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Niche partitioning in the cestode communities of two elasmobranchs

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Several randomization methods have been used to investigate the influence of competitive interactions in shaping parasite community structure. Marine fish parasite communities have often been regarded as unstructured assemblages with little or no resource limitation and, therefore, not prone to competitive influences. In this study, null models were used to assess the niche overlap of cestode communities of two distinct but closely related elasmobranch hosts: the round stingray, *Urobatis halleri*, Cooper (1863) and the skate, *Leucoraja naevus*, Muller and Henle (1841). Cestode species distributions were analyzed for randomness with respect to two niche axes: host size class and location within host spiral intestine. Niche overlap of cestode species was calculated for each niche type using MacArthur and Levins' and Pianka's indices, and compared to overlap values obtained from randomly generated communities. Cestodes of both host species were distributed heterogeneously among valves and host size-classes. The majority of parasite species (including all common ones) within *U. halleri* and all species within *L. naevus* had significantly nonrandom distributions with respect to at least one niche category. Cestode species pairs tended to overlap significantly less than expected in spiral intestine valves and significantly more than expected among host size classes. We conclude that cestode communities are structured deterministically in a way consistent with expectations based on competition.

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There is still debate as to whether and to what extent patterns of species co-existence and habitat selection are determined by competition, particularly within parasite communities. Null model analyses of species co-existence patterns have proven useful and informative in evaluating competitive interactions (Gotteli and Graves 1996, Gotelli 2001). Several such models have been applied to parasite communities, where competitive interactions can be particularly difficult to study by direct observation or experimental manipulation (Lotz and Font 1985, Moore and Simberloff 1990, Haukisalmi and Henttonen 1993, Sousa 1993, Kuris and Lafferty 1994, Rohde et al. 1998, Poulin and Guégan 2000, Šimková et al. 2001, Gotelli and Rohde 2002, Poulin and Valtonen 2002, Mouillot et al. 2003). Despite numerous studies, researchers have failed to reach consensus on whether competition or some other negative interaction, such as spatial segregation to promote conspecific mating and prevent interspecific hybridization or reproductive interference (Rohde 1994), plays a major role in creating parasite community structure. In part, this lack of consensus is attributable to the great variability of parasite and host life histories. Marine fish parasite communities have often been regarded as unstructured assemblages with little or no resource limitation and competitive influence (Rohde et al. 1995, Gotelli and Rohde 2002). However, it can be difficult to assess resource availability, utilization, and limitation as well as the role of competition and reproductive interactions in parasite communities.

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In this study, null models were used to assess the niche overlap of cestode communities of two distinct but closely related elasmobranch hosts, the round stingray, *Urobatis halleri* Cooper (1863) from the northern Gulf of California, and the skate, *Leucoraja naevus* Muller and Henle (1841) from the coast of Aberdeen, Scotland. These are small marine fish (max size 56.0 cm and 70.0 cm, respectively) that inhabit the bottoms of beaches and bays (FishBase web database: www.fishbase.org). Two niche axes are assessed: host size-class and location in the host's spiral intestine. Host size, related to fish age, is often correlated with parasite density and species diversity, and represents a large-scale temporal niche (Polyanski 1961, Rohde 1979). The spiral intestine contains a flap of tissue attached in a continuous spiral down its outer edge forming whorls that serve to increase the absorptive surface of the small intestine. It divides the environmental gradient down the intestine into a discrete series of definable spatial niches in which the cestodes reside (McVicar 1979). Overlap of species and communities with respect to these two niche axes was calculated using MacArthur and Levins' (1967) and Pianka's (1973) niche overlap indices. By examining the distributions of cestodes among niche categories and comparing observed and expected niche overlap among species, we explore the likelihood that these parasite communities have been structured by competition. Specifically, we use the data to address the following questions: 1) are cestode species distributed randomly among host valves and size classes? 2) Are these cestode species distributed similarly to each other with respect to niche categories? and, 3) Are the patterns of niche overlap within the cestode communities similar to those of a randomly constructed community? We conclude that the answer to the above questions are no, no, and no, implying that cestode communities are structured deterministically in a way consistent with expectations based on competition.

Material and methods

Host capture and cestode collection

During the fall of 1994 and 1995, students from the University of New Mexico's Marine Invertebrate Biology (404L) class collected the cestode parasites of 28 round stingrays, *Urobatis halleri*, from the northern Gulf of California near Puerto Peñasco, Sonora, Mexico. In a previous study, McVicar (1977, 1979) collected helminthes from the spiral valve of 205 skates, *Leucoraja naevus*, from Aberdeen, Scotland using techniques similar to those utilized for the *U. halleri* collections. McVicar concentrated his research on the effects of the physiochemical environment on cestode distribution and completed some preliminary community analysis, including an assessment of crowding and worm migration effects. He also noted complimentary niche utilization by these cestode communities where worms with highly overlapping distributions in host size-groups inhabited different regions of the spiral intestine.

