3

Spatial scale and the processes structuring a guild of larval trematode parasites

Wayne P. Sousa

3.1 INTRODUCTION

An individual host is a patch of habitat for a particular stage in the life cycle of a parasite (Price, 1980; Holmes and Price, 1986). It contains resources necessary for growth and development of this infecting stage, and for production of the next, usually dispersing, stage. Each individual host is an inherently bounded, discrete habitat, that is isolated from other similar habitat patches by an external environment that is inhospitable to the parasitic stage that infects the host.

As patches of parasite habitat, hosts are both self-reproducing and ephemeral. Excluding instances of vertical transmission and assuming life-long infection (as is the case for many parasitic infections of invertebrate hosts), empty patches are born via the recruitment of susceptible offspring to a host population, patches increase in size and change in a variety of other characteristics (e.g. morphology, biochemistry, etc.) during host ontogeny, and they disappear (along with their resident parasites) when the host dies. The rates at which these processes occur vary among host populations and in time.

In many ecological systems, the distribution and accessibility of resources vary with spatial and temporal scale, as do the processes that structure populations and communities (e.g. Andrewartha and Birch, 1954; Wiens, 1976; Price, 1980; Allen and Starr, 1982; Connell and Sousa, 1983; Dayton and Tegner, 1984; Sousa, 1984; Addicott *et al.*, 1987). Studies of processes

G. W. Esch et al. (eds.), *Parasite Communities: Patterns and Processes*

operating at different scales within systems of divided habitat patches have provided substantial insight in this regard. When strong asymmetrical interactions on the small scale, i.e. within a patch, preclude the coexistence of competitors, or of predators and their prey, the existence of multiple patches coupled by dispersal often promotes their coexistence on the larger scale (Hutchinson, 1951; Skellam, 1951; Huffaker, 1958; Cohen, 1970; Levins and Culver, 1971; Horn and MacArthur, 1972; Levin, 1974, 1976; Slatkin, 1974; Armstrong, 1976; Hastings, 1977, 1980; Caswell, 1978; Shorrocks *et al.*, 1979; Sousa, 1979; Lloyd and White, 1980; Atkinson and Shorrocks, 1981; Hanski, 1981, 1983; Ives and May, 1985; Murdoch *et al.*, 1985). Differential rates of dispersal among species, independent aggregation of species among patches, and an increased number of patches in the system enhance the likelihood that diversity will be maintained on the large scale, i.e. across all patches in the system.

The spatial scales of resources provided by hosts are hierarchical (Esch *et al.*, 1975; Margolis *et al.*, 1982; Holmes and Price, 1986; see also Chapter 1), and patterns and outcomes of interaction among parasites may vary among these scales. Nested levels in this hierarchy include: (a) tissues within a host, (b) an individual of a particular host species, (c) populations of a particular host species, and (d) communities of host species. The population of a particular parasite species that infects an individual host is called an infrapopulation; the collection of populations of different parasite species within a single host is an infracommunity. The assemblage of parasite species that infect a population of a particular host species is called a component community.

Populations of invertebrates that serve as intermediate hosts are commonly infected by several species of parasitic helminths (Denny, 1969; Wright, 1971; Brown, 1978; Rohde, 1982; Lauckner, 1980, 1983). To understand the processes that structure such assemblages of larval parasites better, I investigated patterns of species diversity of the helminths that infect the salt marsh snail, *Cerithidea californica*, at two different spatial scales. This parasite assemblage is composed solely of larval digenetic trematodes. Because the members are taxonomically similar and exploit a common resource, the assemblage is more appropriately referred to as a guild (*sensu* Root, 1967) than a community. The smaller of the two scales examined in this study is that of the individual snail, which potentially supports an infraguild of larval trematodes. The larger scale is that of the local host population and its component guild of parasites.

This chapter primarily examines patterns and processes at the second, larger scale, but summarizes what is known concerning structure and dynamics at the individual host scale. The latter is the subject of Chapter 3. Here, I examine several characteristics of local host and parasite popu-

lations that may influence the diversity of component guilds of larval trematodes. These characteristics include host population density, size/age distribution, location, and rates of host and parasite recruitment. The study is restricted to infections by redia and sporocyst stages of trematodes that use *Cerithidea* as first intermediate host.

3.2 PATCH DYNAMICS AND COMPLEX PARASITE LIFE CYCLES

The digenetic trematodes that infect *Cerithidea* have life cycles typical of most parasitic helminths (see below). There is an obligate sequence of intermediate and definitive hosts; transmission is effected either by free-living motile larvae or by encysted larvae that are ingested by the host. The complex life cycles of Digenea effectively isolate the patches of habitat afforded by individuals of the same host species, since the stages that infect one such individual cannot be directly transmitted to another. Therefore, in the case of the intermediate snail host, the rate of establishment of new redial and sporocyst infections within a local snail population depends on: (a) the abundance of infective stages (i.e. miracidia) in the local environment, (b) the rate at which hosts come into contact with these stages or ingest them, and (c) the susceptibility of the individual snails that comprise the local host population. The availability of infective stages is mainly determined by processes external to the local host population, e.g. the abundance and habitat use of the definitive hosts, and physical characteristics of the local aquatic environment including water flow, chemistry, temperature, turbidity, depth, etc. These physical characteristics may influence movement and survival of the infective stages. Differential production or mortality during the dispersal phase will cause rates of establishment to differ among species of parasites.

Rates of contact between host and parasite may also be influenced by the behaviour of each. If infective stages are transmitted by ingestion, host feeding habits will affect the rate at which new infections are acquired. If infective stages actively seek hosts using environmental gradients (e.g. light intensity) that are correlated with host abundance, or chemical cues from the host, rates of encounter will be higher. Miracidia appear to employ both of these mechanisms, although behavioural responses to host exudates are only observed when the larva is in close proximity to its host (Wright, 1959, 1971; Ulmer, 1971; Cable, 1972; Chernin, 1974; Shiff, 1974; MacInnis, 1976; Brown, 1978; Smyth and Halton, 1983).

The susceptibility of hosts may vary with the species or genetic strain of parasite and with host characteristics such as age, sex, and genotype

(Richards, 1976; Meuleman *et al.*, 1987). Susceptibility may also be affected by host nutritional state, which may, in turn, be influenced by host population density.

3.3 THE SYSTEM: *CERITHIDEA CALIFORNICA* AND ITS TREMATODE PARASITES

Details of the life history of *Cerithidea californica* are summarized in Sousa (1983). Dense populations of this deposit-feeding gastropod inhabit pickleweed (*Salicornia virginica*) marshes and adjacent high intertidal (+ 1.2–2.1 m mean lower low water) mudflats and tidal creeks in protected bays and estuaries along the Pacific coast of North America. The species' range extends from Tomales Bay (Marin Co., California) to central Baja, California, Mexico (Macdonald, 1969a, b). The snail is iteroparous and its larvae undergo direct development within benthic egg strings. Egg laying begins in late March or April, hatching starts by June and continues into August.

Cerithidea is first intermediate host to at least 18 species of digenetic trematodes in California (Martin, 1955, 1972; Yoshino, 1975). In Bolinas Lagoon (Marin Co., California), the site of this study, 15 species of trematodes were found in the seven annual samples of snail populations on which this chapter is based (Table 3.1). The life cycles of all but one of these species appear to follow the typical digenean sequence (Shoop, 1988): egg, free-living miracidium, intramolluscan sporocyst or redia stage, free-living

Table 3.1 Larval trematodes that infect *Cerithidea californica* in Bolinas Lagoon. The identities of species marked with an asterisk have yet to be determined

Family	*Species*
Cyathocotylidae	*Mesostephanus appendiculatus*
	cyathocotylid #2*
Echinostomatidae	*Acanthoparyphium spinulosum*
	Echinoparyphyum sp.*
	Himasthla rhigedana
Heterophyidae	*Euhaplorchis californiensis*
	Phocitremoides ovale
Microphallidae	microphallid #1*
	microphallid #2*
Notocotylidae	*Catatropsis johnstoni*
Philopthalmidae	*Parorchis acanthus*
Renicolidae	*Renicola buchanani*
	renicolid #2*
	renicolid #3*
Schistosomatidae	*Austrobilharzia* sp.*

cercaria, encysted metacercaria stage in a poikilothermic second intermediate host (invertebrate or fish), and finally, development from an ingested metacercaria, of a parasitic adult worm in the definitive vertebrate host. The life cycle of *Austrobilharzia* sp. is the only exception to this pattern; the metacercaria stage is absent and the definitive host is infected directly by a cercaria. The definitive hosts for most of the trematodes are probably birds, but there is little information concerning the distribution of adult trematodes among potential avian or mammalian hosts that inhabit the study area.

