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Diversity of metazoan parasites of the introduced oyster species *Crassostrea gigas* in the Exe Estuary

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Temporal patterns in metazoan parasite community diversity of *Crassostrea gigas*, (Lamellibranchia: Ostreidae) were studied in the Exe Estuary at monthly intervals over one year and in relation to host age-classes. A total of four metazoan species was found to parasitize *C. gigas* in the Exe Estuary: the turbellarian *Paravortex* sp., cercaria Lepocreadiidae, metacercariae of *Renicola roscovita* and the copepod *Mytilicola intestinalis*. Only *R. roscovita* and *M. intestinalis* were present in all months throughout the year and in all host age-classes. Analysis of the metazoan parasite community at individual host level revealed little variation in community structure with respect to season or host age, as only a slight increase in diversity values was observed during the summer months. However, community diversity does vary from year to year, as shown by comparison between host age group samples in three consecutive years. None of the parasites are specialist to oysters but all appear to be widespread and abundant parasite of other lamellibranch species.

INTRODUCTION

Invertebrates have generally been studied for their role as intermediate hosts in the life cycles of a great variety of helminth parasites, particularly in relation to the transmission of human and economically important animal diseases (Malek, 1980). Although many surveys and some studies of both protozoan and helminth population dynamics have been conducted on a great variety of invertebrate–parasite systems (the majority involving gastropod–digenean systems) (Lauchner, 1980, 1983), the search for patterns of parasite community composition and structure, and their causation, has been limited (Sousa, 1990; Kuris, 1990; Femandez & Esch, 1991a,b; Kuris & Lafferty, 1994). This is despite the fact that it is now widely recognized that invertebrate hosts must play an important role in the processes structuring helminth communities of vertebrates and indeed, helminth communities in invertebrates can determine the structure of the helminth communities of vertebrates (Edwards & Bush, 1989; Bush et al., 1993; Sousa, 1994).

Studies on gastropod hosts indicate that their parasite communities are composed mainly of precercarial stages of digeneans (i.e. miracidium, sporocyst and redia). Furthermore, communities may be rich at component level, whilst they are generally depauperate at infracommunity level (Sousa, 1990; Kuris, 1990; Fernandez & Esch, 1991b; Williams & Esch, 1991; Snyder & Esch, 1993; Kuris & Lafferty, 1994). Infracommunities in gastropods seem to be structured predominantly by antagonistic interactions among the larval digeneans, with dominating redial stages feeding on those of subordinate species (Sousa, 1990; Kuris, 1990; Lafferty et al., 1994). Species presence is thus in turn determined by spatial and temporal heterogeneity in recruitment and by competition over time according to a hierarchy of dominance of the species (Fernandez & Esch, 1991a,b; Snyder & Esch, 1993; Lafferty et al., 1994).

Oysters are one of the most important commercial species of bivalves. They can act as first or second intermediate host for several metazoan parasite species (Cheng, 1967; Lauckner, 1983; Bower et al., 1994) and although many individual helminth species have been investigated in terms of their population dynamics and their effect on the host (Lauckner, 1983; Bower et al., 1994), neither community structure nor temporal variation have been studied.

Communities in general tend to change over the time. Temporal changes in community structure reflect the presence–absence of species, and the absolute and relative density levels of the species (Putman, 1994). Such changes tend to be seasonal and highly dependent on seasonal environmental changes (Wolda, 1987). Helminth parasites have complex life cycles (often including more than a single host) and temporal and seasonal patterns play an important role in processes of recruitment of each of the life cycle stages to their respective host (Chappell, 1969; Esch, 1983). Thus, temporal changes in population densities of species within the community are particularly to be expected.

Summary parameters of helminth communities (such as species richness, diversity and dominance) vary in relation to host age and season in a variety of vertebrate and invertebrate hosts (Cloutman, 1975; Wallace & Pence, 1986; Fernandez & Esch, 1991b; Snyder & Esch, 1993). It is therefore necessary in any community investigation to determine whether there are seasonal and age related changes in community structure before undertaking any other community study. In this paper we present data on metazoan parasite communities of *Crassostrea gigas*

Thunberg, from the Exe Estuary during one year of monthly sampling and in different oyster age groups sampled one year apart in order to identify temporal patterns in species composition, richness and diversity.

MATERIALS AND METHODS

Study area

The Exe Estuary (Figure 1) has been widely studied (see papers in Boalch, 1980). It has been classified as a bar-built estuary distinguished by recent sedimentation, with a bar across the mouth. The estuary consists of a narrow low-tide channel meandering between extensive intertidal mud and sand flats. The sand and muddy sand intertidal flats typically support large populations of the commercially exploited bivalves *Cerastoderma edule* (L.) and *Mytilus edulis* L., smaller populations of *Scrobicularia plana* (daCosta), and *Tellina tenuis* (daCosta), and a large population of different species of resident and wintering shore-birds, feeding mainly on the invertebrate community of the estuary (English Nature, 1993).