A detailed description of the *Urobatis halleri* collection, dissection, and parasite identification is presented elsewhere (Friggens and Duszynski 2005). Briefly, the stomach and spiral intestine of each host was removed, injected with AFA (5 parts glacial acetic acid, 10 parts formalin, and 85 parts 85% EtOH) to kill and fix the worms in situ and then placed in a dish containing AFA for examination. Worms from the stomach and each valve of the spiral intestine were recovered and transferred to an appropriately labeled vial containing 10% formalin. Only worms obtained from freshly dissected valves where worm position could be verified were used in analyses.

Leucoraja naevus were collected off the coast of Aberdeen, Scotland by seine and taken to the laboratory for dissection (McVicar 1977). Hosts were divided into 11 size-classes by length (5 cm increments) and each of the nine valves of the spiral intestine was divided into six areas. Number, prevalence and intensity of each worm species were calculated for each host size-group and each spiral valve area (McVicar 1977, 1979).

Statistical analysis

This paper is based on the cestode communities of 28 *U. halleri* and 204 *L. naveus*. Extremely rare species (in less than 10% of hosts) were recorded but not included in statistical analysis. Cestode counts for the valves of *L. naevus* were available from the published work of McVicar (1977, 1979). Original per host data (Appendix A of McVicar's PhD dissertation, 1973) were used for the host size-class analyses. McVicar's Appendix A listed 205 hosts, one of which, an 11 cm juvenile, was left out of this analysis. *Urobatis halleri* possesses 13 valves within its spiral intestine, whereas *L. naevus* has nine valves. Due to small numbers of most cestode species in the latter half of the spiral intestine, the three posterior valves were combined for most statistical analyses. Host samples were divided into three size-classes; *U. halleri* were grouped in <24 cm, 25–30 cm, and >30 cm size classes and *L. naevus* were grouped in <30 cm, 31–49 cm and >50 cm size classes.

Ecological terminology follows the guidelines of Margolis et al. (1982). Excel, Minitab 6.0, and Statistical Analysis Software (SAS 8.2) were used for analysis and to calculate prevalence, abundance, intensity, as well as mean and median number of each cestode species within each host, each spiral valve, and each host size-class. An analysis of variance procedure (ANOVA) was used to assess whether cestodes were distributed equally among valves and host size-classes. The distribution of all cestodes, each cestode species, and cestode species pairs with respect to host valves and host size-classes were analyzed by Wilcoxon rank score chi-square tests (Kruskal–Wallis tests). To compensate for small and skewed samples, Fisher's exact tests were used where appropriate. Linear regression analysis was performed to assess relationships between total cestode number, cestode species number, and host size. For each host, matrices of cestode species counts by niche classification category were constructed. Niche overlap was quantified using MacArthur and Levins' (1967) equation:

$$O_{21} = \frac{\sum p_{2i} p_{1i}}{\sum (p_{1i})^2}$$

and Pianka's (1973) revised version:

$$O_{21} = O_{12} = \frac{\sum p_{2i} p_{1i}}{\sqrt{\sum p_{2i} \sum p_{1i}}}$$

where p is the frequency of utilization of n different resource states and p_{xi} is the utilization frequency of species x in resource state i (Gotelli and Graves 1996).

The mean of pair-wise overlap values for all parasites species along each of the niche axes was calculated for use as a community-wide summary statistic. To assess whether the overlap values of the cestode communities of *U. halleri* and *L. naevus* would likely have occurred by chance, the original species utilization matrices were randomized by retaining the original values and then shuffling the placement of those values among resource states (from Gotelli and Graves 1996: randomization algorithm 3 of Lawlor 1980). For each of four species utilization matrices (cestode species × *U. halleri* size-class, cestode species × *U. halleri* valves, cestode species × *L. naevus* size-class, and cestode species × *L. naevus* valves), 500 random permutations were generated. Niche overlap values were calculated from each of these randomly generated matrices, and species-pair and community-summary statistics were computed. Actual overlap values were then compared to the distributions of expected values. Multidimensional niche overlap was represented by the geometric mean between niche overlap values of each species pair and each aggregate statistic for each niche axis (host size-class by valve category). As with the analysis of single niche axes, the observed values were compared to the frequency distributions of the randomized values. To assess the effect of the abundant, widely distributed "core" species on niche selection, this analysis was repeated using only species with a prevalence >50%.