3.4 METHODS

Study sites

The study was conducted in Bolinas Lagoon, located 24 km NW of San Francisco, California (37°55′N, 122°41′W). *Cerithidea* populations and their parasites were sampled at two sites within the lagoon. One site is adjacent to the mouth of Pine Gulch Creek (hereafter PGC site) which flows into the lagoon on its western edge, and the other is at the northeast corner of Kent Island (hereafter KI site). The sites are designated 'B' and 'C' respectively, on the map of the lagoon that appears in Stenzel *et al.* (1976), and are about 750 m apart. The freshwater flowing from the creek at PGC is an important resource for birds. Densities of wintering, migrant waterfowl and roosting gulls and terns are much higher at this site than at KI which lacks a source of freshwater. Some of these birds are probably definitive hosts of trematodes that infect *Cerithidea*.

The sites also differ in sediment characteristics. The surface sediment at PGC is a poorly sorted, very fine sandy mud and has a considerably higher organic content than the surface sediment at KI which is a well sorted, fine to medium sand (Ritter, 1969; Sousa, unpublished data). This variation in sediment quality is related to hydrological and biological differences between the sites. KI is closer to the mouth of the lagoon and to its main channel, so that tidal currents are relatively stronger, and deposition of fine particles is less, as compared to PGC. In addition, KI is inhabited by a dense population of ghost shrimp, *Callianassa californiensis*. While feeding and burrowing, *Callianassa* extensively rework the sediment, extracting or resuspending fine particulate matter, leaving a sandy, organically poor sediment (MacGinitie, 1934). In contrast, PGC has a depositional environment. Tidal currents at this site are slow and eddying. It receives a substantial input of allochthonous detrital matter and fine sediment from the creek, particularly following heavy winter rains. Bioturbation is minimal since *Callianassa* is not present at the site, possibly because the silty sediment at PGC is unsuitable for burrow construction, or because the ghost

shrimp cannot tolerate the sharp reductions in salinity associated with high, winter, creek flow (Sousa and Gleason, 1989).

The species composition and abundance of foraging shorebirds also differs between the sites and appears to be related to the spatial variation in sediment and in the associated benthic invertebrates and fishes on which they prey (Stenzel *et al.*, 1976; Page *et al.*, 1979; Quammen, 1984). These birds are definitive hosts, and many of their prey are second intermediate hosts for some of the parasites that infect *Cerithidea* (Robinson, 1952; Russell, 1960a, b; Badley, 1979; Sousa, personal observation). Since shorebird species differ in diet, they probably harbour different infracommunities of parasites (Russell, 1960a, b). The differential use of lagoon habitats by bird species and variation in the abundances of second intermediate hosts between sites may combine to produce spatial differences in the abundance of infective stages of different trematodes.

At both study sites, snails are distributed as a series of subpopulations occupying shallow (5–15 cm deep) depressions or 'pans' in the surface of the mudflat which hold standing water at low tide. These pans range in size from slightly less than $1\,m^2$ to $20\,m^2$. During most months of the year they are flushed daily by high tides.

At PGC, the pans are located along the interface of the tidal mudflats and the higher elevation, *Salicornia*-dominated marsh. Snails rarely move between them (Sousa, unpublished data) presumably because the emergent mudflats (which often consist of hard, dried plates of sediment) and the dense stands of pickleweed that border the pans, represent physical barriers to snail movement. As a consequence of this lack of adult migration and the absence of a planktonic stage in the snails' life history, the demographies of different subpopulations of snails at PGC vary greatly. They differ in size-distribution, rate of recruitment, density, and rate of parasitic infection (Sousa, unpublished data).

At KI, pans occur across the upper tidal mudflat as well as along the mudflat–marsh boundary as at PGC. At the start of the study, densities of ghost shrimp were low in these pans; however, over the course of the study shrimp populations gradually invaded about half the pans, excluding the snails. Their recruitment to the pans followed two stormy winters (1982 and 1983) when a significant amount of sedimentation occurred at the site; however, the precise mechanism(s) responsible for these shifts in local distribution are unknown. Areas between the pans have remained pockmarked with the conical sediment mounds that mark the burrow openings of a dense population of ghost shrimp. Snails are present in these surrounding areas, but at much lower densities than in the pans which are foci of snail feeding and reproduction. The *Callianassa*-dominated areas between the pans remain moist during most low tides, and few of the KI pans have vegetation around their edges. These features, as well as the fact that the

average distance between neighbouring KI pans is only half that of PGC pans (8 versus 16 m), probably account for the fact that rates of snail movement between subpopulation is at least three times greater at KI than PGC. As an apparent consequence of this greater exchange of migrants, demographic characteristics of different subpopulations at KI are very similar within any particular year, and they change quite synchronously over time (Sousa, unpublished data).

Sampling procedures

In August of 1981, a total of 34 subpopulations of *Cerithidea* were selected for long-term monitoring of demographic parameters and parasitic infection, 19 at PGC and 15 at KI. The chosen pans comprised almost all of those that contained snails along the 315 m and 70 m of marsh edge habitat studied at PGC and KI, respectively.

These subpopulations were sampled each August from 1981 through to 1987. The snails were sampled with a 225 cm^2 scoop core which collected all sediment and benthic invertebrates to a depth of 2 cm, sufficient to collect all snails in the area. The contents of each scoop were sieved through 1 mm mesh in the field and returned to the laboratory for analysis. The length (apex to aperture) of each snail was measured to the nearest 0.01 mm, then each was dissected to determine its sex and what species of trematode, if any, infected it.

Five or ten scoop samples were collected from each pan, depending on the density of snails; the greater number was taken in sparser populations. The scoops were made at regularly spaced intervals along the length of a metric tape transecting each pool, parallel to its long axis. These samples provided estimates of snail density (both young of the year and older individuals) and biomass. To ensure an adequate sample size of snails $\geq$ one year old, an additional sample of snails was collected from some pans. This supplemental sample was collected from one to three haphazardly chosen locations within a pool. Starting from the position of the first collected individual, all snails (excluding new recruits) were collected from the immediate area until the total sample numbered at least 100 individuals; a few collections fell short of this goal. Statistical tests verify that the size distributions of snails in these supplemental collections do not differ from those of $\geq$ one year old snails in scoop samples taken in the same pans. For the following analysis of parasite assemblages, the scoop and supplemental samples of $\geq$ one-year-old snails taken in a particular pan and year are pooled. Young-of-the-year snails collected in the scoop samples were never found to harbour trematode infections and are not considered in this analysis.