Crassostrea gigas (Pacific oyster), first introduced as larvae to Britain in 1962, from British Columbia, Canada, it is now cultivated in many estuaries and sheltered coastal waters of the UK (C.G. Askew, personal communication). Since its introduction into the UK, there have been reports of natural settlement in some of the estuaries where it is being cultivated including the Exe Estuary (Spencer et al., 1994).

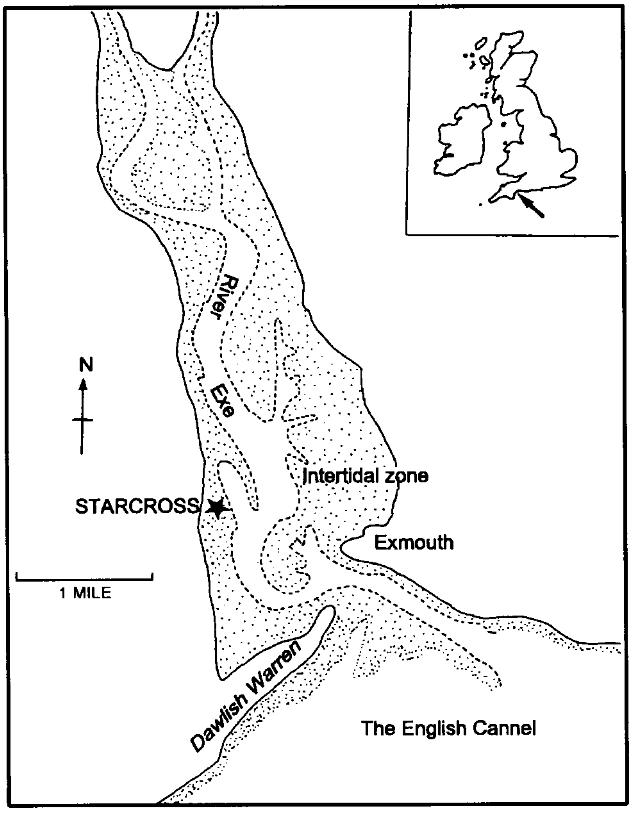

Figure 1. Map of the Exe Estuary, indicating the mudflat of Starcross.

Comparison between monthly samples

Monthly samples of 30 (26 in February) *C. gigas* were collected from November 1993 to October 1994 (except for March) at the mudflat at Starcross on the margin of the upper estuary of the River Exe (Figure 1). Oysters were hand picked during low tide and transported to the laboratory where they were maintained in seawater tanks until examination (always within two weeks of collection). Age was determined in the field by counting the numbers of annual growth rings and only oysters of 5 and 6-y old were collected (this was the most frequent year-class found in Starcross). Oysters were opened by cutting the adductor muscle and each organ was compressed between two slides and examined under the dissection microscope. All parasites were identified and counted *in situ.*

Comparison between host age groups

To investigate changing patterns of helminth communities with respect to host age, year-classes had to be grouped as there were not enough oysters of each year-class to constitute a large enough sample. Three age groups were constructed as follows: group 1, oysters between 2 and 4-y old; group 2, oysters between 5 and 7-y old; group 3, oysters >8-y old. A sample of 30 oysters from each age group was collected in April 1995. An extra sample of 60 oysters (of age groups 1 and 3 only) was collected in April 1996 to check variations in patterns found in the 1995 sample.

Data analysis

The terms prevalence and abundance were used as defined in Margolis et al. (1982). Helminth community analysis was performed at infracommunity level *(sensu* Holmes & Price, 1986). Infracommunities were summarized by: richness (the mean number of helminth species per host), the mean number of helminth individuals per host and the mean value of Brillouin's diversity index. Mean percentage similarity per month was calculated for all possible pair combinations of infected hosts. Community measurements were calculated as in Magurran (1988).

Significance in differences between prevalence and abundance values between seasonal samples and age groups were tested by using a *G*-test with William's correction for independence of prevalence (Sokal & Rohlf, 1981) and a Kruskal–Wallis test for independence of medians for abundance data (Conover, 1980)

Significant differences between monthly samples in the mean number of species per host and Brillouin's diversity index were tested by one-way ANOVA followed by a Tukey test (Sokal & Rohlf, 1981). For significant differences in the mean number of helminth individuals per host, a nonparametric Kruskal–Wallis test was used (Conover, 1980). Significance was taken at $P<0.05$ unless otherwise noted.