Results

The cestode communities

Thirteen cestode species of two orders were identified in 1,505 worms recovered from the spiral intestine of 28 *U. halleri* (Table 1). All hosts were infected with cestodes. These 28 hosts had 1–8 (4.6±1.7) cestode species and 5–324 (53.75±63.7) individuals. Prevalence, intensity, abundance, range and length of each species are listed in Table 1. After considering worm size, prevalence and abundance, it was determined that four rare species, *Acanthobothrium* sp1, A. sp2, *Mecistobothrium myliobati* and *Phyllobothrium* sp. did not represent a substantial source of biomass within these communities, and they were excluded from further analysis. The Trypanorhyncha species and two *Rhinebothrium* species

Table 1. Cestodes of the spiral intestine of 28 *Urobatis halleri* caught in the northern Gulf of California in October of 1994, 1995, and 2001.

Order/species	Total no.	Prevalence	Mean intensity of infection	Abundance (±SD)	Range	Length (mm)
Tetraphyllidea						
Acanthobothrium olseni	35	0.32	3.9	2.7 (±5.0)	1–17	4.4[a]
A. parviuncinatum	265	0.93	10.2	19.0 (±8.8)	1–36	~6.00[a]
Acanthobothrium sp1	4	0.10	1.3	0.3	1	>3.0[b]
Acanthobothrium sp2	1	0.04	1.0	0.1	1	>3.0[b]
Rhinebothrium urobatidium	114	0.71	5.7	8.2 (±4.1)	1–19	3.3[a]
Rhinebothrium sp1	42	0.13	21.0	3.8 (±28.3)	1–41	1.3–5.1[c]
Rhinebothrium sp2	12	0.18	2.4	0.9 (±2.6)	1–7	1.8–5.3[c]
Phyllobothrium sp.	2	0.04	2.0	0.2	2	1.7[c]
Trypanorhyncha						
Eutetrarhynchus sp.	107	0.50	7.6	7.9 (±10.7)	1–36	2.5–6.0[c]
Oncomegas paulinae	31	0.36	3.1	2.3 (±4.3)	1–15	17.4–27.6[a]
Mecistobothrium myliobati	2	0.07	1.0	0.2	1	27.6[a,d]
Prochristianella minima	94	0.46	7.2	6.9 (±5.8)	1–19	2–2.5[a]
Prochristianella sp.	794	0.71	39.7	53.8 (±70.7)	1–289	1.2–2.2[c]

[a] Lengths reported are from original descriptions (Dailey Mudry 1968, Young 1954, 1955, Heinz and Dailey 1974, Appy and Dailey 1977, Toth et al. 1992) and correspond to *U. halleri* specimens.

[b] Only partial specimens were recovered from hosts.

[c] Lengths reported are the averaged measurements taken by MMF for new worm species found in *U. halleri*.

[d] Only immature specimens were recovered from hosts.

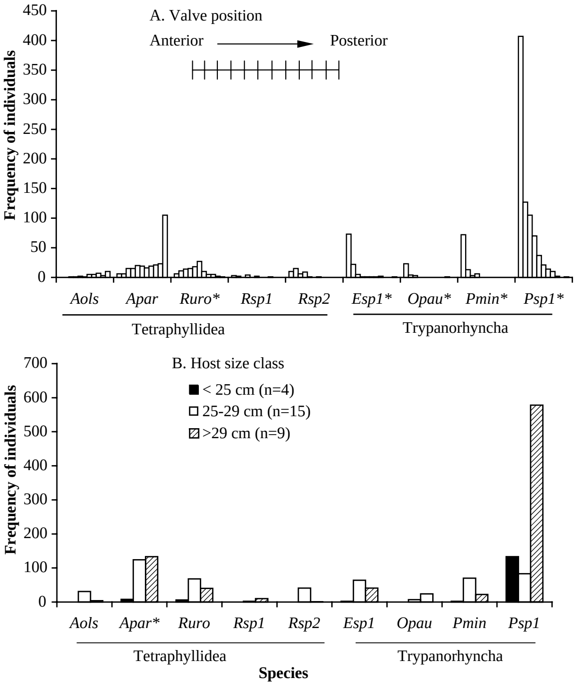

Fig. 1. Distribution (total no.) of nine species of cestodes in 11 spiral intestine valves and three size classes of 28 *Urobatis halleri* from the northern Gulf of California. Valves are numbered from anterior (left) to posterior (right). (*Aols* = *Acanthobothrium olseni*, *Apar* = *A. parviuncinatum*, *Ruro* = *Rhinebothrium urobatidium*, *Rsp1* = *R. sp.1*, *Rsp2* = *R. sp.2*, *Esp1* = *Eutetrarhynchus sp.1*, *Opau* = *Oncomegas paulinae*, *Pmin* = *Prochristianella minima*, *Psp1* = *P. sp.1*). *Distribution of cestode species across niche categories is significantly different ($p < 0.05$) from random.