In most cases, snail subpopulations were dense enough that sampling was unlikely to have an impact on population dynamics. However, due to a variety of factors, but especially storm-related disturbance, the density of snails in certain pans sometimes fell to such low levels that I chose not to collect a sample for fear of affecting subsequent dynamics. Over the course of the seven years, a number of snail populations (and their component parasite assemblages) did become extinct due to physical and biological disturbances. For both these reasons, the number of subpopulations sampled at each site varied from year to year, and gradually diminished over the course of the study. By 1987, only 14 of the original pans sampled at PGC

Table 3.2 Annual rates of trematode infection in ≥ one-year-old *Cerithidea californica* at Pine Gulch Creek (PGC) and Kent Island (KI). Data from sampled subpopulations at each site are pooled

		Uninfected		*Infected by*				
				1 species		*> 1 species**		
Site	*Year*	%	(*N*)	%	(*N*)	%	(*N*)	total *N*
PGC	1981	84.34	(3502)	15.44	(641)	0.22	(9)	4152
	1982	87.96	(2571)	11.87	(347)	0.17	(5)	2923
	1983	72.17	(1079)	26.96	(403)	0.87	(13)	1495
	1984	81.85	(1768)	18.01	(389)	0.14	(3)	2160
	1985	85.80	(1837)	13.97	(299)	0.23	(5)	2141
	1986	74.50	(1461)	25.09	(492)	0.41	(8)	1961
	1987	66.33	(1186)	32.66	(584)	1.01	(18)	1788
KI	1981	74.07	(1631)	25.20	(555)	0.73	(16)	2202
	1982	89.96	(1505)	9.68	(162)	0.36	(6)	1673
	1983	77.16	(456)	21.83	(129)	1.01	(6)	591
	1984	83.19	(886)	16.81	(179)	0.00	(0)	1065
	1985	95.74	(1302)	4.19	(57)	0.07	(1)	1360
	1986	93.91	(1281)	6.09	(83)	0.00	(0)	1364
	1987	94.72	(932)	5.18	(51)	0.10	(1)	984

Average annual per cent uninfected and infected snails

	Uninfected		*Infected by*			
			1 species		*> 1 species**	
Site	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*
PGC	78.99	8.07	20.57	7.74	0.44	0.36
KI	86.96	8.86	12.71	8.55	0.32	0.40

* All are double infections except for one triple infection at KI in 1981.

and seven of those at KI remained. The numbers of ≥ one-year-old snails examined at each site during the seven censuses are listed in Table 3.2.

Measures of community structure

This chapter examines the structure of the larval parasite assemblages infecting subpopulations of *Cerithidea*. For each yearly, pooled collection from a subpopulation (hereafter referred to as a sample of snails), I have estimated several measures of parasite guild structure (Table 3.3). The raw data from which these measures are calculated were the number of infections of each parasite species found in the sample of snails. For mixed species infections, the occurrence of each species was counted as if it were a single infection of that species; i.e. each species' total for the particular sample was incremented by one for every mixed species infection in which it occurred. Since mixed infections are exceedingly rare (see below), this protocol had little influence on the results.

Since the rate of parasitic infection varied among snail subpopulations (see below), as did the number of snails collected from each, the total number of infections (NI) found in each sample of snails varied considerably. Species richness (S), the number of species in an assemblage, is strongly affected by sample size (Hurlbert, 1971; Heck *et al.*, 1975; Simberloff, 1979). In an effort to reduce the effect of small sample size *per se*, samples with fewer than 30 snails or five infections were excluded from the analysis. However, this modification of the data alone did not eliminate a significant correlation in several years at both sites between S and ln NI

Table 3.3 Measures of parasite guild structure within snail subpopulations. p_i is the proportion of infections by parasite species i

Measure	*Symbol*	*Method of computation*
Species richness	S	Total number of parasite species in sample
Expected number of species in a random sample of 15 infections	$E(S_{15})$	Calculated by rarefaction using multinomial formula of Heck *et al.* (1975)
Exponential of Shannon diversity index (Hill's (1973): N_1)	Exp (H')	$\text{Exp}(-\Sigma p_i \ln p_i)$
Reciprocal of Simpson's diversity index (Hill's (1973): N_2)	$1/\Sigma p_i^2$	See symbol
Simple dominance (May, 1975)	Dom	p_i of most abundant species in sample

Table 3.4 Correlations between measures of species richness and the number of infections in a sample. See Table 3.3 for explanation of measures. Log transformation of number of infections improved linearity of the relationships. *n* is number of subpopulations sampled. A dash indicates that the sample size (*n*) was too small for statistical analysis

Site	*PGC*							*KI*						
Year	81	82	83	84	85	86	87	81	82	83	84	85	86	87
Correlation of:														
1. S and ln (number of infections)														
r	0.65	0.87	0.42	0.78	0.38	0.47	−0.07	0.32	0.72	0.91	0.09	0.34	0.94	0.42
n	19	15	14	13	14	13	14	15	14	7	8	7	8	6
p[a]	**	***	+	***	+	+	ns	ns	**	**	ns	ns	***	ns
2. E (S_{15}) and ln (number of infections)														
r	0.17	0.07	0.61	−0.07	−0.20	−0.53	−0.60	0.33	–	0.91	−0.10	–	–	–
n	15	11	13	8	10	10	13	15	2	4	8	0	1	0
p	ns	ns	*	ns	ns	+	*	ns	–	*	ns	–	–	–

[a] All probabilities in table are one-tailed: ns ≥ 0.10, + < 0.10, * < 0.05, ** < 0.01, *** < 0.001.

(Table 3.4). Rarefaction procedures were then used (Heck *et al.*, 1975) to estimate the expected number of trematode species in a sample of 15 infections (E (S_{15})) drawn randomly from the collection of infections found in each sample of snails. The multinomial-based formula of Heck *et al.* (1975) was applied since the infections within each collection of snails is likely to be a very small fraction of those within an entire subpopulation of snails, numbering in the thousands of individuals. In this situation, the successive collection of infected snails is unlikely to affect the relative abundance of infections by different parasites within the snail subpopulation. The sampling and estimation procedures also meet the criteria outlined by Sanders (1968) and Simberloff (1979): (a) the samples are taxonomically similar and come from the same habitat, (b) the method of sampling was consistent for all pans and years, and (c) (E (S_{15})) was computed by interpolation, not extrapolation. As a result of this rarefaction procedure, the sample sizes for analyses of relationships between (E (S_{15})) and host population characteristics were smaller than those for other measures of guild structure, since snail samples containing fewer than 15 infections were not included in the former data set. The correlation between (E (S_{15})) and ln NI is clearly weaker than between S and ln NI (Table 3.4). Partial correlations between (E (S_{15})) and ln Ni with mean length of snails in the sample held constant were not significant in any year, at either site.

The other measures of parasite guild structure (Table 3.3) were chosen for their ease of interpretation (Hill, 1973; Peet, 1974; May, 1975). The two diversity measures, Exp (H′) and $1/\Sigma p_i^2$, differ in their sensitivity to changes in the relative importance of species (Hurlbert, 1971; Peet, 1974). The first index is most sensitive to changes in rare species, while the second is more responsive to changes in common species.

3.5 THE ANALYSIS

Patterns at the level of the individual host

Several lines of evidence indicate that strong antagonistic interactions between larval parasite species occur within individual snails. Circumstantial evidence comes from the observation that mixed-species infections by larval trematodes are exceedingly rare in *Cerithidea* populations. Martin (1955) made 12 monthly collections of adult *Cerithidea* from a salt pond in Upper Newport Bay, California and reported the frequencies of different categories of infection for the pooled collection of monthly samples. A statistical analysis of these pooled data indicates that mixed-species infections were fewer than would be expected under the null hypothesis that parasites are randomly and independently distributed among snails

(Chapter 4). This result suggests negative interactions between species of parasites, but the pooled nature of the data set complicates interpretation of the statistical pattern of negative association. Heterogeneity in the relative abundance of parasite species among the monthly samples alone could produce such a pattern, without any direct interaction between species. Indeed, Martin (1955) found seasonal variation in the prevalance of infection, as did Yoshino (1975) for *Cerithidea* populations in Goleta Slough, California. Cort *et al.* (1937) were among the first to identify this problem with analyses of parasite associations based on heterogeneous data sets.

Mixed species were also very rare in the seven annual samples from Bolinas Lagoon (Table 3.2). Of 4462 infected snails examined during the seven censuses, only 91 (2%) were infected by more than one species. I have statistically compared the observed and expected numbers of mixed infections for each pan within a given year. This pan by pan analysis of samples collected in the same month of each year reduces the influence of spatial and temporal heterogeneity in parasite abundance discussed above. Due to the large number of parasite species involved and relatively low frequencies of infections per species, the expected numbers of mixed-species infections are often too small for the application of standard analyses for discrete data, e.g. contingency tables. Instead, I used Monte Carlo simulations (Sokal and Rohlf, 1981) to estimate the probability of the observed number of mixed infections under the null hypothesis of random, independent assortment of parasites among hosts. The results of this analysis agree with that of Martin's (1955) data discussed above; within a number of snail subpopulations in any given year, the frequency of snails infected by more than one species of larval trematode is less than would be expected by chance (Sousa, in prep).