The expected frequency of double infections in a host as a result of independent random co-occurrence (*fc*) was calculated as in Kuris (1990):

$$fc = \mathrm{A} \times \mathrm{B}/\mathrm{N} \tag{1}$$

where A and B are observed frequencies of species A and species B respectively and N is the total number of hosts examined. A simple 2×2 contingency table analysis was used to contrast expected and observed frequencies. For this analysis pooled data from all monthly samples were used. Independence of occurrence between helminth species was tested by using a *G*-test with Williams' correction (Sokal & Rohlf, 1981).

RESULTS

Comparison between monthly samples

Four metazoan species parasitized *Crassostrea gigas* throughout the year: the turbellarian *Paravortex* sp., occurred in the oyster intestine; cercaria Lepocreadiidae, found in gonad tissue; metacercariae of *Renicola roscovita* (Stunkard), encysted in the palps, digestive gland and, rarely, in the mantle; and the copepod *Mytilicola intestinalis* Stever, living in the intestine. Prevalence and abundance of each species in each month are shown in Table 1.

Only two species were present in all samples: *R. roscovita* and *M. intestinalis*. Prevalence of both species varied over the year (Table 1), but seldom (two occasions) reached or exceeded 50%. *Renicola roscovita* reached a peak of prevalence in September (40%) and a nadir in May (10%) (Table 1). Abundances showed a slightly different trend to prevalence: maximum value was found in January (2.50±1.43 parasites per examined host) and minimum in May (0.13±0.07) with an increase over summer and autumn. However, no differences in either prevalence or abundance between months were significant (G=12.91, $\chi^2=18.3$, df=10 and H=11.64, df=10).

Prevalence and abundance values of *M. intestinalis*, by contrast, reached their maxima during the summer months, and minima between November and January (Table 1). Maximum value of prevalence was recorded during June (53.33%) and minimum value of abundance during August (0.76±0.23 individuals per examined host). Minimum values for both parameters were recorded in November (3.33% prevalence and 0.03±0.0 abundance). Monthly samples were significantly different between the winter and summer (G=51.08, $\chi^2=18.3$, df=10 and H=51.95).

In view of their rarity, no conclusions can be reached concerning seasonality in *Paravortex* sp. and cercaria Lepocreadidae.

Parameters of infracommunities are summarized in Table 2. Mean values of number of species per host ranged from 0.37±0.11 (January) to 0.83±0.12 (July). Values remained low between November and February then rose through the spring months to reach their peak in July and August. Mean values of numbers of species per host were significantly different between months

Table 1. *Composition, prevalence and abundance (±SE) of the metazoan parasite fauna of* Crassostrea gigas *in monthly samples from the Exe Estuary.*

		Paravortex sp.		Cercaria Lepocreadiidae		*Renicola roscovita*		*Mytilicola intestinalis*	
	N	%	Abundance	%	Abundanc	%	Abundance	%	Abundance
November 1993	30	3.33	0.03±0.03	0	0	36.66	2.23±0.97	3.33	0.03±0.03
December	30	0	0	0	0	33.33	1.03±0.33	6.66	0.06±0.05
January 1994	30	3.33	0.03±0.03	0	0	20.00	2.50±1.43	13.33	0.16±0.08
February	26	0	0	0	0	15.38	0.26±0.14	34.61	0.50±0.16
April	30	0	0	3.33	0.03±0.03	30.00	0.73±0.23	40.00	0.73±0.21
May	30	0	0	0	0	10.00	0.13±0.07	30.00	0.56±0.18
June	30	0	0	0	0	23.33	1.10±0.63	53.33	0.66±0.12
July	30	3.33	0.03±0.03	0	0	30.00	0.80±0.30	50.00	0.73±0.17
August	30	0	0	0	0	30.00	1.00±0.38	40.00	0.76±0.23
September	30	0	0	0	0	40.00	2.06±0.65	10.00	0.43±0.13
October	30	3.33	0.03±0.03	0	0	23.33	1.56±1.19	20.00	0.40±0.21

Table 2. *Characteristics of the metazoan parasite infracommunity of* Crassostrea gigas *in monthly samples from the Exe Estuary.*