(*Rhinebothrium* sp.1 and *R. urobatidium*) accounted for 82% of the cestodes inhabiting *U. halleri.* These parasites occurred primarily in the anterior portion of the spiral intestine (valves 1–5). Two *Acanthobothrium* species were found primarily in the posterior portion of the spiral intestine (valves 6–11) (Fig. 1). *Oncomegas paulinae* and *Prochristianella* sp. were most numerous in the largest host size-class, whereas most of the other species were concentrated in the middle size-class (Fig. 1). There was a significant positive correlation between the number of parasite species and host body length ($p = 0.015$) and between number of parasite individuals and host length ($p = 0.021$), although the relationship was weak in both cases ($R^2 = 0.211$ and 0.188, respectively).

Five species of cestodes from three different orders were reported from 204 *L. naevus* (Table 2). Hosts harbored 1–5 (4.6) cestode species and 6–1,419 individuals. Prevalence, intensity, abundance and ranges of each cestode species are given in Table 2. *Acanthobothrium quadripartitum* and *E. harfordi* numbers were highest in the 2nd valve of the spiral intestine, while *Echeneibothrium* sp. and *P. piriei* were most numerous in the 4th valve (Fig. 2). *Grillotia erinaceus* had its highest numbers in the 1st valve, although, overall, this species did not show a strong pattern of spatial segregation. *Acanthobothrium quadripartitum* was concentrated in the largest size-class, whereas *Echeneibothrium* sp. and *E. harfordi* occurred in the smallest size-classes, *P. piriei* showed no pattern, and the numbers of *G. erinaceus* were highest at the mid-size class (Fig. 2). There was a significant positive correlation between number of parasite individuals and host length ($p < 0.0001$, $R^2 = 0.515$) and also between number of parasite species and host length, although as in *U. halleri* this relationship was weak ($p < 0.0001$; $R^2 = 0.088$).

Cestode distributions

The numbers of each cestode species were distributed heterogeneously with respect to both valve and host size-classes for both host species. Five of nine species within *U. halleri* and all species within *L. naevus* had significantly heterogeneous distributions among host valves (Fig. 1A). *Acanthobothrium parviuncinatum* was the only species within *U. halleri* to show a significantly heterogeneous distribution among host size-classes (Fig. 1B). All species of cestodes found in *L. naevus* had significant, nonrandom distributions across host spiral intestine valves and host size-classes (Fig. 2). Cestodes were distributed non-randomly with respect to each other in the majority of cases. Of 36 species pairs in *U. halleri*, 26 had significantly nonrandom distributions (Table 3). All 10 species pairs

Table 2. Cestodes of the spiral intestine of 204 *Leucoraja naevus* caught in the North Sea off the coast of Aberdeen, Great Britain over 11 months in 1968 and 1969.

Order/Species	Total no.	Prevalence	Mean intensity of infection	Abundance (±SD)	Range
Tetraphyllidea					
Acanthobothrium quadripartitum	17,804	0.99	87.7	87.3 (±158.6)	1–1260
Echeneibothrium sp.	2,274	0.94	11.9	11.1 (±11.5)	1–104
Phyllobothrium piriei	6,526	0.99	32.1	32.0 (±44.1)	1–355
Diphyllidea					
Echinobothrium harfordi	406	0.53	3.8	1.99 (±3.4)	1–23
Trypanorhyncha					
Grillotia erinaceus	195	0.47	2.0	0.96 (±1.4)	1–7

