically important bivalve—before and after the onset of significant human influence in shoreface ecosystems of the Adriatic Sea, one of the most heavily altered marine regions globally (Lotze et al., 2011). Specifically, by integrating radiocarbon dating with analyses of parasite intensity (the number of pits per host) and size distributions of trematode-induced pits, we expand the temporal and geographical scope of neontological studies supporting claims of anthropogenic declines in parasitism in marine environments (Wood et al., 2023). We hypothesize a decline in parasite-host interactions during the past 2 k.y., which was characterized by decreased parasite prevalence and intensity (accounting for differences in depositional environment, time averaging, and host body size) and the extirpation of parasite taxa. In this work, we reveal, from sedimentary succes-

sions in Italy, a case for the collapse of parasitic infection in *C. gallina* that occurred during the transition of the Adriatic into an “urban sea” (coastal estuaries and marginal seas with drainage basins that are extensively developed and populated by humans). While a collapse in parasitism may seem positive, it signals a simplification of the trophic structure and a loss of crucial ecological functions along with the parasites.

METHODS

We analyzed trematode-induced pits from *C. gallina* valves sourced from five samples (0.375 dm³ each) of two sediment cores (cores 240-S8 and 223-S5, drilled by the Emilia-Romagna Geological Survey) from late-Holocene variably fluvial-influenced shoreface deposits, and 11 modern death assemblages (MDAs; 0.375 dm³) from shoreface settings of the Adriatic Sea (Fig. 1; Table 1). The Holocene stratigraphic architecture of the study area was reported by Amorosi et al. (2016). Sediment samples were dried at 45 °C for 24 h, soaked in 4% H₂O₂, and wet-sieved with a 1 mm sieve (Huntley and Scarponi, 2012). We selected 31 well-preserved, non-parasitized valves for low-precision radiocarbon dating (Bush et al., 2013).

We took scaled photomicrographs of all valves with trematode-induced pits oriented perpendicular to the commissural plane. Using ImageJ 1.53t (<https://imagej.net/ij/>; Schneider et al., 2012), we measured bivalve anterior-posterior length, dorsal-ventral height, and the primary and secondary axes of the trematode-induced pit (Fig. 1). Trematode prevalence is the proportion of valves within a sample with at least one trematode-induced pit. Trematode pits are equally likely to occur on both valves, and no correction is needed to calculate prevalence, as with predatory drill holes (Huntley, 2007). Pit size is the geometric mean of the primary and secondary axes, and host body size is the geometric mean of valve length and height. We

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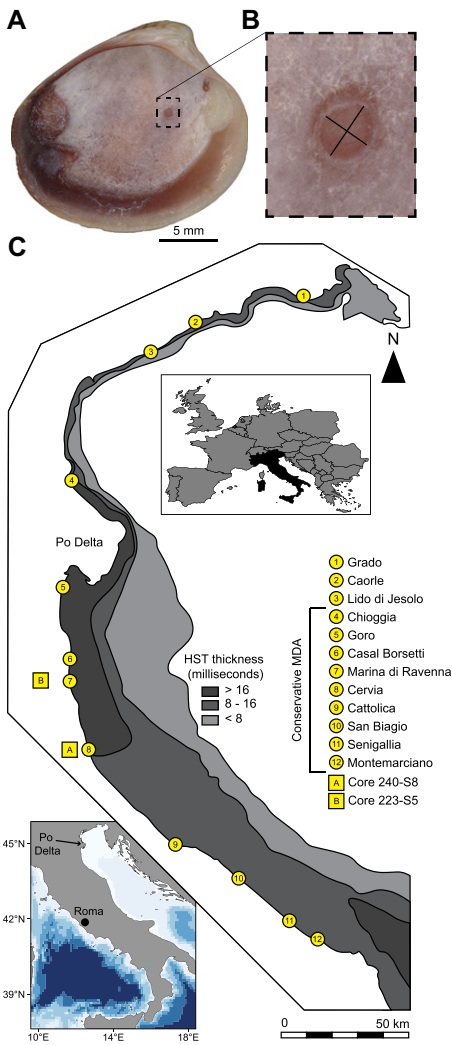


Figure 1. (A) *Chamelea gallina* (Lido di Jesolo, Po Delta, Italy) with trematode-induced pits. (B) Enlarged view of a pit from the valve in panel A showing the primary and secondary axes measured. (C) Index map of sampling locations of modern death assemblages (MDAs, circles) and Holocene sediment core samples (squares). HST—highstand systems tract.