	N	No. of helminth species per host (±SE)	No. of helminth individuals (±SE)	Brillouin's index (±SE)	% similarity (±SE)	% of hosts with 0 or 1 parasitic species
November 1993	30	0.43±0.10	2.30±0.97	0.01±0.01	75.76±4.74	90.00
December	30	0.40±0.10	1.10±0.32	0.01±0.01	76.97±5.03	96.66
January 1994	30	0.37±0.11	2.70±1.48	0.02±0.01	42.65±7.69	93.33
February	26	0.50±0.13	0.77±0.22	0.03±0.02	56.67±5.68	92.30
April	30	0.73±0.10	1.50±0.27	0.02±0.01	45.79±3.36	95.00
May	30	0.40±0.09	0.70±0.19	0.0	59.09±6.10	100.00
June	30	0.76±0.11	1.76±0.62	0.03±0.01	57.14±3.14	90.00
July	30	0.83±0.12	1.56±0.34	0.06±0.02	48.77±2.94	84.37
August	30	0.70±0.12	1.76±0.49	0.05±0.02	50.12±3.41	86.11
September	30	0.50±0.10	2.20±0.66	0.01±0.01	69.67±4.43	94.11
October	32	0.46±0.13	2.00±1.20	0.05±0.02	47.44±5.31	78.12

($F_{10,325}=2.69$). Mean number of helminth individuals per host fell from the minimum value in January (2.71 ±1.48) to the minimum value in May (0.7 ±0.12) before increasing throughout the summer (differences were not significant H=16.42; df=10).

Mean values of Brillouin's diversity index were always <0.1 (Table 2). They remained relatively constant from November to June before increasing slightly during the summer months, but monthly differences were not significant ($F_{10,325}=1.26$). Mean percentage similarity between months varied between 42.65 ±7.69 in January and 76.97 ±5.03 in December (Table 2) but values remained fairly similar between January and August. With the exception of July, August and October >90% of the oysters examined each month were parasitized by either one or no species (Table 2). The percentage of uninfected hosts was >50% in most months, except during the months of higher diversity where there was a clear decrease in the percentage of uninfected hosts and a corresponding increase in the proportion of hosts infected with two species (Figure 2). The maximum number of helminth species ever found in a single host was two (Figure 2).

Evidence of interactions

Of the total number of oysters sampled over the year (326), 70 were infected with *R. roscovita* only, 69 with *M. intestinalis* only, 24 with both species and 163 were uninfected. The expected frequency of double infections assuming independent and random co-occurrence was 15 lower than the observed frequency. Therefore there was no evidence to suggest interactions in the patterns of co-occurrence ($G=0.585$; $\chi^2=3.84$, df=2, $P>0.05$).

Comparison between oyster age groups

The 1995 sample

With the exception of cercaria Lepocreadiidae all metazoan parasite species were found parasitizing the different host age groups. Their prevalence and abundance values are shown in Table 3. *Renicola roscovita* and *M. intestinalis* were the only species present in all age groups. Differences in prevalence and abundance between age groups were not significant (*R. roscovita*, $G=0.264$, $\chi^2=5.991$, df=2, $H=0.18$; *M. intestinalis*, $G=3.8488$, $\chi^2=5.991$, df=2, and $H=4.57$).

No significant differences between the mean number of species per host were found between host age-classes ($F_{2,87}=0.58$), and although mean number of individuals per host increased with oyster age, differences were not significant ($H=3.22$, df=2; $\chi^2=5.99$). Values of Brillouin's index were under 0.06 and no significant differences between age groups were detected ($F_{2,87}=0.77$). Percentage similarities within host age groups were above 80%. More than 86% of hosts examined in each age group harboured zero or one parasite species (Table 4).

The 1996 sample

Oyster age groups were infected with the same three parasite species as in 1995 (Table 3). Prevalence and abundance of *R. roscovita* were quite similar in both age groups examined. Prevalence values had increased slightly compared to the same groups examined the year before, but values of abundance were considerably higher. In contrast, values of prevalence and abundance of *M. intestinalis* were notably lower than in 1995. Moreover, both prevalence and abundance of *M. intestinalis* in oysters sampled in 1996 increased significantly with oyster age ($G=5.5\%$ df=1; $\chi^2=3.84$ for differences in prevalence and $H=6.72$, for differences in abundance).

Helminth infracommunity parameters are summarized in Table 4. The number of species per host increased significantly with oyster age groups ($F_{59,1}=5.28$; $P<0.05$). In contrast to 1995, age groups showed lower species richness (Table 4). No significant differences were found in mean number of individuals per host or mean values of Brillouin's diversity index between oyster age groups in 1996. Also, neither of these two parameters were very different from those of the corresponding oyster age groups in the year before. Mean percentage similarity values were much lower in contrast with those of 1995