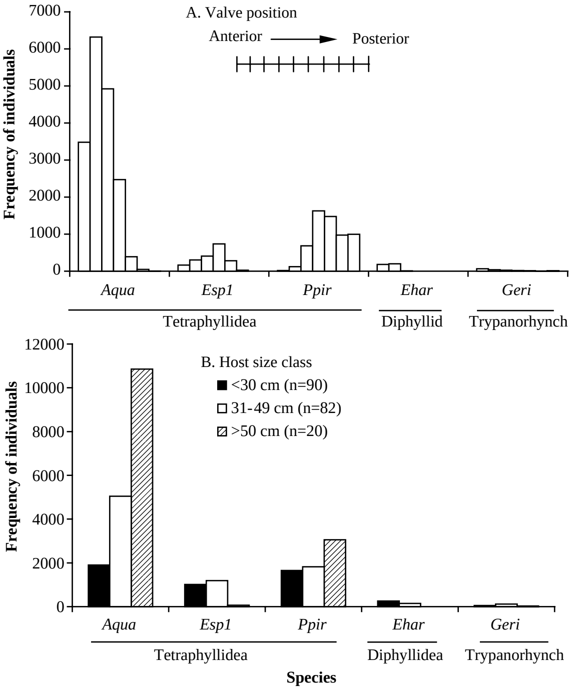

Fig. 2. Distribution (total no.) of five species of cestodes within seven spiral intestine valves and three size classes of 204 *Leucoraja naevus* from the coast of Aberdeen, Scotland. Valves are numbered from anterior (left) to posterior (right). The distribution of cestode species across niche categories is significantly different ($p < 0.05$) from random for all species. (*Aqua* = *Acanthobothrium quadripartum*, *Esp1* = *Echeneibothrium sp.*, *Ppir* = *Phyllobothrium piriei*, *Ehar* = *Echinobothrium harfordi*, *Geri* = *Grillotia erinaceus*).

within *L. naevus* showed significantly distinct distributions among valves and host size-groups ($p \leq 0.001$).

Cestode niche overlap

Within the valve and size classes of *U. halleri,* observed community-wide niche overlap was significantly higher than the expected distribution for both MacArthur and Levins' (1967) and Pianka's (1973) overlap measures.

Observed overlap between species pairs in valves was significantly different (chance of co-occurring is 5% or less when compared to random distribution) from expected in the majority of cases. Lower than expected observed pair-wise overlap values outnumbered higher than expected values (Table 4), although significant differences in both directions were observed. Acanthobothrians were involved in all lower than expected associations, while intrageneric pairs within the Trypanorhyncha accounted for the majority of the higher than expected observations. There were fewer significant species pair overlap values within *U. halleri* size-classes than for valve groups and the majority of observed values were greater than expected from a random assemblage (Table 4). All lower than expected values were for intrageneric pairs within the Trypanorhyncha, whereas higher than expected values were seen in a variety of pairs. Analysis using the five most common species strengthened the above results showing lower than expected niche overlap within valves and higher than expected overlap in size-groups (MacArthur and Levins' 1967 measure). The community-wide niche overlap of the cestode community of *L. naevus* did not differ significantly from random for valves or group size classes using either equation. Overlap of species pairs within *L. naevus* followed a pattern similar to *U. halleri*; overlap within valves was generally lower than expected, while overlap of pairs within size-groups was generally higher than expected by chance (Table 4). *Phyllobothrium piriei* was involved in all higher than expected overlap values within spiral valves. No other clear patterns were evident, and analysis using only four species did not reveal additional information.

Fewer than 35% of species pairs deviated significantly from random in the analysis of multidimensional niche overlap. Comparisons of observed to expected multidimensional niche overlap showed a predominance of higher than expected values using both MacArthur and Levins' (1967) and Pianka's (1973) equations. Within *U. halleri*, niche overlap of 15 species pairs was significantly higher than expected, whereas overlap of eight species pairs was significantly lower than expected

Table 3. Results (Prob $>X^2$) of Kruskal–Wallis tests for independent distribution of species pairs of the cestode assemblage of 28 *Urobatis halleri* among host spiral intestine valves (above diagonal) and size classes (below diagonal). Significant values are in bold.

	Aols[1]	*Apar*	*Rsp1*	*Rsp2*	*Ruro*	*Esp1*	*Opau*	*Pmin*	*Psp1*
Aols		<**0.0001**	0.1086	<**0.0001**	**0.0058**	<**0.0001**	<**0.0001**	<**0.0001**	<**0.0001**
Apar	**0.0174**		<**0.0001**	0.0782	**0.0216**	<**0.0001**	<**0.0001**	<**0.0001**	<**0.0001**
Rsp1	<**0.0001**	<**0.0001**		<**0.0001**	<**0.0001**	<**0.0001**	**0.0007**	<**0.0001**	**0.0039**
Rsp2	**0.0001**	<**0.0001**	**0.0443**		**0.005**	<**0.0001**	**0.0007**	<**0.0001**	<**0.0001**
Ruro	**0.0001**	<**0.0001**	<**0.0001**	0.1242		<**0.0001**	<**0.0001**	<**0.0001**	<**0.0001**
Esp1	**0.007**	0.0732	<**0.0001**	**0.0114**	0.3841		**0.0006**	0.075	<**0.0001**
Opau	<**0.0001**	**0.0143**	<**0.0001**	0.669	**0.0001**	0.5967		0.1314	**0.0001**
Pmin	0.2012	<**0.0001**	**0.0056**	**0.0001**	0.0678	0.1699	<**0.0001**		**0.001**
Psp1	<**0.0001**	<**0.0001**	<**0.0001**	0.2695	<**0.0001**	**0.0004**	**0.0096**	<**0.0001**	