Such negative associations are not proof of direct antagonistic interactions among species. One alternative explanation is that miracidia of one parasite species may actively avoid, or be unable to infect, snails that are already parasitized by a different species (for a discussion of possible mechanisms of indirect antagonism see Lim and Heyneman, 1972).

A second alternative explanation for the rarity of mixed infections is that parasite species may preferentially infect hosts of different size, although this pattern itself might be an evolutionary response to negative interactions in the past, i.e. niche partitioning (MacArthur and Levins, 1967; but see Connell, 1980). *Cerithidea* infected by different trematode species do differ in mean length (Sousa, 1983; Sousa and Gleason, 1989; see also Chapter 4), but the ranges of snail lengths in which the different species are found overlap considerably. While these distinctive patterns of distribution may reduce rates of interspecific interaction, two lines of evidence indicate that intramolluscan antagonistic interactions do occur, and that they are strongly

hierarchical in outcome (Sousa, in prep.). While dissecting snails from the annual samples, I have observed a number of mixed infections in which rediae of one species are preying on rediae, sporocysts, or cercariae of another. These interactions are hierarchical: species with large rediae dominate, especially *Himasthla* and *Parorchis*. Redial species of intermediate size are, in turn, dominant over species with small rediae or sporocysts. I have also examined temporal patterns of parasite species replacement in marked snails carrying known infections that have been released in the field and recaptured at a later date. These sequences of replacement are also strongly hierarchical. Species with large rediae (*Himasthla* and *Parorchis*) most frequently invade and displace infections by other species; in contrast, infections by these two species are very rarely invaded and, if so, only by the other member of the pair.

In summary, the rarity of mixed-species infections, direct observations of hierarchical antagonism between co-occurring species, and the record of hierarchical species replacement over time, all suggest that negative interspecific interactions among larval trematodes occur at the scale of the individual snail, the infraguild (i.e. infracommunity) level. The next section addresses the question of whether these interactions are common enough to affect the structure of the component guild (i.e. component community) of parasites within a subpopulation of snails.

Patterns at the level of the host subpopulation

Hypotheses and predictions

In this section, I present two alternative hypotheses which may explain parasite guild structure at the level of the host population in this system. The first hypothesis is that the hierarchical, negative, interspecific interactions seen at the infraguild level strongly influence component guild structure. The second is that the spatial and temporal patterns of parasite recruitment and the duration of host exposure, rather than interspecific competition, are the primary determinants of guild structure at the component level.

Infraguild interactions will affect the structure of component parasite guilds if the host resource is sufficiently limiting that a few antagonistically-dominant species of parasites come to monopolize the infections. These conditions could result in two ways: (a) from high rates of recruitment and infection by these dominant species, or (b) from low rates of recruitment of new hosts to the population and the gradual accumulation of infections by the dominant parasites with time. If intramolluscan antagonism was the primary determinant of component-level structure, the following patterns would be predicted. First, assuming that the mean length of snails in a population is an index of mean age, species richness and diversity should

exhibit a hyperbolic relationship when plotted against mean length of snail. Young populations composed predominantly of small snails will have only been exposed to infective parasite larvae for a short time. Therefore, only a small number of parasite species will have had the opportunity to infect them, and those parasite species with the highest recruitment rates will be most abundant. Species richness and diversity of parasite guilds infecting such snail populations will be low. At the opposite extreme, populations composed primarily of larger, older snails will have been exposed to infective miracidia for a relatively long time. For this reason, and the fact that infections appear to be life-long in *Cerithidea* (Sousa, 1983, in prep.), prevalence of infection should be high in these older populations and antagonistic interspecific interactions common. These interactions should result in most snails being infected by a few dominant trematode species, and diversity should decline. The highest species richness and diversity should be seen in populations of intermediately-sized snails which are old enough to have accumulated several parasite species, but are not so old that one or a few species have had sufficient time to dominate the majority of the infections. The pattern for species dominance should be the mirror image of that for species richness and diversity. This hypothesized hyperbolic relationship is analogous to that predicted by the Intermediate Disturbance Hypothesis for patterns of species diversity in assemblages of free-living organisms (Connell, 1978; Sousa, 1984).

The assumption that snail length is an index of snail age is certainly true in a relative sense (i.e. snails grow longer with time); however, the precise age of a snail cannot be predicted from its length. For example, snail growth can be stunted under conditions of high density. As a result, in populations of different density, snails of the same age may differ by several mm in length. In addition, parasitic infection can alter snail growth rate, either slowing or accelerating it depending on the species of trematode (Sousa, 1983, unpublished data). As a consequence, while a strong relationship between size and age exists, there is undoubtedly some variation in it.

A second prediction from the interspecific interaction hypothesis is that all else being equal, the species richness and diversity of parasites should increase with greater variation in host size within a snail subpopulation, since the distributions of different species among host size classes are heterogeneous (see references cited earlier). Partitioning of hosts by size may promote coexistence of parasite species by reducing the rates at which they antagonistically interact.

A third prediction is that, all else being equal, parasite species richness and diversity should be higher in host populations with a greater availability of uninfected, susceptible individuals since the frequency of mixed-species infections and antagonistic interactions should be lower under these conditions.

Under the second general hypothesis, a very different pattern of component guild structure is predicted. If rates of parasite recruitment and infection are low relative to the rate at which uninfected, susceptible new hosts recruit, the number of open patches of host resource may never become so limited that intramolluscan interactions would reduce the diversity of the component guild. Further, mortality of old, infected hosts may limit the accumulation of infections by dominant species. Under these conditions, an equilibrium assemblage, dominated by a few species would seldom if ever develop. Species richness and diversity would rise monotonically with mean snail age (length) as parasite species and infections accumulate with time. These indices of guild diversity might even display a faster than linear increase with mean length of snails in a subpopulation, if the range of mean host sizes is sufficiently large. This is because a snail's rate of growth slows with increasing length (Sousa, unpublished data); therefore, the mean age of a host population increases as a power function of mean length.

Conversely, species dominance should exhibit a monotonic decline with mean snail length. Neither variation in host size within a population, nor variation in the availability of uninfected, susceptible hosts would have a marked effect on guild structure, since the host resource is not limiting. Under these circumstances, guild structure would be determined primarily by temporal and spatial patterns of parasite recruitment. This situation is roughly equivalent to Wilson's (1969) non-interactive phase of community development. Price (1980) argues that this kind of nonequilibrium situation is typical of many, if not most, host-parasite systems.

Results

Scatterplots (Figs 3.1–3.3) and correlation analysis (Table 3.5) reveal that in five of the seven annual samples from PGC, rarefied species richness (E (S_{15})), and at least one of the two diversity indices (Exp(H′) and $1/\Sigma p_i^2$) exhibited a significant monotonic increase with the mean length of snails in a subpopulation. There was no significant correlation between these variables in 1982 or 1987. Simple dominance (Dom) declined significantly and monotonically with mean snail length in three of the seven years (Table 3.5; Fig. 3.4); similar, but non-significant, negative relationships were detected in the other four. The combined probability (Fisher, 1954) for all seven years was highly significant for each of the above correlations ($p < .001$ in each case).

