1989

Comparative ecology of the parasites of the spot, Leiostomus xanthurus Lacepede, and the Atlantic croaker, Micropogonias undulatus Linnaeus (Sciaenidae), in the Cape Hatteras region

Dennis A. Thoney
College of William and Mary - Virginia Institute of Marine Science

Order number 8923062

Comparative ecology of the parasites of the spot, Leiostomus xanthurus Lacepede, and the Atlantic croaker, Micropogonias undulatus Linnaeus (Sciaenidae), in the Cape Hatteras Region

Thoney, Dennis Allan, Ph.D.

The College of William and Mary, 1989

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

COMPARATIVE ECOLOGY OF THE PARASITES OF THE SPOT, _LEIOSTOMUS XANTHURUS_ LACEPEDE, AND THE ATLANTIC CROAKER, _MICROPOGONIAS UNDULATUS_ LINNAEUS (SCIAENIDAE), IN THE CAPE HATTERAS REGION

A DISSERTATION

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Doctor of Philosophy

---

by

Dennis A. Thoney

1989

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Dennis A. Thoney

Approved, May 1989

Dr. William J. Hargis, Jr.
Committee Chairman/Advisor

Dr. Eugene M. Burreson

Dr. John A. Musick

Dr. Evon P. Ruzecki

Dr. Mark W. Luckenbach

Dr. Robin M. Overstreet
Gulf Coast Research Laboratory, Ocean Springs, Mississippi

TABLE OF CONTENTS

ACKNOWLEDGMENTS

I thank Jess Hawkins, Mac Currin, and John Miller for collecting fish in Pamlico Sound and the National Marine Fisheries Service (NOAA) for allowing me to participate in their ground fish surveys. I also thank Robin M. Overstreet and Tom Mattis for assistance in identification of digenean and cestode parasites. Constructive comments of the manuscript by Drs. William J. Hargis, Jr., Eugene M. Burreson, and Robin M. Overstreet are also greatly appreciated.

LIST OF TABLES

LIST OF FIGURES

Chapter II

ABSTRACT

Parasite communities of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, were examined to determine if (1) their structure changed with host age, (2) geographical location affects community structure, (3) food habits affect community structure, and (4) their parasite communities are predictable. Juvenile fish were collected monthly from Chesapeake Bay and Pamlico Sound and adult fish were collected offshore north of Cape Hatteras in the fall, and offshore south of Cape Hatteras in the spring and fall. A total of 21 parasitic species occurred in juvenile spot with 19 in juvenile croaker from Chesapeake Bay and Pamlico Sound. The parasite communities of juvenile fishes varied with size, season, and area. Additional parasites were acquired as juveniles diversified their diets and fed on more intermediate host species. Equibility and, thus, diversity were depressed due to large numbers of the digenean *Diplomonorchis leiostomi* that dominated the parasite communities of both species. Although juvenile spot and croaker shared eight and six parasites between estuaries, respectively, many nonspecific parasites (generalists) were more common in both spot and croaker from one estuary than the other. All species occurring in both hosts have indirect life cycles suggesting that the availability of certain intermediate hosts as prey was important. The estuary of residence was clearly as important as host species identity in determining parasite community structure. Twenty-three species of metazoan parasites were recorded from adult spot and 26 from adult croaker. Of the 33 parasitic species found, 17 occurred in both spot and croaker. No significant differences in intensity of parasites occurred between sexes of either spot or croaker. All of the parasites had overdispersed or clumped distributions among hosts. Adult spot and croaker collected offshore had much greater species-richness, diversity, and total number of individual parasites than juvenile fishes collected in the estuaries. The number of species and diversity of parasites in adult fish was greater in croaker than spot. However, when only gastrointestinal helminths were considered, spot had greater species-richness as well as greater numbers of individual helminths, suggesting that they had a more diverse diet and fed on more infected intermediate hosts than croaker. In both adult spot and croaker the mean number of parasitic species was greater than those of freshwater fishes and fewer than those for birds and mammals. The total number of individual parasites found in spot and croaker was similar to that of freshwater fishes. Comparison of adult spot and croaker parasite faunas collected offshore indicated that their respective parasite component communities were distinct and that similar infracommunity variability existed in both hosts. Although the parasite dominance hierarchy in adults of both species varied slightly between areas and seasons sampled, there appeared to be predictable dominant species consisting of *D. leiostomi* and *Scolex polymorphus unilocularis* in spot and *S. polymorphus unilocularis* in croaker. The core species were accompanied by subordinate, less-predictable species. The variability in both relative intensities and

presence absence of parasites within communities resulting from their diverse diets make them less predictable than those of other vertebrates with less diverse diets.