[1] *Aols* = *Acanthobothrium olseni*, *Apar* = *A. parviuncinatum*, *Ruro* = *Rhinebothrium urobatidium*, *Rsp1* = *R. sp. 1*, *Rsp2* = *R. sp. 2*, *Esp1* = *Eutetrarhynchus sp.*, *Opau* = *Oncomegas paulinae*, *Pmin* = *Prochristianella minima*, *Psp1* = *P. sp. 1*.

Table 4. Results of pairwise comparisons between observed (O) and expected (E: mean of 500 random permutations) niche overlap values calculated from two equations (MacArthur and Levins, 1967, left column, and Pianka, 1973, right column) for two niche categories, spiral intestine valve and host size-class, for all cestodes and only the most common (prevalence >50%) cestode species inhabiting *Urobatis halleri* and *Leucoraja naevus*.

Host	MacArthur and Levins 1967		Pianka 1973	
Cestodes	O>E	O<E	O>E	O<E
Niche	No. significant pairs (%)		No. significant pairs (%)	
Urobatis halleri				
All cestode species				
Valves	18/72 (25)	26/72 (36)	9/36 (25)	13/36 (36)
Size-classes	19/72 (26)	2/72 (2.7)	13/36 (36)	0
Common species				
Valves	3/20 (15)	7/20 (35)	3/10 (30)	3/18 (30)
Size-classes	5/20 (20)	0	2/10 (20)	0
Leucoraja naevus				
All cestode species				
Valves	3/20 (15)	4/20 (20)	0	4/10 (40)
Size-classes	3/20 (15)	0	3/10 (30)	0
Common species				
Valves	2/12 (16)	2/12 (16)	1/6 (16)	1/6 (16)
Size-classes	4/16 (25)	0	0	0

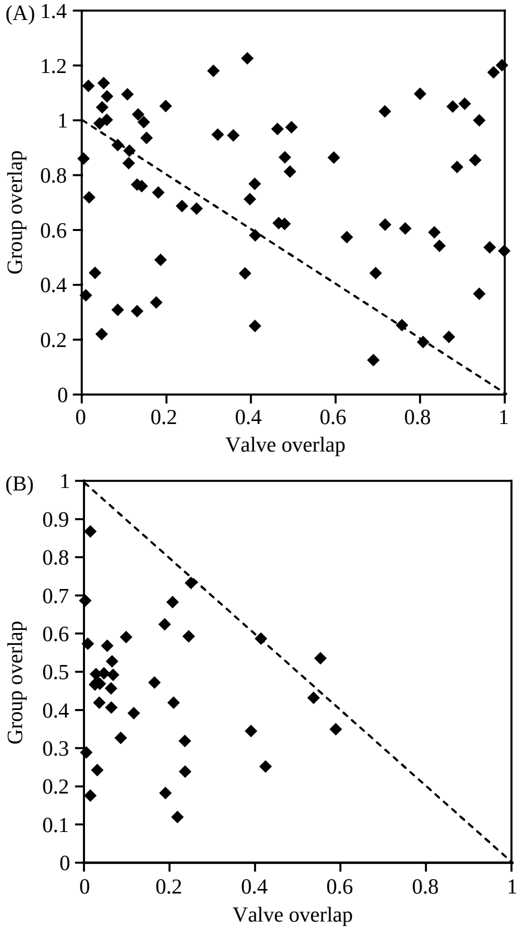

Fig. 3. Comparison of two measures of niche overlap values for nine species of cestodes inhabiting two niches categories, spiral intestine valve and host size classes, within 28 *Urobatis halleri*. (A) MacArthur and Levins (1967) (B) Pianka (1973).

using MacArthur and Levins' (1967) measure. Using Pianka's (1973) measure, seven pairs overlapped greater than expected and three lower than expected from a randomly generated community.