used the *mclust* package (Scrucca et al., 2016; <https://mclust-org.github.io/mclust/>) in R (R Core Team, 2021) to produce Gaussian finite mixture models of pit size separately for Holocene and modern samples. This function has two model types for univariate size data: one assuming equal variance, and one assuming varying variance values of the Gaussian distributions. Bayesian information criterion (BIC) values are calculated for one to nine Gaussian distributions under both model types, and the preferred model is the one with the highest BIC value (see Supplemental Material¹ for assumptions of this

¹Supplemental Material. Supplemental data, methods, results, and R script. Please visit <https://doi.org/10.1130/GEOL.S.25776909> to access the supplemental material; contact editing@geosociety.org with any questions.

approach). We conducted Spearman correlation analyses comparing the median pit size to the number of pits per valve in the Holocene and modern samples.

RESULTS

The ten radiocarbon dates of *C. gallina* from core 240-S8 are consistent with their stratigraphic position with a median calendar age of 175 BCE (interquartile range of valve calendar ages [IQR] = 267 yr) for the 13.1 m sample and a median of 679 BCE (IQR = 88 yr) for the 13.7 m sample (Table 1). The median age for pooled core samples is 543 BCE (IQR = 444 yr), which is significantly older than the median age (1819 CE, IQR = 297 yr) of the 21 pooled MDA dates (Fig. 2; Table 1; Table S1 in the Supplemental Material). Three outliers from Grado are more than 1 k.y. older than the other specimens, leading us to be concerned about greater time averaging (and possible spurious trends) in the northern MDA samples from such starved coastal settings. Therefore, we conducted analyses on both MDA data and a subset that excludes samples from Grado, Caorle, and Lido di Jesolo (conservative MDA [CMDA]; median age = 1913 CE, IQR = 190 yr; comparable to Holocene sample time averaging).

We identified 838 trematode pits in 240 infested valves out of 4567 examined *C. gallina* valves (Table 1). Trematode prevalence, measured by either pooled valves or median of sample prevalence, is significantly higher in Holocene samples than in the CMDA or MDA samples (Fig. 2; Table S2). Because trematode pits tend to be found on larger valves (Huntley, 2007; Huntley and Scarponi, 2012, 2021), we investigated valve size. CMDA and MDA *C. gallina* median host valve sizes (21.3 mm and 22.1 mm, respectively) are significantly larger than those from Holocene cores (14.2 mm) and are not distinguishable from one another (Fig. 2; Table S3). Trematode-induced pit size ranged from 0.117 mm to 1.708 mm. The median Holocene pit size (0.497 mm) is significantly larger than that of CMDA and MDA pits (both 0.335 mm, $p = 7.99 \times 10^{-9}$; Fig. 2; Table S4). No significant ($r_{\text{Pearson}} = -0.025$, $p = 0.48$) correlation exists between host size and pit size (Fig. S1).

The Gaussian finite mixture models established that the Holocene ($n = 715$) and MDA ($n = 123$) samples are best interpreted as two Gaussian distributions with differing variance structures (Fig. 3; Figs. S2–S4; Tables S5 and S6). The Holocene pit sizes are characterized by a component with a mean size of 0.475 mm, which comprises ~84% of the data, and a second component with a mean size of 0.745 mm for the remaining ~16%. MDA pits are characterized by two components with mean sizes of 0.379 mm (78%) and 0.777 mm (22%) (Fig. 3). The CMDA ($n = 62$) data are best interpreted as three components with mean sizes of 0.320 mm

(20%), 0.518 mm (70%), and 0.814 mm (10%). The median number of pits per infested valve is 3 for Holocene samples and 2 for both MDA and CMDA samples ($p = 0.02$ and $p = 0.003$, respectively). There is a significant negative correlation ($\rho = -0.193$, $p = 0.01$) between median pit size and the number of pits per valve among Holocene samples. These relationships among MDA and CMDA samples are non-significant ($\rho = -0.027$, $p = 0.88$; $\rho = -0.271$, $p = 0.13$, respectively; Fig. 3; Table S7).