Patterns at KI were similar to those at PGC, but not as strong. The smaller number of subpopulations sampled at this site reduces the statistical power of the correlation analysis. This problem is aggravated by the fact that within any particular year, KI subpopulations varied little in mean length (Figs

Table 3.5 Correlations between measures of parasite guild structure and average length of snails in a subpopulation. See Table 3.3 for explanation of measures. *n* is number of subpopulations sampled. Dom was normalized with an angular transformation. A dash indicates that the sample size (*n*) was too small for statistical analysis

Site	*PGC*							*KI*						
Year	81	82	83	84	85	86	87	81	82	83	84	85	86	87
Correlation of average length and														
1. E (S_{15})														
r	0.46	0.27	0.58	0.78	0.82	0.70	0.40	−0.20	–	0.11	0.90	–	–	–
n	15	11	13	8	10	10	13	15	2	4	8	0	1	0
p[a]	+	ns	*	*	**	*	ns	ns	–	ns	**	–	–	–
2. Exp (H′)														
r	0.55	0.40	0.40	0.61	0.73	0.66	0.34	−0.21	0.56	0.44	0.92	−0.44	0.66	0.65
n[b]	19	15	14	13	14	13	14	15	14	7	8	7	8	6
p	*	ns	ns	*	**	*	ns	ns	*	ns	***	ns	+	ns
3. $1/\Sigma p_i^2$														
r	0.48	0.31	0.30	0.69	0.74	0.67	0.43	−0.18	0.47	0.46	0.83	−0.43	0.57	0.75
p	*	ns	ns	**	**	*	ns	ns	+	ns	*	ns	ns	+
4. arcsin Dom														
r	−0.36	−0.26	−0.25	−0.69	−0.75	−0.63	−0.49	0.02	−0.24	−0.39	−0.54	0.25	−0.28	−0.79
p	ns	ns	ns	**	**	*	+	ns	ns	ns	ns	ns	ns	+

[a] All probabilities in table are two-tailed: ns ≥ 0.10, + < 0.10, * < 0.05, ** < 0.01, *** < 0.001.
[b] Sample sizes are the same for measures 2, 3, and 4 this table.

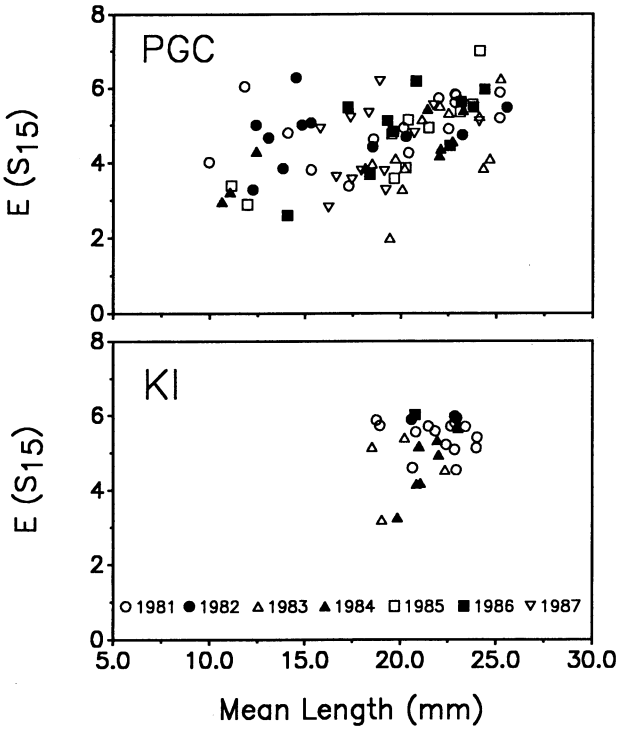

Fig. 3.1 Plot of rarefied number of trematode species versus mean length of snails in a subpopulation at each study site. Each symbol represents the pooled sample of snails collected from an individual pan in the indicated year (see text for further explanation).

3.1–3.4), as discussed earlier. Even so, significant positive correlations between rarefied species richness or the indices of diversity and mean snail length were detected in two of the seven years. Simple dominance appeared to be negatively correlated with mean snail length, but this relationship was never statistically significant.

Figure 3.5 is identical to Fig. 3.4, but indicates which species of parasite was the most prevalent in each pan. Note that the predominant species differed considerably between sites, even though the number of parasite species infecting a host subpopulation of a given mean length did not differ between sites (Fig. 3.1). Also note that *Echinoparyphium* was a conspicuous dominant in those PGC populations whose size distributions were dominated by small snails.

No significant relationship was found in any year, at either site, between the standard deviation of snail length and any of the measures of parasite guild structure. The same was true for a partial correlation analysis of these

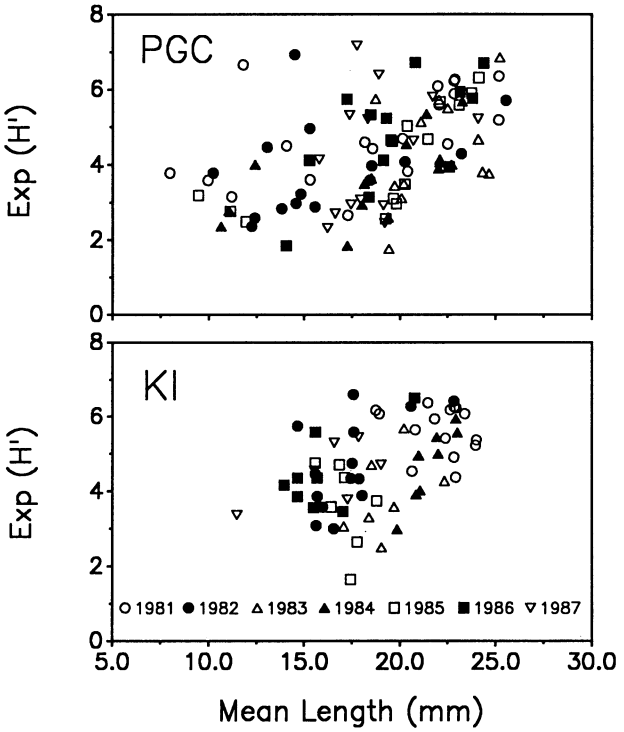

Fig. 3.2 Plot of antilogarithm of Shannon diversity index versus mean length of snails in a subpopulation at each study site. Symbols as in Fig. 3.1.

variables with mean snail length held constant. Scatterplots of the variables did not reveal any hidden, non-linear relationships.

Similarly, only three out of 38 partial correlations (mean length held constant) between rarefied species richness, or the diversity indices, and the mean density of uninfected snails were statistically significant. Two of these significant correlations were positive, favouring the Antagonistic Interaction Hypothesis; the third was in the opposite direction.

When no adjustment for differences in mean snail length is made, species richness and diversity were sometimes negatively related to the density of uninfected hosts. Significant negative relationships of these measures to the density of uninfected snails were found at PGC in three of the seven years (1984–86; r ranged from -0.57 to -0.76, $p < .05$ or .01). These were years in which the proportionately fewer infections in dense, younger, populations of small snails were dominated by one parasite species, *Echinoparyphium*. In each of these years, simple dominance was also significantly correlated with the density of uninfected snails, but in the opposite direction

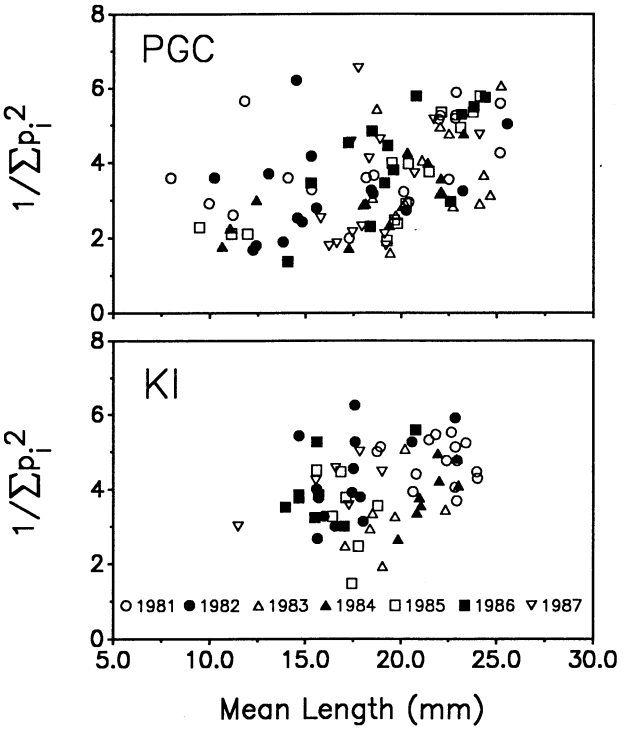

Fig. 3.3 Plot of reciprocal of Simpson diversity index versus mean length of snails in a subpopulation at each study site. Symbols as in Fig. 3.1.

to the diversity measures (r ranged from 0.65 to 0.73, $p < .05$ or $< .01$). None of these relationships were significant in any year at KI, where *Echinoparyphium* infections never dominated a component guild (Fig. 3.5).