It is helpful to use both MacArthur and Levins' (1967) and Pianka's (1973) equations to measure niche overlap when analyzing communities such as the one in *U. halleri*, where there is a large variation in species occurrence patterns. MacArthur and Levins' (1967) asymmetric overlap measure is more sensitive to niche restriction between species than Pianka's (1973) symmetrical version (Haefner 1988). However, Pianka's (1973) is more straightforward to interpret. Although these two measures are similar (May 1975), quite different results can be obtained as seen in Table 4. MacArthur and Levins' (1967) measure shows no pattern when niche overlap values are plotted against one another, which might be taken to imply little interaction (Fig. 3A). However, there is evidence of complimentary cestode distributions for *U. halleri* with Pianka's measure; values that are high along one axis are low along the other and few points are high for both (Fig. 3B). This result is illuminating: while MacArthur and Levins' (1967) equation provides better resolution for viewing species interaction, it is also more sensitive to combinations of rare and common species. The high values for overlap in both size-class and valve position are largely a result of two species, one rare and one common, having highly asymmetric niche overlap values depending upon which species is in the denominator of the equation. Pianka's (1973) overlap measure shows a much clearer pattern.

Similar patterns of niche overlap occurred within *L. naevus* cestode communities. Values obtained from MacArthur and Levins' (1967) measure for *L. naevus* cestode pairs were relatively high for both axes (Fig. 4A). However, when values derived from Pianka's (1973)

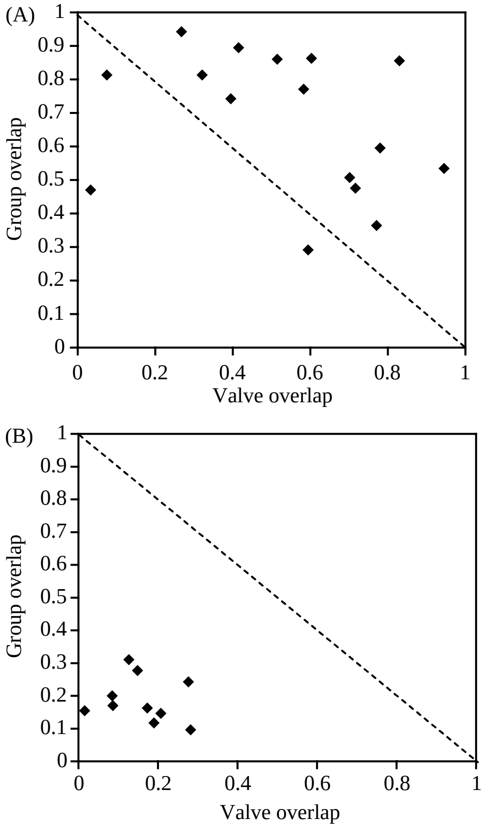

Fig. 4. Comparison of two measures of niche overlap values for five species of cestodes inhabiting two niches categories, spiral intestine valve and host size classes, within 204 *Leucoraja naevus*. (A) MacArthur and Levins (1967) (B) Pianka (1973).

measure were plotted against one another, overlap was complimentarily distributed along both axes (Fig. 4B). Again, the substantial overlap seen in the size classes using MacArther and Levins' (1967) measure is an artifact of comparing a well-dispersed species with a relatively rare species. A potential problem with both equations is the lack of resolution when using community-wide values, and it has been recognized that community-wide overlap values often misrepresent the interactions within a given population (Haefner 1988).

Discussion

Overall, the results presented in this paper demonstrate that the cestode communities of *U. halleri* and *L. naevus* were highly structured assemblages. First, cestodes were distributed non-randomly along niche axes. Species were distributed unequally among valves and body-size classes. All common species (prevalence greater than 46%) had non-random distributions along at least one niche axis. Secondly, results of niche overlap analysis shows that, within the spiral intestine, species clumped more than would be expected in a randomly structured community. Finally, there were patterns of complementary niche selection: Species that tended to inhabit the same host size classes were more segregated within the spiral valve, and vice versa. This pattern has been noted before within *L. naevus* (McVicar 1979). Within *U. halleri*, complementary niche selection was best demonstrated among the trypanorhynchs where, using MacArthur and Levins' (1967) measure, all species overlapped more than expected among valves, whereas, overlaps were significantly lower than expected within size groups (data not shown).