DISCUSSION

Pre-Anthropogenic Impact Baseline

Conservation paleobiology uses geohistorical data to address modern conservation challenges and provides baseline data beyond direct ecological monitoring (Dietl et al., 2015). We determined the baseline for trematode-bivalve interactions prior to anthropogenic impact and demonstrate their collapse in the Adriatic Sea over the past ~2 k.y. Specifically, in settings dominated by *C. gallina*, trematode prevalence decreased by nearly an order of magnitude (Fig. 2). Even though there is substantial geographic variation in parasitic prevalence within our MDA samples, the highest prevalence value in the modern samples (0.145, Montemarcano; Fig. 1) is less than half of the highest prevalence in Holocene samples (0.402, 13.5 m of core 240-S8; Fig. 2, Table 1), suggesting a real temporal difference. Our previous work demonstrated that trematode pits are positively associated with starved depositional conditions, sea-level rise, and large host body size (Huntley, 2007; Huntley and Scarponi, 2012, 2015, 2021; Huntley et al., 2014; Scarponi et al., 2017). All Holocene samples are from similar sediment types and deposited in a progradational setting, further highlighting their high prevalence values. A slight increase in relative sea level since the late nineteenth century (an average rise of 1.2 mm/yr; Carbone et al., 2011) does not seem to have had a significant effect on modern parasite prevalence values. Despite host sizes being significantly higher in the modern samples, prevalence is significantly lower relative to the Holocene. This size difference is likely due to the 10-cm-diameter Holocene cores. Nevertheless, this strengthens our argument for declining parasite prevalence. Concurrently, the median number of pits per infested valve decreased significantly. Trematode-induced pits are generally highly aggregated among their Holocene *C. gallina* hosts, meaning that most hosts have only a few pits, and a few hosts have many (Huntley and Scarponi, 2021). This pattern is common among macroparasite-host interactions and effectively increases the parasite population density (Shaw and Dobson, 1995). The strong decrease in aggregation of parasites indicates a collapse in the effective parasite population density in the study area.

TABLE 1. TREMATODE PARASITISM AND RADIOCARBON RESULTS BY SAMPLE

Sample Location	<i>Chamelea gallina</i> examined	Infested	Pits not obscured	Prevalence	Mean intensity	¹⁴ C dated specimens	Median age (calendar)	IQR
Grado	198	20	46	0.101	2.3	7	1576.0	1783.5
Caorle	585	5	12	0.009	2.4	—	—	—
Lido di Jesolo	538	1	3	0.002	3.0	—	—	—
Chioggia	344	23	20	0.067	0.9	—	—	—
Casal Borsetti	456	0	0	0.000	—	—	—	—
Marina di Ravenna	746	3	14	0.004	4.7	7	1786.0	50.5
Cervia	85	0	0	0.000	—	—	—	—
Catollica	213	13	14	0.061	1.1	—	—	—
San Biagio	319	13	3	0.041	0.2	—	—	—
Senigallia	279	0	0	0.000	—	7	1984.0	0.5
Montemarciano	62	9	11	0.145	1.2	—	—	—
240-S8 12.5 m	29	4	18	0.138	4.5	—	—	—
240-S8 13.1 m	358	111	499	0.310	4.5	5	-175.0	267.0
240-S8 13.5 m	87	35	190	0.402	5.4	—	—	—
240-S8 13.7 m	—	—	—	—	—	5	-679.0	88.0
240-S8 14.8 m	248	2	4	0.008	2.0	—	—	—
223-S5 14.9 m	20	1	4	0.050	4.0	—	—	—

Notes: Pits not obscured: number of pits completely visible in the photomicrographs. Prevalence: number of infested per number examined. Mean intensity: number of pits not obscured per number infested. IQR—interquartile range of valve calendar ages in a sample. Dashes indicate no data.

At first glance, the significant decrease in median pit size through geological time could indicate the extinction of a larger-sized trematode taxon. However, the density estimation modeling results (Fig. 3) for the Holocene and MDA samples indicate that both samples are made up of two Gaussian distributions: one commonplace small-sized taxon and one that is less common, large, and with greater size variation. An analysis of the CMDA samples suggests similar results, with the presence of a third component that is even smaller, comprising ~20% of the observations. We are hesitant to interpret these latter results at face value because the sample size for the CMDA model ($n = 62$) approaches the minimum needed to model one-dimensional data with high certainty (Psutka and Psutka, 2019). The important point is that even with the most conservative approach, there was no decrease in the number of trematode pit size groups. In other words, there is no evidence for the loss of a trematode taxon over the past ~2 k.y. in the northern Adriatic Sea.

These results are consistent with Zuschin et al.'s (2024) work demonstrating a recent col-

lapse in predator-prey interactions in the northern Adriatic Sea due to anthropogenic habitat degradation and an increase in eutrophication-driven hypoxia. Specifically, they found a decrease in predator abundance, a turnover toward less-preferred prey organisms, and a size increase in a dominant hypoxia-related prey species. The depletion of large predators and consumers has caused a strong simplification of the food web in the region. Importantly, both studies documented parasitism and predation beyond the temporal range of ecological monitoring and provided direct insights into the transition of the nearshore settings of the Adriatic into its current urban sea state.