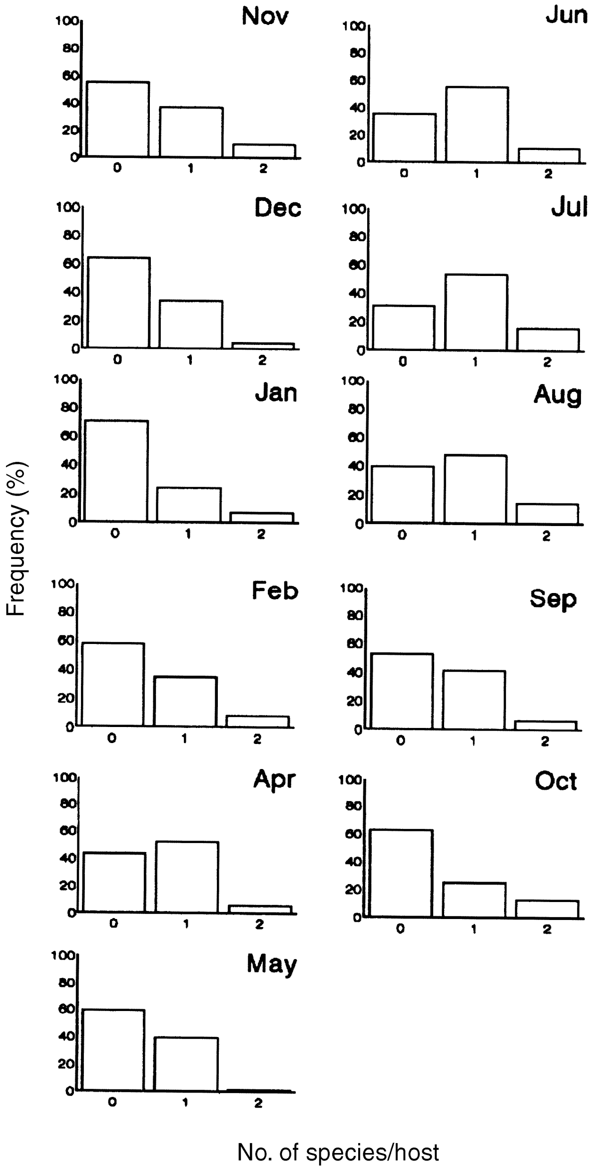

Figure 2. Monthly frequency distribution of the number of helminth species per host in oysters (*Crassostrea gigas*) from the Exe Estuary.

Table 3. *Prevalence and abundance (±SE) of the metazoan parasite species in different age groups of* Crassostrea gigas *in the Exe Estuary.*

	N	*Paravortex* sp.	*Renicola roscovita*	*Mytilicola intestinalis*
April 1995				
Age group 1	30			
Prevalence		0	6.66	66.66
Abundance			0.33±0.25	2.26±0.47
Age group 2	30			
Prevalence		6.66	10.00	83.33
Abundance		0.06±0.05	0.16±0.11	2.90±0.48
Age group 3	30			
Prevalence		0	10.00	86.66
Abundance			0.2±0.12	3.83±0.40
April 1996				
Age group 1	30			
Prevalence		0	16.66	6.66
Abundance			2.83±1.72	0.06±0.04
Age group 3	30			
Prevalence		3.33	16.16	30.00
Abundance		0.03±0.03	2.33±1.39	0.46±0.18

Table 4. *Characteristics of the metazoan parasite infracommunity (±SE) of the three age-classes of* Crassostrea gigas *of the Exe Estuary.*

	N	No. of species per host (±SE)	No. of individuals per host (±SE)	Brillouin's index (±SE)	% similarity (±SE)	% of individual hosts with 0 or 1 species
April 1995						
Age group 1	30	1.06±0.10	2.60±0.49	0.01±0.01	85.33±5.83	93.33
Age group 2	30	1.0±0.09	3.13±0.48	0.05±0.02	81.61±5.35	86.66
Age group 3	30	0.96±0.09	4.03±0.60	0.04±0.02	91.13±3.42	90.00
April 1996						
Age group 1	30	0.23±0.08	2.9±1.72	0	52.00±10.80	100
Age group 3	30	0.53±0.10	2.86±1.37	0.01±0.01	48.07±4.60	96.66

(52±10.8 for age group 1 and 48.07±4.60 for age group 3). Percentages of individual hosts infected with zero and one species were slightly larger than the previous year. In age group 1, no host was infected with more than one species, while in age group 3, 96.66% harboured zero or one species (Table 4).

DISCUSSION

Independent of the season and host age, metazoan parasite communities of oysters, were poor in number of species and individuals, and exhibited low diversity. Communities showed no evidence of interspecific interactions. Such characteristics place them as 'isolationist', non-interactive communities, *sensu* Holmes & Price (1986) and Sousa (1994).