3.6 DISCUSSION AND CONCLUSIONS

There is little evidence from this analysis that the antagonistic interactions between parasite species which occur within individual hosts have a strong impact on patterns of parasite species richness or diversity at the level of the host population. In particular, parasite diversity did not decline in older populations of hosts as would be predicted if uninfected hosts were a limited resource for parasites in such populations and infections came to be monopolized by a small number of antagonistically dominant species. In addition, neither the density of uninfected, susceptible hosts, nor the variation in host size within a snail subpopulation showed any relationship to

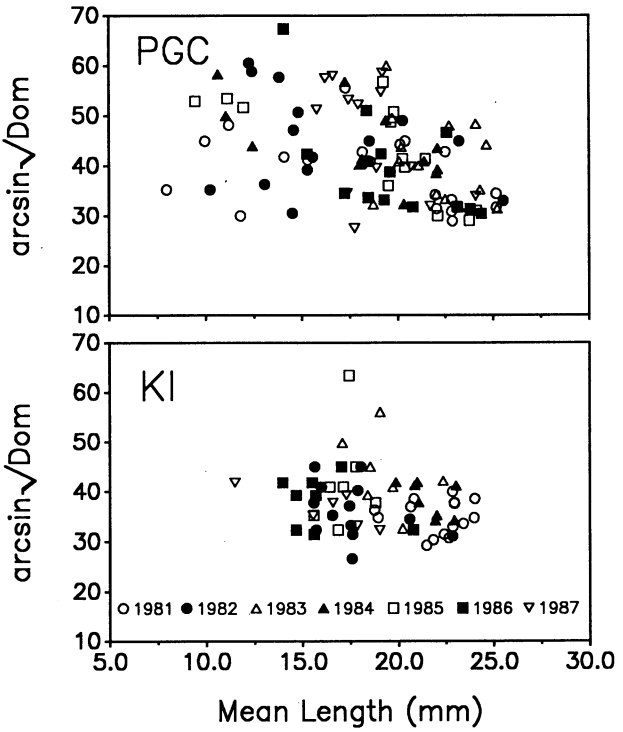

Fig. 3.4 Plot of arcsin-transformed simple dominance index versus mean length of snails in a subpopulation at each study site. Symbols as in Fig. 3.1.

parasite diversity. Indeed, the percentage of hosts infected by larval trematodes is generally greater in populations comprised of larger, older individuals (for full data set: PGC: $r = 0.46, n = 103, p < .001$; KI: $r = 0.86$, $n = 70, p < .001$). Apparently the number of uninfected, susceptible hosts never becomes sufficiently limiting, given the rates of snail and parasite recruitment in this system, to drive parasite diversity downward. Instead, species richness and diversity rise monotonically with mean snail length, or roughly, the mean age of the host population. This is not to say that competition has no influence on the structures of the component parasite guilds examined in this study. Indices of guild structure such as those computed for this analysis hide the population dynamics of individual species; some species may well be less abundant at the component level as a consequence of infra-level antagonistic interactions. It is clear, however, that any such reductions are more than compensated for by increases in both the number and equitability of other parasite species in older host populations. The competitive interactions that prevent the coexistence of

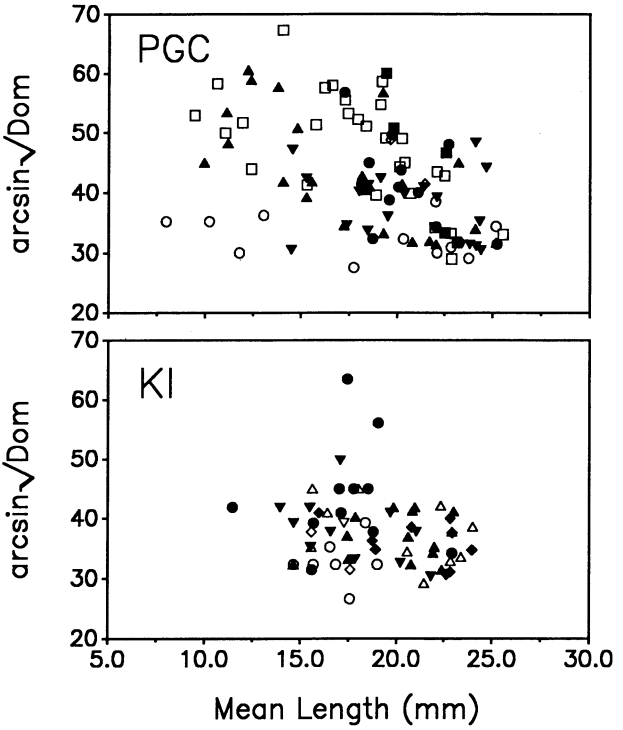

Fig. 3.5 Plot of arcsin-transformed simple dominance index versus mean length of snails in a subpopulation at each study site. Symbols indicate dominant species of parasite in each subpopulation: *Acanthoparyphium* (filled circle), *Euhaplorchis* (open triangle), *Parochis* (filled triangle), *Echinoparyphium* (open square), cyanthocotylid #2 (filled square), *Catatropis* (open inverse triangle), *Himasthla* (filled inverse triangle), renicolid #2 (open diamond), microphallid #1 (filled diamond), co-domination by two or more species (open circle).

parasite species within individual hosts have far less impact on the structures of the component parasite guilds infecting subpopulations of hosts. The population dynamics of the different parasite species in each of the host subpopulations will be examined separately (Sousa, in prep.).

Under a condition of relatively unlimited resources, which appears to characterize the component level of this system, spatial and temporal variation in the abundance and/or infectivity of miracidial stages will be the primary determinant of component guild structure. The observations that the dominant parasite species differ markedly between the sites (Fig. 3.5) and that the relative prevalence of different parasite species fluctuates greatly from year to year (Sousa, unpublished data) support this interpretation.

This study demonstrates that distinct processes are primarily responsible for the structure of assemblages of larval trematodes at different spatial scales; a similar conclusion has been reached for a number of assemblages of free-living organisms (see references cited earlier). If more than one species of parasite recruits to an individual snail, deterministic antagonistic interactions almost always result in the exclusion of one of the two species. Most larval trematodes exploit the gonad or digestive gland of their molluscan hosts (e.g. Wright, 1971; Brown, 1978; Kuris, 1974; Lauckner, 1980, 1983; Sousa, 1983), tissues which are not as easily partitioned as are the complex organ systems of the definitive vertebrate hosts (e.g. Crompton, 1973; Holmes, 1973; Kennedy, 1975; Bush and Holmes, 1983, 1986a, b). Consequently, parasite species rarely coexist on the small scale, and infraguilds are depauperate.

In contrast, the component guild of trematodes that infects populations of *Cerithidea* in Bolinas Lagoon appears to be structured largely by external processes, in particular those that determine spatial and temporal variation in the abundance of infective stages in the parasite life cycle. Interspecific antagonism on the small spatial scale does not have a detectable effect on patterns at this larger scale. Thus, it appears that very different processes determine the organization of larval parasite guilds at the two spatial scales examined in this study, the infra- and component guild levels of parasite resources.

