Patterns in metazoan parasite communities of some oyster species

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Abstract

Metazoan parasite communities of *Crassostrea gigas* and *Ostrea edulis* from Great Britain, *Crassostrea virginica* from Mexico, and *Saccostrea commercialis* from Australia are described and summarized in terms of species composition, species richness, total number of individuals and dominance. Metazoan parasite communities in all host species were composed of turbellarians and the metacercarial stage of digeneans, with the exception of *S. commercialis* where only metacercariae were found. Arthropods, including one copepod and one mite species, were present only in British oyster species. All metazoan parasite communities of oysters had few species and low density of individuals. Richest communities were found in *C. virginica* at both component and infracommunity level. The least diverse component community occurred in *S. commercialis*. Infracommunities in *O. edulis* and *S. commercialis* never exceeded one species per host. The host response against parasites is suggested as the principal factor responsible for depauperate parasite communities of oysters. Environmental factors characteristic of tropical latitudes are likely to have enhanced both the number of species and the densities of parasites per host in the infracommunities of *C. virginica*.

Introduction

The interest of parasitologists in explaining patterns and processes influencing the number of parasite species a host can support increased notably after the publication of Dogiel's (1964) book. He suggested that '. . . more or less a definitive number of species is characteristic of different animal host groups differing perhaps from one part of their distribution range to another.' During the last two decades a sustained effort has been made to determine whether helminth parasite communities are predictable, structured assemblages of species, or the result of chance colonization processes (Holmes, 1987; Esch *et al.*, 1990).

Despite the extensive literature on oyster diseases, few papers discuss metazoan parasites and even fewer consider the metazoan parasite fauna as a whole. Rather, references relate more to taxonomic findings and to new records of particular species. A recent study on metazoan communities of the introduced pacific oyster (*Crassostrea gigas*) in Great Britain attempts to fill this gap (Aguirre-Macedo & Kennedy, 1999). Low diversity and species poor communities were found in monthly samples throughout one year in oysters collected from the Exe estuary. Explanations advanced for this were the recent introduction of this oyster species to Britain together with a strong response of the host to helminth invasions. The objectives of the present study were to determine whether there are patterns in species composition and structure of the metazoan parasite communities at component and infracommunity level of *C. gigas* from other localities where it has been introduced in Britain

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and to contrast metazoan parasite community patterns found in *C. gigas* with metazoan parasite communities of the native oyster *Ostrea edulis* and two other oyster species from different geographical areas in their native land (Mexico, and Australia) in relation to their temperate or tropical origin.

Material and methods

Samples of 163 *Crassostrea gigas* and 69 *Ostrea edulis* from several localities in southern England and Wales (Starcross 50°38′N, 3°27′W, Falmouth 50°08′N, 5°04′W, Swale Estuary 51°21′N, 0°44′E, Torquay 50°28′N, 3°30′W, Helford 50°05′N, 5°13′ W and Menai Strait 53°14′N, 4°10′W), 90 *Crassostrea virginica* collected from localities in Tabasco State, Mexico (Mecoacan 18°16′N, 93°04′W, Carmen 18°14′N, 93°45′W and Machona 18°20′N, 93°55′W lagoons), and 32 *Saccostrea commercialis*, from New South Wales, Australia (Hawkesbury river 33°25′S, 151°18′E) were examined for metazoan parasites (for details on each locality see Aguirre-Macedo, 1996). British and Mexican oysters were examined live immediately after collection and in the following two weeks, while the Australian specimens were fixed in 10% formalin. British localities were chosen according to availability of wild surviving populations of native oysters and where spatfalls of the introduced oyster species were found. Mexican and Australian oyster samples were taken where we had opportunity to get them. Each host was dissected and the organs separately compressed between two slides under a dissecting microscope. All individual parasites were counted and identified in accordance with Cheng (1967), Yamaguti (1975), and Lauckner (1983). Copepods and mites were considered as part of the community for all calculations.