High percentages of uninfected hosts and low percentages of hosts infected with more than two parasite species were responsible for the very low values in all helminth infracommunity parameters. The recruitment of *Mytilicola intestinalis* and *Renicola roscovita* during the summer months was responsible for the slight increase in both species richness and mean number of parasite individuals per host at this time, as the percentage of hosts infected with at least one helminth species increased and so did the hosts infected with two species (Figure 2).

Possible negative interactions and antagonism between the species composing the helminth communities of gastropods have been found to be responsible for low diversities and poor species richness (Sousa, 1990; Kuris, 1990; Fernandez & Esch, 1991b; Esch & Fernandez, 1993; Sousa, 1994; Kuris & Lafferty, 1994) at the infracommunity level. However, helminth communities of oysters did not meet the assumptions for an interactive community (*sensu* Holmes & Price, 1986; Kuris & Lafferty, 1994; Sousa, 1994). Firstly, there are few species to interact; only four species were found infecting oysters in monthly samples and just three in age-class samples, of which only two were relatively frequent. Secondly, prevalence of these species was often <50% and no real dominance hierarchies were detected as, most of the time, communities were dominated by *R. roscovita* in monthly samples and by either *R. roscovita* or *M. intestinalis* in age groups. Finally, these two species (i.e. *R. roscovita* and *M. intestinalis*) exhibit different microhabitat preferences, as *R. roscovita* is most frequently found in palps and *M. intestinalis* inhabits the oyster gut.

Additionally, *R. roscovita* and *M. intestinalis* species differ in their colonization strategy with regard to the definitive host. *Renicola roscovita* is an allogenic species which uses the gastropod *Littorina littorea* L. as its first intermediate host, the oyster as the second intermediate host and *Larus argentatus* as its definitive host. Thus, the presence of *R. roscovita* is determined by the presence of all three suitable hosts. Seasonal patterns in oyster infections will depend on the time of cercaria shedding by the first intermediate host and on the lifespan of the metacercaria, i.e. recruitment and mortality. Laukner (1983) mentioned that the onset of emission of cercariae of *R. roscovita* in some European localities occurs during late May to early June, stopping completely before October. This period coincides with the months in which values of abundance of *R. roscovita* seem to start increasing in the Exe Estuary, even though changes in prevalence were more variable (Table 1). Despite the fact that mussels and cockles accumulate large numbers of metacercariae during the first two and three years (in the order of hundreds to thousands; Lauckner, 1983), oysters appear to harbour far smaller numbers and there is no accumulation of metacercariae with respect to oyster age (Table 3). It is thus possible that mortality of the metacercariae in the oyster might be occurring. Observed patterns in prevalence and abundance of *R. roscovita* in different oyster age groups in 1995 and 1996 reflect, then, the great variability in transmission rates from year to year. Furthermore, the results in the comparison of oyster age groups suggest that oyster defence mechanisms against parasites are operating in maintaining low levels of infection, either by preventing the establishment of the cercariae or by increasing metacercarial mortality.

By contrast, *M. intestinalis* is an autogenic species which can reach maturity in the oyster host. Infections, then, will depend on recruitment of the new generation of first and second copepodite stages which are presumably ingested by the lamellibranch host (Cheng, 1967; Laukner, 1983) and mortality of the previous generation, soon after reproduction (Davey, 1989). Recruitment of *M. intestinalis* to mussels has been reported to occur twice a year, most commonly during late summer and early winter (Davey, 1989). Gresty (1990) reported two periods of recruitment in mussels of the Exe Estuary, during late autumn and early summer, which coincides with the increased levels of prevalence and abundance noted over this period in this study. Davey (1989) found little evidence of a relationship between infection levels and mussel size; instead, he reported broad variations in infection levels from year to year in a ten-year study. He related such variation to changes in climatic factors, especially to yearly temperature ranges, which could also explain the variations in infections over 1995 and 1996 observed in the present study.

It is possible that helminth communities of *Crassostrea gigas*, as a recently introduced species to the UK, are still increasing in richness and diversity. Guègan & Kennedy (1993) pointed out that species introduced by man into new localities will have far less rich helminth faunas than related native species and that eventually the introduced species will become infected by helminth species of native hosts. On the other hand, the fact that oysters possess a strong response against parasites (Cheng & Rificin, 1970) could explain why communities remain poor and low in diversity through the year and oyster age groups. Cheng et al. (1966) mentioned that oysters can prevent the encystment of metacercariae of *Himasthla quissetensis* (Miller & Nothrup) by immobilization of the cercaria before penetration by some host-elaborated substance seeping into the mantle. Also, it is known that oysters respond quickly to the presence of foreign particles, by intracellular digestion and phagocytosis followed by immediate migration of the host cells across the epithelium to the exterior (Tripp, 1975). This process could be one of the principal reasons for the poor helminth communities observed in oysters.