GENERAL INTRODUCTION

Several questions regarding parasite community ecology have been proposed recently by Kennedy et al. (1986), Bush and Holmes (1986), and Holmes (in press). These questions pertain to diversity and predictability of parasite communities and how host life histories affect these parameters. Very few studies have addressed these ecological questions with respect to parasite communities of marine fishes. Since spot and croaker are closely related, have similar life histories and rich parasite faunas, they make ideal hosts for examining these questions in marine fishes.

Spot, *Leiostomus xanthurus* Lacepede, and Atlantic croaker, *Micropogonias undulatus* Linnaeus, are sciaenid fishes that inhabit estuarine and nearshore oceanic waters from southern New England to Texas (Chao and Musick 1977). In the Atlantic Ocean, they are most abundant from Chesapeake Bay, Virginia to the Carolinas (Grosslein and Azarovitz 1982). Spot and croaker along the middle Atlantic coast spawn offshore of the Carolinas. Large numbers of both species are transported as larvae and postlarvae or migrate as adults north of Cape Hatteras in the spring where they use estuarine and nearshore areas as nursery and feeding grounds for juveniles and adults. Both juveniles and adults migrate south of Cape Hatteras in the fall as water temperature decreases. Although spot and croaker are opportunistic "generalists" feeding on many of the same most readily available resources, croaker tend to feed on larger, more mobile epibenthic prey, whereas spot have larger percentages of infaunal invertebrates in their diets (Chao and Musick, 1977; Overstreet and Heard, 1978; Currin et al., 1984).

Spot and croaker are important to the local commercial fisheries, as well as being important forage fishes for several other important commercial fishes. In addition, spot are widely used in various research activities, including toxicology, immunology, and pathology studies, which makes knowledge of their parasitic fauna essential.

Most studies of parasites of the spot and the croaker have been taxonomically oriented (Linton 1940; Hopkins 1941a, b; Hargis 1956; Goldstein 1963; Overstreet 1970, 1973; Hendrix and Overstreet 1977; Fusco and Overstreet 1978; Deardorff and Overstreet 1980, 1981a, b, c; Roberts 1970; and many others). Life cycles have been elucidated for a few species. Very few studies have examined the ecology of parasites and most of those only considered one species (Schlicht and McFarlan 1967; Joy 1974; Joy and Price 1976; Voorhees and Schwartz 1979; Collins et al. 1984). Joy (1976) examined the population dynamics of six species of gill parasites from spot collected in Texas and Overstreet and Howse (1977) examined parasite communities of croaker and spot in polluted and relatively pristine areas of Mississippi.

Although Govoni (1983) examined the parasite fauna in larvae of both species from the northern Gulf of Mexico, there have been no attempts to study ecological aspects of the parasite fauna of either species from the time they enter estuaries as postlarvae until they depart in fall. Most significantly, the parasite faunas of spot and croaker have not been carefully studied along the mid-Atlantic coast of the U. S. A. where both species of fish are extremely abundant and important food and recreational fishes. Therefore, the objective of the first portion of this study was to determine the prevalence and intensity of helminth parasites of juvenile spot and croaker and to assess variation in these parameters with regard to species, area, season, and size of host. The objective of the second phase was to determine how predictable and diverse parasite communities of adult spot and croaker are by examining parasite distributions among these hosts.

Population Dynamics and Community Analysis of the Parasite Fauna of Juvenile *Leiostomus xanthurus* and *Micropogonias undulatus* (Sciaenidae)in Two Estuaries Along the Middle Atlantic Coast of the United States

INTRODUCTION

Along the mid-Atlantic coast, spot and Atlantic croaker spawn offshore of the Carolinas. Spot spawn during winter (Warlen and Chester 1985) and the young-of-the-year enter estuaries in spring. Of the juveniles that enter Chesapeake Bay, most leave by December, but a few over-winter (Chao and Musick 1977) in the deeper, warmer areas of the Bay. Croaker apparently spawn from late summer throughout the following winter because Chao and Musick (1977) found that young-of-the-year appeared in Chesapeake Bay in August and continued recruiting into the Bay through May.