Ecological Implications of Declining Parasitism

The seeming persistence of parasite taxa during this time of decreasing prevalence does not preclude other significant changes in the life history of trematodes. In the Holocene samples, there was a negative correlation between average pit size and the abundance of pits within a valve—a common pattern among

parasites—but this relationship broke down in the modern samples. This situation highlights interesting developmental trade-offs, as metacercaria (infective cyst stage) size can predict adult trematode size in the definitive host, which strongly predicts reproductive output (Saldanha et al., 2009). Thus, the higher aggregation of pits indicates higher population density of trematodes in the late Holocene. Conversely, lower pit aggregation in the modern samples results in reduced population density, making it less likely for metacercariae to reach adulthood in their definitive host. This is concerning because parasites are key components of healthy ecosystems. Parasite diversity often mirrors that of the community on which they depend for transmission (Kamiya et al., 2014). Studies of restored ecosystems display a rebound in the prevalence and richness of digenetic parasites (Huspeni and Lafferty, 2004), and parasitism exhibits a strong positive correlation with diversity and negative correlations with origination and extinction rates across the Phanerozoic (De Baets et al., 2021b). However, anthropogenic impacts can decouple the relationship between

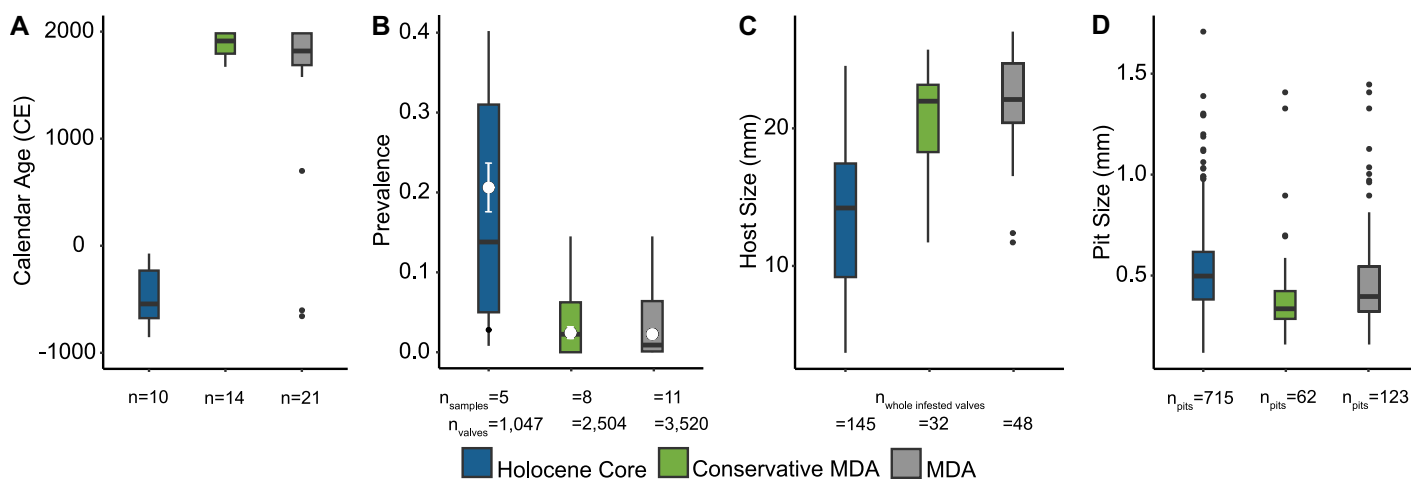


Figure 2. (A) *Chamelea gallina* calendar ages. (B) Trematode prevalence: boxplots (sample prevalence values) and data point with binomial-derived 95% confidence interval (in white; based on pooled individuals). (C) *C. gallina* body size of whole infested valves. (D) Trematode pit size. MDA—modern death assemblage.