All metazoan parasite species found infecting oysters in the Exe have previously been reported as parasitizing other lamellibranchs (Cheng, 1967; Laukner, 1983), i.e. none are specialists of oysters. *Renicola roscovita* and *M. intestinalis* have been found parasitizing other bivalves (mainly mussels) in several localities around Europe with prevalence and abundance values far larger than those found here in oysters (Laukner, 1983). In the Exe Estuary in particular, there are no native oyster populations, but instead, large populations of mussels (*Mytilus edulis*) and cockles (*Cerastoderma edule*) are predominant (Harris, 1980). Between 90 and 100% of the mussel population has been found to be infected with *R. roscovita*, with between 1 and 855 cysts per host (Goater, 1989) and 100% of the cockle (*C. edule*) population with between 70 and 2000 cysts (Goater, 1989; Aguirre-Macedo, 1996). *Mytilicola intestinalis*, on the other hand, has been found infecting 40–100% of the mussel population of the Exe Estuary with mean abundances between 0.7 and 3.5 parasites per host (Gresty, 1990). Oysters appear to exhibit more resistance to parasites (i.e. *R. roscovita* and *M. intestinalis*) than mussels or cockles, but are nevertheless susceptible to infections. Their parasites thus seem to be acquired from the neighbouring lamellibranch-parasite systems (spillovers) where parasite populations seem to be far larger.

Despite some temporal variations in prevalence and abundance of individual helminth species, no significant seasonal variation was observed in community structure and although some significant differences were found between age host groups, such variations seem to be due largely to seasonal changes in recruitment and transmission of individual species from year to year. Therefore, time of collection or age composition of samples could be of minimal importance in determining community structure of metazoan parasites of *C. gigas*.

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REFERENCES

Aguirre-Macedo, M.L., 1996. *Study on helminth and other parasite communities of oysters*. PhD thesis, University of Exeter, Exeter.

Boalch, G.T., ed., 1980. *Essays of the Exe Estuary*, special volume, no. 2. Exeter: Devonshire Association.

Bower, S.M., McGladdery, S.E. & Price, I.M., 1994. Synopsis of infectious diseases and parasites of commercial exploited shellfish. *Annual Review of Fish Diseases*, **4**, 1–199.

Bush, A.O., Heard, R.W. & Overstreet, R.M., 1993. Intermediate hosts as source communities. *Canadian Journal of Zoology*, **71**, 1358–1363.

Chappell, L.H., 1969. The parasites of the three-spined stickleback, *Gasterosteus aculeatus* L. from a Yorkshire pond. I. Seasonal variation of parasite fauna. *Journal of Fish Biology*, **1**, 137–152.

Cheng, T.C., 1967. Marine molluscs as hosts for symbiosis. With a review of known parasites of commercially important species. *Advances in Marine Biology*, **5**, 1–424.

Cheng, T.C. & Rifkin, E., 1970. Cellular reaction of marine molluscs in response to helminth parasites. In *A symposium of diseases of fish and shellfishes* (ed. S.F. Snieszko), pp. 443–496 Washington, DC: American Fisheries Society.

Cheng, T.C., Shuster, C.N. & Anderson, A.H., 1966. A comparative study of the susceptibility and response of eight species of marine pelecypods to trematode *Himasthla quissetensis*. *Transactions of the American Microscopical Society*, **85**, 284–295.

Cloutman, D.G., 1975. Parasite community structure of large-mouth bass, warmouth and blugeill in Lake Fort Smith, Arkansas. *Transactions of the American Fisheries Society*, **1975**, 277–283.

Conover, W.J., 1980. *Practical non parametric statistics*. New York: John Wiley & Sons.

Davey, J.T., 1989. *Mytilicola intestinalis* (Copepoda: Cyclopoida): a ten year survey of infected mussels in a Cornish estuary, 1978–1988. *Journal of the Marine Biological Association of the United Kingdom*, **69**, 823–836.

Edwards, D.D. & Bush, A.O., 1989. Helminth communities of avocets: importance of compound community. *Journal of Parasitology*, **75**, 225–238.

English Nature, 1993. Important areas for marine wildlife around England. *Report. English Nature, Campaign for a Living Coast*, August 1993.

Esch, G.W., 1983. The population and community ecology of cestodes. In *Biology of Eucestoda* (ed. P. Papas and C. Arme), pp. 81–137. New York: Academic Press.

Esch, G.W. & Fernandez, J., 1993. *A functional biology of parasitism*. London: Chapman & Hall.

Fernandez, J. & Esch, G.W., 1991a. Guild structure of larval trematodes in the snail *Helisoma anceps*: patterns and processes at the individual host level. *Journal of Parasitology*, **70**, 528–539.