Although spot and croaker share nursery grounds and feed on many of the same prey there are significant differences in details of their life histories. In contrast to spot, croaker recruit to estuaries over a longer period resulting in cohorts of various sizes being present at any one time. In addition, croaker tend to feed on larger, more mobile prey than spot. Since many of the parasites have indirect lifecycles requiring one or more intermediate hosts for completion, these factors should have a significant influence on parasite community patterns. Determination of facts relating to these features was the principal objective of this study. To better understand the ecology and seasonal dynamics of their parasites, samples of young-of-the-year fishes were examined the time from when they first entered either Chesapeake Bay, Virginia or Pamlico Sound, North Carolina until they left in fall. With respect to these two estuarine systems and the two closely- related hosts, several hypotheses were considered. (1) Juvenile fishes should acquire both more parasitic species and numbers of each species as they grow. (2) If many of the parasites acquired by juvenile spot and croaker are host specific, then their respective parasite faunas should be distinct even in two different estuaries. (3) Since many parasites are acquired from prey, prey composition should have an affect on both the numbers and species of parasites present in juvenile spot and croaker.

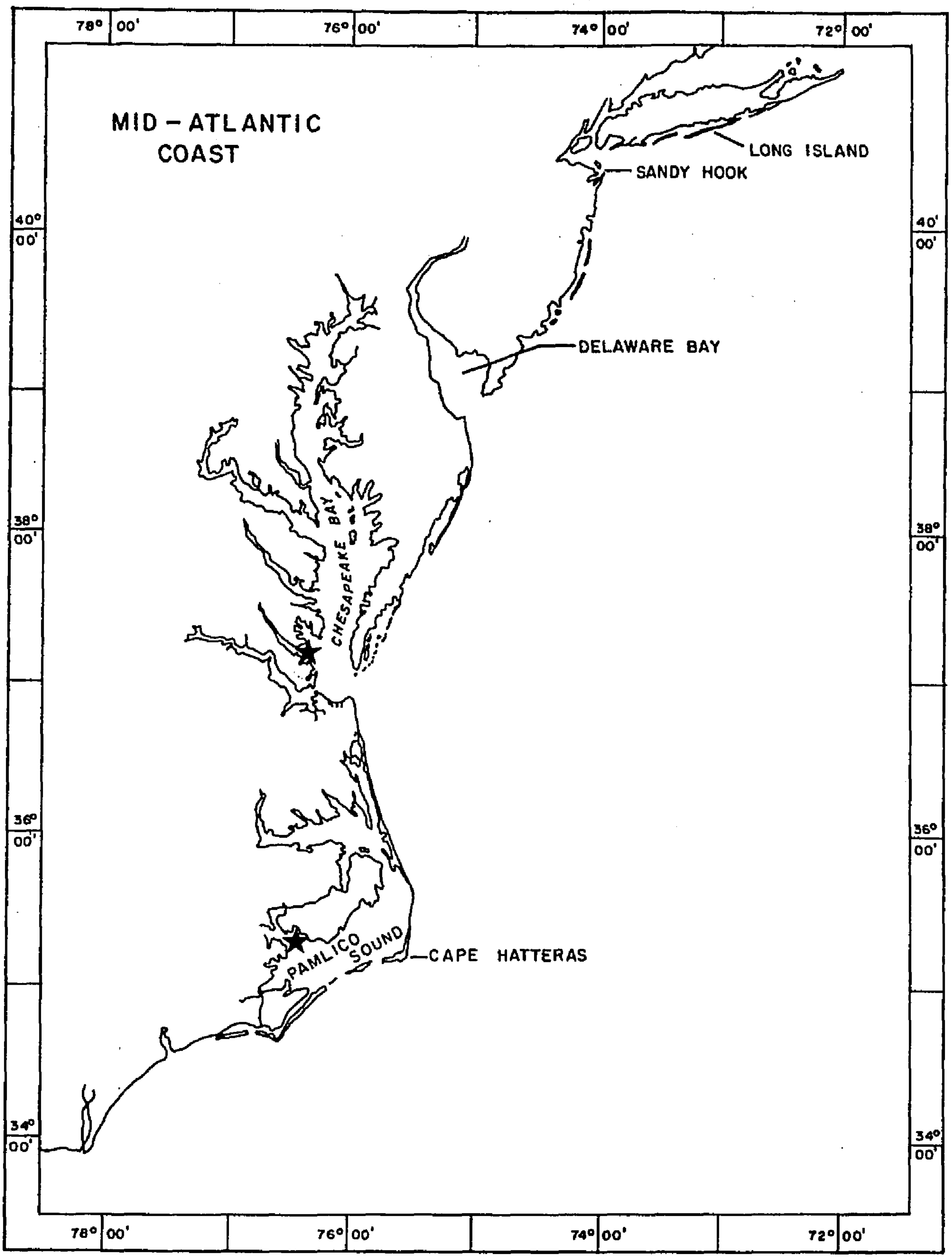
MATERIALS AND METHODS

Young-of-the-year spot were collected by trawl and seine at the mouth of the York River, Chesapeake Bay, Virginia monthly from April 1984 through October 1984 (Figure 1). Young-of-the-year croaker were collected by trawl as near as possible to the mouth of the York River in October and November 1983 and in January, March, April, and May 1984 (Figure 1). Salinities at the mouth of the York River ranged from 16 - 25 ppt. One trawl sample of croaker was collected near the mouth of the James River in July, 1984.