Prevalence and abundance were used as in Bush *et al.* (1997). Analysis of community structure was carried out at two levels: component and infracommunity (*sensu* Holmes & Price, 1986). At component community level, richness was analysed by determining the total number of species and the total number of individuals in the host sample. The Berger-Parker dominance index, as described by Magurran (1988), was used as a measure of dominance ($d = N_{max}/N$; where N_{max} is the number of individuals in the most abundant species and N is the total number of individuals in the community). The terms, allogenic and autogenic species, were used as in Esch *et al.* (1988) (i.e. allogenic parasites have aquatic organisms as intermediate hosts and then mature sexually in birds or mammals; in autogenic parasites the entire life cycle is completed within an aquatic ecosystem). Infracommunities were summarized as the mean number of species and the mean number of individuals per host. No diversity indices were calculated because a high proportion of individual hosts were infected with just one metazoan species. The locality with the maximum local species richness (*sensu* Guegan & Kennedy, 1993) for each host species was used to compare helminth infracommunities among host species. For *S. commercialis*, only the single available sample was used. One-way ANOVA was performed to test significant differences in the mean number of species per host and the transformed mean of the number of individuals per host ($\ln (n+1)$) within and between localities. Significance was taken at $P < 0.05$ unless noted otherwise. When significant differences between means were found, a Tukey test for contrast of means was applied (Sokal & Rohlf, 1981).

Results

Five species (one turbellarian, two digeneans and two arthropods) parasitized *C. gigas* in the four localities sampled in Great Britain. Between two and three species were found in each locality (table 1). Prevalence and abundance of all species were generally low (table 1). The only species found in samples from all localities was the copepod *Mytilicola intestinalis*. This copepod exhibited the highest values of prevalence (table 1) in all the localities, with the exception of Starcross, where metacercariae of *Renicola roscovita* (Stunkard) exhibited the highest prevalence and abundance (tables 1). Of the five metazoan species found, two were allogenic: *R. roscovita* and *Metacercaria mytili* Labour, using birds as definitive hosts. The other three species were autogenic.

Ostrea edulis from Britain was parasitized by a total of four metazoan species with a maximum of two species found per locality. No metazoan parasites were recovered from the Torquay sample and none of the metazoan species was recovered from more than one locality. Prevalence and abundance values for each species in each locality are shown in table 1. As in *C. gigas,* prevalence of all species was low. *Renicola roscovita* from the Menai Strait sample exhibited the maximum values of prevalence (40%) and abundance per host (0.5 ± 0.11); none of the other species attained values >6% prevalence and 0.1 individuals per host.

A total of four helminth species parasitized *C. virginica* in southern Mexico: the turbellarian *Urastoma cyprinae* (Graff) and metacercarial stages of three species of digeneans: *Proctoeces maculatus* Prévot, *Gymnophalloides* sp. and a gymnophallid gen. sp. Table 1 summarizes the prevalence and abundance values of each parasite species. All species prevalence exceeded 10%, but only *Gymnophalloides* sp. and the gymnophallid metacercariae attained >70% prevalence in two of the localities sampled. The most prevalent and abundant species was the gymnophallid, encysted in the digestive diverticula. Of the four species found in *C. virginica*, two were allogenic; the gymnophallid and *Gymnophalloides* sp. which have birds as final hosts. The other two species were autogenic: *U. cyprinae,* with an aquatic life cycle and the metacercariae of *P. maculatus* which uses fish as definitive hosts.

Australian oysters, *S. commercialis,* were parasitized by an unidentified species of digenean in its metacercarial stage. This helminth was encysted in the palps of 59% of the hosts examined (n = 32) with an abundance of 2.9 ± 1.19 cysts per host.

Table 1 compares the characteristics of the metazoan parasite communities of all four oyster species in each locality. At the component level, metazoan parasite species richness was low for all oyster species; the maximum number of species (four) was found in *C. virginica* and the minimum in *S. commercialis* (one). The highest number of individuals occurred in *C. virginica* (694 individuals at Carmen lagoon) while the lowest was

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Table 1. Prevalence, abundance ± SE and community measurements of metazoan parasites found in British, Mexican and Australian oysters.