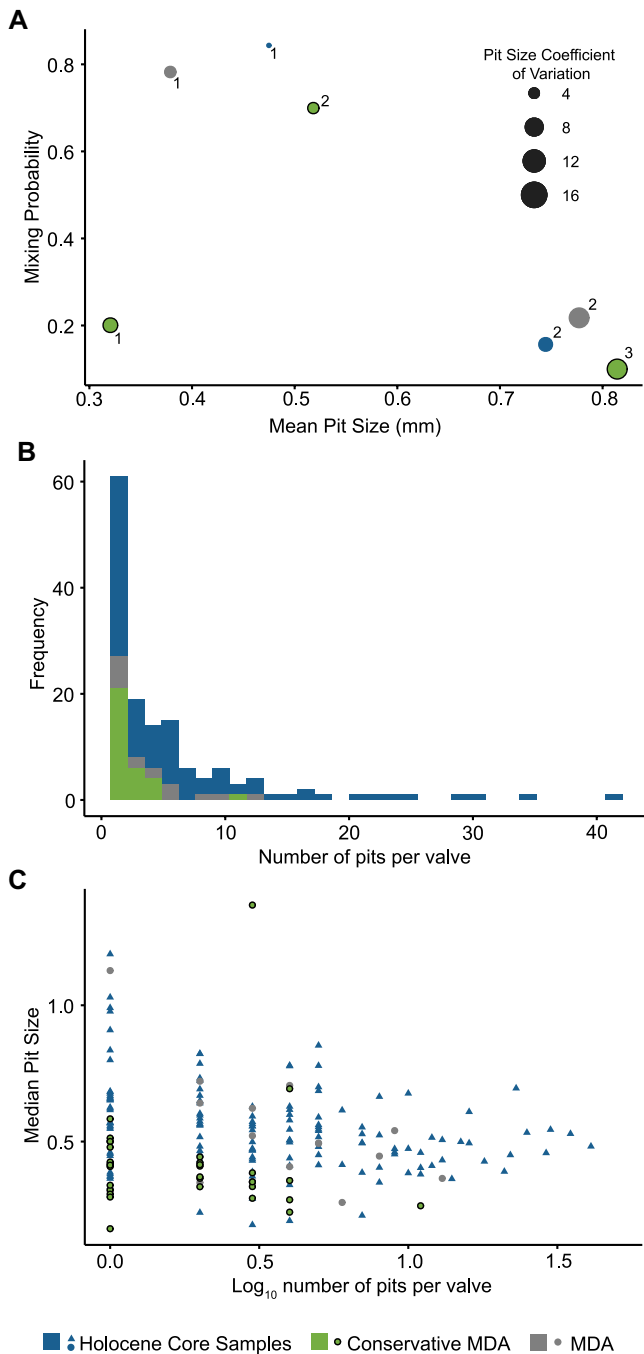


Figure 3. (A) Gaussian finite mixture models for Holocene core samples, modern death assemblages (MDAs), and conservative MDAs. Numbered points refer to the components produced by each model (see Supplemental Material [see text footnote 1] for details). (B) Frequency distribution of intensity values for infested *Chamelea gallina*. (C) Intensity values and median pit size per valve.

host and parasite biodiversity (Wood et al., 2018). Our findings are consistent with other studies that show a decrease in the equitability of *C. gallina*-dominated communities and a reduction of the targeted bivalve over time in the Adriatic Sea (Scarponi et al., 2023; Carlucci et al., 2024), raising concern about the near-future status of *C. gallina*.

What Causes the Significant Decline of Adriatic Trematodes in the Past ~2 k.y.?

Approximately 2.5 k.y. ago, the study area saw a general trend toward a dryer climate (Stefani, 2017) and rapid complex progradational coastal dynamics south of the Po Delta (Amo-

rosi et al., 2017). The region experienced sustained local anthropogenic impacts beginning in Roman times, which became more widespread and intense since the mid-twentieth century (Trincardi et al., 2023). The timing of the collapse of parasitism suggests a link to anthropogenic causes, but testing the specific drivers is not possible with our data. However, pollution and other anthropogenic-related stresses are often associated with a reduction in parasite species richness (Marcogliese, 2004). Parasite transmission may be hindered when intermediate hosts are reduced and free-living life stages (cercariae) are directly affected by these stressors (Mackenzie, 1999). Ocean acidification

could be one such factor. The pH of northern Adriatic Sea water decreased by 0.063 units between 1983 and 2008 CE (Luchetta et al., 2010), twice the current global average rate (Hönisch et al., 2012). Experiments have shown that lowered pH reduces cercarial longevity and metacercarial survival (MacLeod and Poulin, 2015). The timing of ocean acidification as a driver of the pattern of parasitism decline is consistent with the ages of our CMDA samples.

SUMMARY

Our study shows that the dynamics of certain parasite-host relationships reconstructed from recent sedimentary successions can offer a quantitative benchmark against which to evaluate the status of present-day ecosystems. In this case, trematodes became much less common with the onset of human influence, infecting their hosts less frequently and less intensely. We interpret this decline in parasitism to be cause for concern and consistent with numerous other lines of evidence for plummeting ecosystem function and health.

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