One sample of postlarval spot was collected by trawl from Ocracoke Inlet as individuals entered Pamlico Sound, North Carolina (Figure 1) in February 1985. Two trawl samples of postlarval croaker were collected from the mouth of the Pamlico River in September and November 1984. Other trawl samples of juvenile spot and croaker were collected monthly from March 1985 through November 1985 (except April) from various stations near the mouth of the Pamlico River (Figure 1). Salinities taken monthly ranged from 16.2 to 23.3 ppt. for the Pamlico River except the August sample which was from Broad Creek, a tributary near the mouth of the Pamlico River, where the salinity was 9.5 ppt.

Most of the fish were fixed immediately in 10% neutral-buffered formalin and later transferred to 70% ethanol until examined for parasites. Some hosts from the York River were examined fresh. Standard length was measured on all fish. The skin, gills, and gastrointestinal tracts were examined for parasites using a stereo-microscope. Platyhelminths recovered were stained in Van Cleave's Hematoxylin and

Figure 1. Estuaries in the Cape Hatteras region from which juvenile spot and croaker were collected (*, sampling sites).


MID - ATLANTIC
COAST
78° 00'
76° 00'
74° 00'
72° 00'
40° 00'
38° 00'
36° 00'
34° 00'
LONG ISLAND
SANDY HOOK
DELAWARE BAY
CHESAPEAKE BAY
PAMLICO SOUND
CAPE HATTERAS

mounted on slides in Clear Mount for identification. N ematodes and copepods were cleared in glycerin or lactic acid, respectively, for identification. Prey recovered from the entire length of the gut were identified to class or ordinal level.

The Shannon-Wiener index of diversity (H) and its components species richness (S) and species evenness (E) were calculated as: $H = - p_i \log_2 p_i$, where $p_i = n_i/N$ and is the proportion of the collection belonging to the ith species; S = total number of parasite species; $E = H/\log_2 S$. These indices were calculated for both component communities (parasites within a sample of hosts) and infracommunities (parasites within an individual host). Jaccard's index of species overlap was used to compare pairs of samples qualitatively and was calculated by the methods of Leong and Holmes (1981): $J = 100\ c/(a+b-c)$, where a = number of species in first sample, b = number species in second sample, and c = number of species common to both. Percentage similarity was used to compare pairs of samples quantitatively and was calculated by the methods of Hurlburt (1978): $PS = 100\ [1-0.5(\ p_{ia}-p_{ib}\ )]$, where P_{ia} and P_{ib} are the proportions of taxon, i, in samples a and b, respectively. Ecological terminology follows that recommended by Margolis et al. (1982). Abundance refers to the mean number of parasites per individual host in a sample.

RESULTS

A total of 21 parasites occurred in young-of-the-year spot from Chesapeake Bay and Pamlico Sound. Only eight (38%) parasites were shared between the two estuaries (Table 1). The four most abundant (dominant) parasite species of spot collected in Chesapeake Bay (Table 2) are generalists, in that they occur in several other sympatric fishes. Fish of the smallest size class (0-40 mm) collected in April did not have any of the dominant parasite species; however, 33% were infected (mean intensity = 1.3) with *Scolex polymorphus unilocularis*. By May all four of the dominant parasite species were present. The four most abundant parasite species occurring in spot collected in Pamlico Sound are also generalists (Table 3). Thirteen percent of the fish (0-20 mm) collected in February were already infected with a few *Diplomonorchis leiostomi*. The other three dominant species were not present in fish less than 41 mm. *Diplomonorchis leiostomi* was the only dominant species shared by spot between the two estuaries. Other less abundant parasites present were considered to be minor components of the parasite community of spot.

A total of 19 parasites occurred in young-of-the-year croaker from Chesapeake Bay and Pamlico Sound (Table 1). Only six (32%) parasites were shared between the two estuaries. Three of the four most abundant parasite species which occurred in croaker are generalists; the monogenean *Macrovalvitrematoides micropogoni* is specific to croaker (Table 4). The four most abundant parasite species in croaker collected in Pamlico Sound also are generalists, except *M. micropogoni* (Table 5). Three of the dominant parasites were shared between estuaries. Other less abundant

TABLE 1. Abundances of Parasites (mean number per host) found in juvenile *Leiostomus xanthurus* and *Micropogonias undulatus*.