Helminth species	Great Britain							Mexico		Australia	
	Crassostrea gigas				*Ostrea edulis*			*Crassostrea virginica*		*Saccostrea commercialis*	
Localities	Starcross n=30*	Falmouth n=56	Kent n=40	Menai Strait n=37	Menai Strait n=35*	Helford n=17	Torquay n=17	Mecoacan n=30	Carmen n=30*	Machona n=25	Hawkesbury n=32*
Turbellaria											
Paravortex sp.	3 0.3 ± 0.03	0 0.0	2 0.3 ± 0.03	0 0.0	2 0.1 ± 0.08	0 0.0	0 0.0				
Urastoma cyprinae								10 0.1 ± 0.06	28 0.8 ± 2.94	40 0.7 ± 0.19	
Digenea											
Renicola roscovita	36 2.2 ± 0.97	0 0.0	0 0.0	0 0.0	40 0.5 ± 0.11	0 0.0	0 0.0				
Metacercaria mytili	0 0.0	2 0.01 ± 0.01	0 0.0	0 0.0	0 0.0	6 0.1 ± 0.10	0 0.0				
Gymnophallidae sp.								31 0.9 ± 0.32	96 17.4 ± 3.78	77 4.5 ± 1.38	
Gymnophalloides sp.								25 0.3 ± 0.9	88 8.6 ± 1.59	73 2.3 ± 0.48	
Proctoeces maculatus								0 0.0	32 1.0 ± 0.41	23 0.8 ± 0.21	
Metacercariae sp.1											59 2.9 ± 1.19
Arthropoda											
Mytilicola intestinalis	3 0.03 ± 0.03	57 2.5 ± 0.49	10 0.1 ± 0.01	14 0.1 ± 0.05	0.0 0.0	6 0.05 ± 0.05	0				
Mite (unidentified)				3 0.02 ± 0.02							
Total no. of species	3	2	2	2	2	2	0	3	4	4	1
Total no. of individuals	70	142	5	6	20	3		37	694	259	92
Berger-Parker Dominance Index	0.97	0.99	0.8	0.83	0.85	0.66		0.68	0.62	0.54	1
No. of species/host ($\bar{x}$ ± SE)	0.5 ± 0.10	0.5 ± 0.07	0.1 ± 0.05	0.2 ± 0.07	0.4 ± 0.50	0.1 ± 0.08	0	0.6 ± 0.12	2.4 ± 0.18	2.1 ± 0.15	0.6 ± 0.08
No. of individuals/host ($\bar{x}$ ± SE)	2.3 ± 0.96	2.5 ± 0.49	0.1 ± 0.05	0.2 ± 0.07	0.6 ± 0.84	0.2 ± 0.01		1.2 ± 0.36	27.7 ± 3.98	8.6 ± 1.46	2.9 ± 0.96
% of individual hosts with 0 and 1 species	97	98	100	100	100	100		86	12	17	100

Samples marked with (*) were used for helminth community comparison between host species.

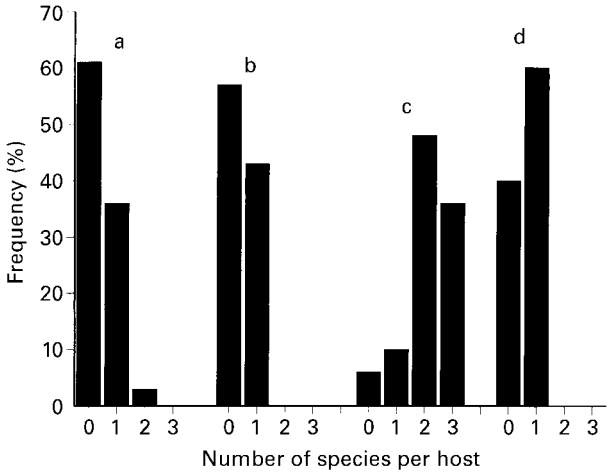

Fig. 1. Frequency distribution of the number of helminth species per individual oyster for each oyster species in samples used for analysis at the component community level: a, *Crassostrea gigas*; b, *Ostrea edulis*; c, *C. virginica*; d, *Saccostrea commercialis*.

found in *O. edulis* from Helford (three individuals). In *C. virginica,* the values of the Berger-Parker index (*d* between 0.54 and 0.68) showed communities less dominated by one species; with the exception of metazoan communities of *O. edulis* from Helford where two of the three individuals found were copepods, in all others hosts species dominance values were above 0.8 (table 1). The metazoan parasite communities of all four oysters species were dominated by allogenic species.