Of the theories put forth to explain niche selection in parasites, three are relevant here: environmental tolerance, reproductive segregation, and competitive displacement. Detailed work on variation in the morphological and chemical environment along the elasmobranch spiral intestine has been used to suggest that the distribution of cestodes is limited, at least in part, by environmental tolerances (Williams 1960, McVicar 1979, Borucinska and Caira 1993). However, these mechanisms have never been able to fully explain the niche specificity of all cestodes within the elasmobranch spiral intestine (Williams 1982, Borucinska and Caira 1993), and it is possible that interspecific interaction has led to the current observed species specialization within the host microhabitats. Spatial segregation of marine ectoparasites and nematodes has been attributed to avoidance of interspecific reproductive interactions (Rohde 1991, 1994). Features of cestode reproductive biology, including their capacity for self-fertilization, would seem to make this mechanism less likely within cestode communities. Additionally, the fact that the most closely related species (e.g. congeners) within *U. halleri* tended to have more overlapping and/or adjacent distributions than more distantly related species (Fig. 1) suggests that reproductive isolation is not a driving mechanism of cestode species segregation (Rohde 1994). Competition likely accounts for at least some of the niche segregation observed here, even when the species-specific distributions can also be related to morphological and chemical variation along the intestine and may be influenced to some extent by reproductive biology.

Results for *U. halleri* were strengthened when niche overlap was analyzed using only common or core species. Core species tend to be both locally abundant and widely distributed with respect to niche axes (Hanski 1982). The results seen in Table 4 indicate that pairs of core species had much lower than expected niche overlap among valves, but not among size groups. This is even more apparent when the analysis was repeated combining valves into three discrete categories: anterior, middle and posterior valve areas. Then, 70% of species pairs had significantly lower than expected overlap within valves and none had significantly greater (data not shown).

This is particularly interesting with respect to the hypothesis presented in Hanski (1982): if interspecific competition is important in structuring communities, core species should be more segregated in niche space than rare, restricted "satellite" species.

Within these cestode communities, spatial niche separation appears to be an important means of specialization to avoid interspecific competition, whereas temporal niche selection, as reflected in host size class, is less so. The greater importance of spatial niches than temporal niches in segregating species and defining community structure has been recognized in previous studies (Pianka 1973, Sasal et al. 1999). It is likely that higher than expected species overlap in host size groups is a result of cestode life history. Cestodes are multi-host parasites, which first infect an invertebrate intermediate host that then must be consumed by a suitable vertebrate, final host before the worms can mature and reproduce. It is not surprising, therefore, that these cestodes appear to accumulate over time and occur together more frequently as the host survives and grows. Positive correlations between host length and helminth burden have been noted in other elasmobranch cestode species (Tanzola et al. 1998, Sanmartin et al. 2000).

It is striking that the cestode communities of two different hosts from very different habitats, in terms of latitude, water temperature, salinity, and seasonal temperature fluctuation show such similar patterns of niche overlap. The cestode communities of *L. naevus* appeared to have stronger nonrandom patterns of distribution, but it is likely that either the smaller sample size of *U. halleri* or the low prevalence of some species within *U. halleri* may have accounted for this apparent difference between host species (i.e. there is some type-II error).

This paper suggests that cestode parasite communities contain species that compete for resources and tend to have non-overlapping distributions in the host intestine. There are three ways to consider parasite responses to competition (Esch et al. 1990). First, competitive exclusion allows one species to completely displace another. This mechanism is not addressed in this study, because overlap and segregation were not analyzed at the level of individual hosts. Competitive exclusion is best evaluated in experimental studies (Holmes 1973). There are too many alternative explanations to competition to infer why one species appears to be absent in the presence of another from observational studies such as this one. Second, interactive site segregation causes a shift in a species niche location or breadth in response to the presence of another. This mechanism is not readily apparent within these elasmobranch communities, again in large part because this analysis was unable to document niche shifts at the level of individual hosts. However, there may be some evidence for this mechanism with the differing distribution of the acanthobothrians between the two hosts. Within *U. halleri*, where there were large numbers of Trypanorhynchs in the anterior spiral intestine, both acanthobothrian species tended to be concentrated in the posterior valves. However, within *L. naevus*, where trypanorhynch numbers were much lower, acanthobothrian species had an anteriorly biased distribution. This may be evidence of displacement of acanthobothrians by the trypanorhynchs within *U. halleri*. Again, these patterns of displacement between distantly related taxa would not be expected if reproductive interference were the primary mechanism of spatial segregation. Finally, competition can manifest as selective site segregation where currently observed niches are a result of evolutionary competitive pressures that caused parasites to select narrow niches. As illustrated in both the host species of this study, selective site segregation is a strong mechanism of cestode separation within the spiral valves. Given these results, we expect that null models based on randomization and other quantitative methods will be useful for characterizing patterns of parasite community structure and for identifying the processes that generate and maintain these patterns. It remains to be determined, however, whether the high degree of community structure and inferred competition seen in these cestodes in elasmobranch hosts will also be found in other parasite assemblages.

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