Finally, it is apparent that the discrete, divided nature of resources provided by hosts promotes coexistence of parasite species on the large scale. This structure and the complex life cycle of the parasites preclude the direct spread between snails of asexual parasitic stages (rediae) of antagonistically dominant species. In effect, this provides a refuge for less aggressive parasites, similar to that demonstrated in Huffaker's (1958) classic study of predator–prey interactions in a patchy, experimental system. Independent aggregation of parasites among hosts, as a consequence of both asexual reproduction and differential exploitation of different-sized hosts, makes coexistence even more likely (Shorrocks *et al.*, 1979; Atkinson and Shorrocks, 1981; Dobson, 1985; Ives and May, 1985). In addition, the ephemeral nature of host patches, and the high rate at which new ones are created via host reproduction, make it all the more difficult for one or a few species to monopolize the host resource.

ACKNOWLEDGEMENTS

I am deeply indebted to many people for their assistance and support during this study. I owe a huge thanks to the seven annual 'snail crews' without whose help in the field and laboratory this study would not have been

possible. G. Roderick and E. Adams wrote excellent, tailor-made computer programs for this analysis. B. Mitchell, A. Bush, G. Esch, and E. Grosholz provided many helpful comments on the manuscript. Parasite species indentifications were confirmed by H. Ching. Access to the study sites was kindly allowed by the Marin County Department of Parks and Recreation. This research was supported by National Science Foundation grants DEB-8004192, BSR-8300082, BSR-8505871, and BSR-8516522.

REFERENCES

Addicott, J. F., Aho, J. M., Antolin, M. F. *et al.* (1987) Ecological neighborhoods: scaling environmental patterns. *Oikos*, **49**, 340–46.

Allen, T. F. H. and Starr, T. B. (1982) *Hierarchy*, University of Chicago Press, Chicago.

Andrewartha, H. G. and Birch, L. C. (1954) *The Distribution and Abundance of Animals*, University of Chicago Press, Chicago.

Armstrong, R. A. (1976) Fugitive species: experiments with fungi and some theoretical considerations. *Ecology*, **57**, 953–63.

Atkinson, W. D. and Shorrocks, B. (1981) Competition on a divided and ephemeral resource: a simulation model. *J. Anim. Ecol.*, **50**, 461–71.

Badley, J. E. (1979) *The Endohelminth Fauna of Willets, Catoptrophorus semipalmatus (Gmelin 1789) (Charadriformes: Scolopacidae) from West Bay, Texas*. MS Thesis, Texas A and M University.

Brown, D. S. (1978) Pulmonate molluscs as intermediate hosts for trematodes. In *Pulmonates, vol. 2A. Systematics, Evolution, and Ecology* (eds, V. Fretter and J. Peake), Academic Press, New York, pp. 287–333.

Bush, A. O. and Holmes, J. C. (1983) Niche separation and the Broken-stick Model: use with multiple assemblages. *Am. Nat.*, **122**, 849–55.

Bush, A. O. and Holmes, J. C. (1986a) Intestinal helminths of lesser scaup ducks: patterns of association. *Can. J. Zool.*, **64**, 132–41.

Bush, A. O. and Holmes, J. C. (1986b) Intestinal helminths of lesser scaup ducks: an interactive community. *Can. J. Zool.*, **64**, 142–52.

Cable, R. M. (1972) Behavior of digenetic trematodes. In *Behavioural Aspects of Parasite Transmission*, (eds, E. U. Canning and C. A. Wright), Suppl. 1 to the Zool. J. Linnean Soc., Academic Press, London, pp. 1–18.

Caswell, H. (1978) Predator-mediated coexistence: a non-equilibrium model. *Am. Nat.*, **112**, 127–54.

Chernin, E. (1974) Some host-finding attributes of *Schistosoma mansoni* miracidia. *Am. J. Trop. Med. Hyg.*, **23**, 320–27.

Cohen, J. E. (1970) A Markov Contingency Table Model for replicated Lotka-Volterra systems near equilibrium. *Am. Nat.*, **104**, 547–59.

Connell, J. H. (1978) Diversity in tropical rainforests and coral reefs. *Science*, **199**, 1302–10.

Connell, J. H. (1980) Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, **35**, 131–8.

Connell, J. H. and Sousa, W. P. (1983) On the evidence needed to judge ecological stability or persistence. *Am. Nat.*, **121**, 789–824.

Cort, W. W., McMullen, D. B. and Brackett, S. (1937) Ecological studies on the cercariae in *Stagnicola emarginata angulata* (Sowerby) in the Douglas Lake region, Michigan. *J. Parasitol.*, **23**, 504–32.

Crompton, D. W. T. (1973) The sites occupied by some parasitic helminths in the alimentary tract of vertebrates. *Biol. Rev.*, **48**, 27–83.

Dayton, P. K. and Tegner, M. A. (1984) The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In *A New Ecology: Novel Approaches to Interactive Systems*, (eds, P. W. Price, C. N. Slobodchikoff and W. S. Gaud), John Wiley and Sons, New York, pp. 457–81.

Denny, M. (1969) Life-cycles of helminth parasites using *Gammarus lacustris* as an intermediate host in a Canadian lake. *Parasitology*, **59**, 795–827.

Dobson, A. P. (1985) The population dynamics of competition among parasites. *Parasitology*, **91**, 317–47.

Esch, G. W. Gibbons, J. W. and Bourque, J. E. (1975) An analysis of the relationship between stress and parasitism. *Am. Midl. Nat.*, **93**, 339–53.

Fisher, R. A. (1954) *Statistical Methods for Research Workers*, 12th edn, Oliver and Boyd, Edinburgh

Hanski, I. (1981) Coexistence of competitors in patchy environment with and without predation. *Oikos*, **37**, 306–12.

Hanski, I. (1983) Coexistence of competitors in patchy environment. *Ecology*, **64**, 493–500.

Hastings, A. (1977) Spatial heterogeneity and the stability of predator–prey systems. *Theor. Popul. Biol.*, **12**, 37–48.

Hastings, A. (1980) Disturbance, coexistence, history, and competition for space. *Theor. Popul. Biol.*, **18**, 363–73.

Heck, K. L. Jr, Van Belle, R. and Simberloff, D. (1975) Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology*, **56**, 1459–61.

Hill, M. O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, **54**, 427–32.

Holmes, J. C. (1973) Site segregation by parasitic helminths: interspecific interactions, site segregation, and their importance to the development of helminth communities. *Can. J. Zool.*, **51**, 333–47.

Holmes, J. C. and Price, P. W. (1986) Communities of parasites. In *Community Ecology: Patterns and Process*, (eds, J. Kikkawa and D. J. Anderson), Blackwell Scientific Publications, Melbourne, pp. 187–213.

Horn, H. S. and MacArthur, R. H. (1972) Competition among fugitive species in a harlequin environment. *Ecology*, **53**, 749–52.

Huffaker, C. B. (1958) Experimental studies on predation: dispersion factors and predator–prey oscillations. *Hilgardia*, **27**, 343–83.

Hurlbert, S. H. (1971) The non-concept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577–86.

Hutchinson, G. E. (1951) Copepodology for the ornithologist. *Ecology*, **32**, 571–7.

Ives, A. R. and May, R. M. (1985) Competition within and between species in a patchy environment: relations between microscopic and macroscopic models. *J. Theor. Biol.*, **115**, 65–92.

Kennedy, C. R. (1975) *Ecological Animal Parasitology*, John Wiley and Sons, New York.

Kuris, A. M. (1974) Trophic interactions: similarity of parasitic castrators to parasitoids. *Q. Rev. Biol.*, **49**, 129–48.

Lauckner, G. (1980) Diseases of mollusca: gastropoda. In *Diseases of Marine Animals, vol. I: General aspects, protozoa to gastropoda*, (ed. O. Kinne), John Wiley and Sons, New York, pp. 311–424.

Lauckner, G. (1983) Diseases of mollusca: bivalvia. In *Diseases of Marine Animals, vol. II: Introductions, bivalvia to scaphopoda* (ed. O. Kinne), Biologische Anstalt Helgoland, Hamburg, pp. 477–961.

Levin, S. A. (1974) Dispersion and population interactions. *Am. Nat.*, **108**, 207–28.