At the infracommunity level, the mean values of number of species and number of individuals per host were generally low. Mexican oysters (*C. virginica*) harboured the richest communities, as judged by the number of species and individuals per host and percentage of individual hosts with none or one species in comparison with the other three hosts (table 1, fig. 1). Neither *S. commercialis* nor *O. edulis* was parasitized by more than one species per individual host (table 1, fig. 1). There were significant differences in the number of species per host (one way ANOVA $F_{3,123}=54.69$; $P<0.001$) and number of individuals per host ($F_{3,123}=24.15$; $P<0.001$) among the metazoan parasite communities of the different host species form the localities with the maximum local species richness. Multiple comparison test (Tukey) indicated that both the mean number of species and the mean number of individuals per host in *C. virginica* are significantly different with respect to *O. edulis, C. gigas* and *S. commercialis.* However, no significant differences were found among these latter three host species. Percentage of individual hosts with only 0–1 metazoan parasite species in *C. gigas, O. edulis* and *S. commercialis* was far greater than that of *C. virginica* (table 1, fig. 1).

Discussion

These results show that metazoan parasite communities of *C. gigas* proved to be depauperate in all localities examined in Great Britain and, despite the recent introduction of *C. gigas* into Great Britain, there are no differences in species richness and composition of metazoan parasite communities with respect to those of the native oyster *O. edulis*. Both oyster species were parasitized by the same parasites and strongly dominated by only one parasite species of the community. Variation in community parameters (mainly total number of individuals and mean number of individuals per host) in each locality and host seem to be more related to seasonal variations in the abundance values of the dominant species, as has been found in metazoan parasite communities of *C. gigas* from the Exe Estuary (Aguirre-Macedo & Kennedy, 1999).

Depauperate metazoan parasite communities also found in oysters like *C. virginica* from Mexican localities and *S. commercialis* from Australia suggest that poverty in species number and low density of parasite communities are characteristic of oyster hosts.

Other surveys of oyster parasites have also demonstrated depauperate helminth communities. Burton (1961), for example, recorded only *Bucephalus cuculus* (McCrady) cercariae in 12 of 663 oysters examined in Chesapeake Bay (USA), and Turner (1985), who examined 1242 oysters from a Louisiana estuary, found just four oysters infected with *B. cuculus.* These findings confirm the low susceptibility of oysters to infections with helminth parasites.

A striking similarity between the groups forming the species composition was evident among the different oyster species. Digeneans in the metacercarial stage and turbellarids were present in all host species except *Saccostrea commercialis,* where turbellarids could have been lost during fixation procedures. Arthropods such as mites and copepods of *Mytilicola intestinalis* seem to be a particular group of the metazoan parasite communities of British oysters since they were found only in *C. gigas* and *O. edulis*. However, another species of *Mytilicola* (*M. porrecta* Humes) has previously been reported in the American oyster *C. virginica* from the USA (Lauckner, 1983). Therefore, it is possible not only that members of the parasite genus *Mytilicola* are restricted in their distribution to temperate latitudes, but also that levels of infection in oysters are related to levels of infection in the proximate populations of mussels (i.e. Starcross, Falmouth, Swale Estuary, Menai Strait and Helford), since mussels are the preferential host of this genus of parasites (Lauckner, 1983).