Fernandez, J. & Esch, G.W., 1991b. The component community structure of larval trematodes in the pulmonate snail *Helisoma anceps*. *Journal of Parasitology*, **70**, 540–550.

Goater, C.P., 1989. *Patterns of helminth parasitism in the oystercatcher,* Haematopus ostralegus, *from the Exe Estuary, England.* PhD thesis, University of Exeter, Exeter.

Gresty, K.A., 1990. *The feeding biology of* Mytilicola intestinalis *Steur, in the mussel host* Mytilus edulis *L., and other host–parasite relationships*. PhD thesis, University of Exeter, Exeter.

Guègan, J.F. & Kennedy, C.R., 1993. Maximum local helminth parasite community richness in British freshwater fish: a test of colonization time hypothesis. *Parasitology*, **106**, 91–100.

Harris, T., 1980. Invertebrate community structure on, and near, Bull Hill in the Exe estuary. In *Essays on the Exe Estuary*, special volume, no. 2 (ed. G.T. Boalch), pp. 135–160. Exeter: Devonshire Association.

Holmes, J.C. & Price, P.W., 1986. Communities of parasites. In *Community ecology: patterns and processes* (ed. J. Kikkawa, and A.D. Anderson), pp. 187–213. Oxford: Blackwell Scientific Publications.

Kuris, A., 1990. Guild structure of larval trematodes in molluscan host: prevalence, dominance and significance of competition. In *Parasite communities: patterns and processes* (ed. G.W. Esch et al.), pp. 69–100. New York: Chapman & Hall.

Kuris, A. & Lafferty, K.D., 1994. Community structure: larval trematodes in snail hosts. *Annual Review of Ecology and Systematics*, **25**, 189–217.

Lafferty, K.D., Sammond, D.T. & Kuris, A.M., 1994. Analysis of larval trematode communities. *Ecology*, **75**, 2275–2285.

Laukner, G., 1980. Diseases of Mollusca: Gastropoda. In *Diseases of marine animals*. Vol. 1. *General aspects*, *Protozoan to Gastropoda* (ed. O. Kinne), pp. 311–424. Chichester: John Wiley & Sons.

Laukner, G., 1983. Diseases of Mollusca: Bivalvia. In *Diseases of marine animals*. Vol. II. *Introduction Bivalvia to Scaphopoda* (ed. O. Kinne). Hamburg: Biologisch Anstalt Hergoland.

Magurran, A.E., 1988. *Ecological diversity and its measurements*. London: Chapman & Hall.

Malek, E.A., 1980. *Snail-transmitted parasite diseases*. Boca Raton and New York: CRC Press.

Margolis, L., Esch, G. & Holmes, J., 1982. The use of ecological terms in parasitology. *Journal of Parasitology*, **68**, 131–133.

Putman, R.J., 1994. *Community ecology*. London: Chapman & Hall.

Snyder, S.D. & Esch, G.W., 1993. Trematode community structure in the pulmonate snail *Physa gyrina*. *Journal of Parasitology*, **79**, 205–215.

Sokal, R.R. & Rohlf, F.J., 1981. *Biometry. The principles and practices of statistics in biological research*, 2nd ed. San Francisco: W.H. Freeman & Co.

Sousa, W., 1990. Spacial scale and the processes structuring a guild of larval trematodes parasites. In *Parasite communities: patterns and processes* (ed. G.W. Esch et al.), pp. 41–67. New York: Chapman & Hall.

Sousa, W., 1994. Patterns and processes in communities of helminth parasites. *Trends in Ecology and Evolution*, **9**, 52–57.

Spencer, B.E., Edwards, B.D. & Kaiser, M.J., 1994. Spatfalls of the non-native Pacific oyster, *Crassostrea gigas* in British waters. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **4**, 203–217.

Tripp, M.R., 1975. Humoral factors and molluscan immunity. In *Invertebrate immunity* (ed. K. Maramorosch and R.E. Shope), pp. 201–223. London: Academic Press.

Wallace, B.M. & Pence, D.B., 1986. Population dynamics of helminth community from migrating blue-winged teal, loss of helminths without replacement on wintering grounds. *Canadian Journal of Zoology*, **64**, 1765–1773.

Williams, J.A. & Esch, G.W., 1991. Infra and component community dynamics in the pulmonate snail *Helisoma anceps* with special emphasis on hemiurid trematode *Halipegys occidentalis*. *Journal of Parasitology*, **72**, 246–253.

Wolda, H., 1987. Seasonality and the community. In *Organization of communities, past and present* (ed. J.H.R. Gee and P.S. Giller), pp. 69–95. London: Blackwell Scientific Publications.

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