Levin, S. A. (1976) Population dynamic models in heterogeneous environments. *Ann. Rev. Ecol. Syst.*, **7**, 287–310.

Levins, R. and Culver, D. (1971) Regional coexistence of species and competition between rare species. *Proc. Nat. Acad. Sci. USA.*, **68**, 1246–8.

Lim, H. K. and Heyneman, D. (1972) Intramolluscan inter-trematode antagonism: a review of factors influencing the host–parasite system and its possible role in biological control. *Adv. Parasitol.*, **10**, 191–268.

Lloyd, M. and White, J. (1980) On reconciling patchy microspatial distributions with competition models. *Am. Nat.*, **115**, 29–44.

MacArthur, R. H. and Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.*, **101**, 377–85.

Macdonald, K. B. (1969a) Molluscan faunas of Pacific coast salt marshes and tidal creeks. *Veliger*, **11**, 399–405.

Macdonald, K. B. (1969b) Quantitative studies of salt marsh mollusc faunas from the North American Pacific coast. *Ecol. Monogr.*, **39**, 33–60.

MacGinitie, G. E. (1934) The natural history of *Callianassa californiensis*. *Am. Midl. Nat.*, **15**, 166–77.

MacInnis, A. J. (1976) How parasites find hosts, some thoughts on the inception of host–parasite integration. In *Ecological Aspects of Parasitology*, (ed. C. R. Kennedy), North-Holland Publ. Co., Amsterdam, pp. 3–20.

Margolis, L., Esch, G. W., Holmes, J. C. *et al.* (1982) The use of ecological terms in parasitology. *J. Parasitol.*, **68**, 131–3.

Martin, W. E. (1955) Seasonal infections of the snail *Cerithidea californica* Haldeman, with larval trematodes. In *Essays in the Natural Sciences in Honor of Captain Allan Hancock*, Allan Hancock Foundation, University of Southern California Press, Los Angeles, pp. 203–10.

Martin, W. E. (1972) An annotated key to the cercariae that develop in the snail *Cerithidea californica*. Bull. South. Cal. Acad. Sci., **71**, 39–43.

May, R. M. (1975) Patterns of species abundance and diversity. In *Ecology and Evolution of Communities*, (eds, M. L. Cody and J. M. Diamond), Belknap Press, Cambridge, Mass., pp. 81–120.

Meuleman, E. A., Bayne, C. J. and Van der Knaap, W. P. (1987) Immunological aspects of snail–trematode interactions. In *Developmental and Comparative Immunology* (eds, E. L. Cooper, C. Langlet and J. Bierne, Progress in Clinical and Biological Research, vol. 233, Alan R. Liss, Inc, New York, pp. 113–27.

Murdoch, W. W., Chesson, J. and Chesson, P. L. (1985) Biological control in theory and practice. *Am. Nat.*, **125**, 344–66.

Page, G. W., Stenzel, L. E. and Wolfe, C. M. (1979) Aspects of the occurrence of shorebirds on a central California estuary. *Stud. Avian Biol.*, **2**, 15–32.

Peet, R. K. (1974) The measurement of species diversity. *Ann. Rev. Ecol. Syst.*, **5**, 285–307.

Price, P. W. (1980) *Evolutionary Biology of Parasites*, Princeton University Press, Princeton.

Quammen, M. L. (1984) Predation by shorebirds, fish, and crabs on invertebrates in intertidal mudflats: an experimental test. *Ecology*, **65**, 529–37.

Richards, C. S. (1976) Genetics of the host–parasite relationship between *Biomphalaria glabrata* and *Schistosoma mansoni*. In *Genetic Aspects of Host–parasite relationships*, (eds, A. E. R. Taylor and R. Muller), Symposia of the British Society for Parasitology, vol. 14, Blackwell Scientific Publications, pp. 45–54.

Ritter, J. R. (1969) *Preliminary Studies of the Sedimentology and Hydrology in Bolinas Lagoon, Marin County, California, May 1967–June 1968*, U.S. Department of the Interior, Geological Survey, Water Resources Division, Menlo Park, California.

Robinson, E. J. (1952) A preliminary report on the life cycle of *Cloacitrema michiganensis* McIntosh 1938. *J. Parasitol.*, **38**, 368.

Rohde, K. (1982) *Ecology of Marine Parasites*, University of Queensland press, St. Lucia.

Root, R. (1967) The niche exploitation pattern of the blue-grey gnatcatcher. *Ecol. Monogr.*, **37**, 317–50.

Russell, H. T. (1960a) Trematodes from shorebirds collected at Morro Bay, California. *J. Parasitol.*, **46** (5 : 2), 15 [Abstr.].

Russell, H. T. (1960b) *Trematodes From Shorebirds Collected at Morro Bay, California*, PhD. thesis, University of California, Los Angeles, C.A.

Sanders, H. L. (1968) Marine benthic diversity: a comparative study. *Am. Nat.*, **102**, 243–82.

Shiff, C. J. (1974) Seasonal factors influencing the location of *Bulinus (Physopsis) globosus* by miracidia of *Schistosoma haematobium* in nature. *J. Parasitol.*, **60**, 578–83.

Shoop, W. L. (1988) Trematode transmission patterns. *J. Parasitol.*, **74**, 46–59.

Shorrocks, B., Atkinson, W. and Charlesworth, P. (1979) Competition on a divided and ephemeral resource. *J. Anim. Ecol.*, **48**, 899–908.

Simberloff, D. (1979) Rarefaction as a distribution-free method of expressing and estimating diversity. In *Ecological Diversity in Theory and Practice*, (eds, J. F. Grassle, G. P. Patil, W. Smith and C. Taillie), International Co-operative Publishing House, Fairland, Maryland, pp. 159–76.

Skellam, J. G. (1951) Random dispersal in theoretical populations. *Biometrika*, **38**, 196–318.

Slatkin, M. (1974) Competition and regional coexistence. *Ecology*, **55**, 128–34.

Smyth, J. D. and Halton, D. W. (1983) *The Physiology of Trematodes*, 2nd edn, Cambridge University Press, Cambridge.

Sokal, R. R. and Rohlf, F. J. (1981) *Biometry*, 2nd edn, W. H. Freeman and Co., San Franscisco.

Sousa, W. P. (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, **60**, 1225–39.

Sousa, W. P. (1983) Host life history and the effect of parasitic castration on growth: a field study of *Cerithidea californica* Haldeman (Gastropoda: Prosobranchia) and its trematode parasites. *J. Exp. Mar. Biol. Ecol.*, **73**, 273–96.

Sousa, W. P. (1984) The role of disturbance in natural communities. *Ann. Rev. Ecol. Syst.*, **15**, 353–91.

Sousa, W. P. and Gleason, M. (1989) Does parasitic infection compromise host survival under extreme environmental conditions: the case for *Cerithidea californica* (Gastropoda: Prosobranchia)? *Oecologia*, in press.

Stenzel, L. E., Huber, H. R. and Page, G. W. (1976) Feeding behavior and diet of the long-billed curlew and willet. *Wilson Bull.*, **88**, 314–32.

Ulmer, M. J. (1971) Site-finding behavior in helminths in intermediate and definitive hosts. In *Ecology and Physiology of Parasites*, (ed. A. M. Fallis), University of Toronto Press, Toronto, pp. 123–60.

Wiens, J. A. (1976) Population responses to patchy environments. *Ann. Rev. Ecol. Syst.*, **7**, 81–120.

Wilson, E. O. (1969) The species equilibrium. *Brookhaven Symp. Biol.*, **22**, 38–47.

Wright, C. A. (1959) Host location by trematode miracidia. *Ann. Trop. Med. Parasit.*, **53**, 288–92.

Wright, C. A. (1971) *Flukes and Snails*, Hafner Press, New York.

Yoshino, T. P. (1975) A seasonal and histologic study of larval digenea infecting *Cerithidea californica* (Gastropoda: Prosobranchia) from Goleta Slough, Santa Barbara County, California. *Veliger*, **18**, 156–61.