It would be expected that oysters from tropical latitudes would have richer communities than those from temperate ones, and this was found to be the case in Mexican *C. virginica*. Nevertheless, the paucity of the metazoan parasite communities of the four host species from such different geographical areas might be related to specific physiological characteristics common to these bivalve hosts. Such characteristics could be related to the host response mechanism, precluding helminth establishment and survival. It is well known that oysters can develop a strong host response against helminth parasites (Feng, 1988). There is evidence that cellular responses in *C. virginica* and *C. gigas* can result in the encapsulation and elimination of helminth parasites (Cheng & Rifkin, 1970). Cheng *et al.* (1966) found that oysters can prevent

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infections by echinostomid cercariae by inducing the encystment of the cercaria before the cercaria penetrates the mantle tissue of the oyster. Additionally, high concentrations of lysozyme-like substances occurring in the oyster's mantle are responsible for a lytic effect against a great variety of microorganisms, including cercaria and other helminth larval stages. It seems likely that these substances, together with mobile cells, are able to quickly and effectively clean foreign materials in oyster tissue (Tripp, 1975). Clearly, these mechanisms make the establishment and survival of helminth parasites rather difficult. *Crassostrea virginica* from Mexico, however, seem to be more susceptible to helminth infections. Of all hosts examined, 93% harboured at least one helminth species and more than 80% between two and four. In all other oyster species, with the exception of *C. gigas*, 100% were infected with only one species or uninfected.

These differences could result from the ecological conditions of the localities inhabited by each oyster species. Harsher conditions in temperate latitudes, for example, could explain why British and Australian oysters harboured poorer infracommunities compared with Mexican oysters. On the other hand, the period of availability of infective stages might be shorter in temperate latitudes because: (i) in most temperate localities there are strong seasonal patterns of infection, due mainly to the drop of temperature during the winter season; (ii) there must be some influence of tides and water currents on the time exposure of the host to the parasites. In tropical latitudes, patterns in seasonality are less pronounced because of the constancy in climatic characteristics. Furthermore, Mexican oysters are primarily subtidal. In other words oysters in Mexican localities are always under water, and these conditions might produce longer periods of host exposure to the parasites and therefore slightly richer metazoan parasite communities in Mexican *C. virginica.* Nevertheless, it would be desirable to have data from more localities within the natural geographical distribution of *C. virginica* and *S. commercialis*.

On the other hand, there are no community studies as such on which to base comparison of oyster metazoan parasite communities with any other bivalves. Bowers (1965) in his survey of parasites of molluscs and birds from several localities along Wales, Scotland and southern England, recorded a maximum of ten helminth species from cockles (*Cerastoderma edule*), between three and five from *Mytilus edulis*, *Macoma baltica*, *Donax vitatus*, *Ensis ensis*, *Hiatela artica*, and *Scrobicularia plana*, and one from *Tellina tenuis* and *Modiolus modiolus*. Thus, with the exception of *C. edule*, depauperate metazoan parasite communities at component level seem to characterize most lamellibranchs. In spite of the low diversity parasite component communities, the picture can be different at the infracommunity level. Goater (1989) recorded five species of metazoan parasites (four metacercariae and one copepod) in mussels (*M. edulis*) and four species (three metacercariae and one cestode larvae) in *C. edule* in the Exe Estuary (UK). He did not report full component or infracommunity data but rather he recorded parasite densities between 50 and 200 on average in four of the five species (excluding the copepod) in mussels and between 500 and 1500 on average per cockle examined. Therefore, even when metazoan parasite component communities in other lamellibranchs look as poor as those in oysters, infracommunities can be far richer, and even richer than those of some of freshwater fishes (see Kennedy *et al.*, 1986).

Metazoan parasite communities of oysters were slightly richer in species number than those of gastropods at infracommunity level, but richer communities at component level have been observed in marine and freshwater gastropods (Rohde, 1981; Kuris, 1990; Sousa, 1990; Fernandez & Esch, 1991; Curtis & Hubbard, 1993; Snyder & Esch, 1993; Williams & Esch, 1993). Processes structuring helminth communities of marine and freshwater gastropods are different from those found in metazoan parasites of oysters because of the high host-specificity of digeneans parasitizing gastropods. Furthermore, mechanisms acting at infracommunity level are related more to interspecific interactions (Kuris & Lafferty, 1994; Lafferty *et al.*, 1994). By contrast, none of the metazoan parasite species parasitizing oysters are specific to the level of species or genus: all have previously been found in other genera of bivalves (Lauckner, 1983). More importantly, the strong host response produced by oysters against parasites seems to be the principal factor structuring metazoan parasite communities of oysters. Therefore, only those species that are able to overcome the host response become established.

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