Host Species	*Leiostomus xanthurus*		*Micropogonias undulatus*		
Area	Chesapeake Bay	Pamlico Sound	Chesapeake Bay	Pamlico Sound	Site in Host*
n=	116	140	103	127	
Myxozoa					
Kudoa branchiata Joy 1972	0.1				G
Digenea					
Apocreadium manteri Overstreet 1970	<0.1		0.1		I
Diplomonorchis leiostomi Hopkins 1941	8.0	46.5	1.0	46.3	I
Zoogonus rubellus (Olsson 1868)	2.8		<0.1		IR
Lepocreadium setiferoides (Miller & Northup 1926)	3.1	<0.1	0.1		I
Opecoeloides vitellosus (Linton 1907)				<0.1	I
Parahemiurus merus (Linton 1910)	0.5	0.4			S
Lecithaster confusus Odhner 1905			<0.1	<0.1	I

Table 1 (cont.)

Lecithaster leiostomi Overstreet 1970	1.3	<0.1			IR
Lecithochirium microstomum Chandler 1935			<0.1		S
Ascocotyle sp. (encysted metacercaria)	0.6		<0.1		F
Aspidocotylea					
Lobatostoma ringens (Linton 1907)				0.4	R
Monogenea					
Absonifibula bychowsky Lawler & Overstreet 1976			0.1	<0.1	G
Macrovalvitrematoides micropogoni (Pearse 1949)			0.2	0.2	G
Heteraxinoides xanthophilis (Hargis 1956)	0.4	0.2			G
Cestoda					
Psuedophyllidea (metacestode)				<0.1	I
Scolex polymorphus unilocularis	0.1	0.3	0.1	0.2	I
Echineibothrium sp. (metacestode)		<0.1		<0.1	I
Lacistorhynchus sp. (metacestode)		1.6		0.1	M

Table 1 (cont.)

Nematoda					
Goezia sp.		<0.1			I
Hysterothylacium sp.	<0.1		<0.1		M
Spirocamallus cricotus Fusco & Overstreet 1978		0.9		0.1	I
Acanthocephala					
Dollfusentis chandleri Golvan 1969	0.4		0.2	<0.1	R
Hirudinea					
Aestabdella leiostomi Burreson & Thoney 1988	<0.1				G
Myzobdella lugubris Leidy 1851	<0.1				E
Myzobdella uruguayensis Mane-Garzon & Montero 1977		0.1		<0.1	G
Copepoda					
Ergasilus lizae Kroyer 1863	0.1	3.8			G
Paraergasilus sp.	<0.1	0.4			G

*E, skin; F, fins, muscle, heart; G, gills; I, intestine; M, mesentery; R, rectum; S, stomach.

Table 2. Abundance of parasites (mean number per host) from <u>Leiostomus xanthurus</u> from Chesapeake Bay (numbers of hosts examined in parentheses).

Fish Length	Apr	May	Jun	Jul	Aug	Sep	Oct	Total
				<u>Diplomonorchis leiostomi</u>				
101-120						8.7(3)	3.6(5)	5.5(8)
81-100					18.5(6)	9.5(11)	4.2(9)	9.7(26)
61-80				63.8(5)	13.8(9)	2.0(1)	1.0(1)	27.9(16)
41-60		0.6(8)	0.1(9)	17.6(10)				7.0(27)
21-40		0.2(14)	0(6)					0.1(20)
0-20	0(18)	0(1)						0(19)
Total	0(18)	0.3(23)	0.1(15)	33.0(15)	15.7(15)	8.8(15)	3.8(15)	8.0(116)
				<u>Lepocreadium setiferoides</u>				
101-120						0(3)	0.2(5)	0.1(8)
81-100					0(6)	0(11)	0.8(9)	0.3(26)
61-80				0(5)	0(9)	0(1)	1.0(1)	<0.1(16)
41-60		38.1(8)	0(9)	0.6(10)				12.0(27)
21-40		2.6(14)	0(6)					1.8(20)
0-20	0(18)	0(1)						0(19)
Total	0(18)	14.9(23)	0(15)	0.4(15)	0(15)	0(15)	0.6(15)	3.1(116)

Table 2 (cont.)

				Zoogonus rubellus				
101-120						0(3)	1.8(5)	1.1(8)
81-100					0(6)	0.3(11)	0.3(9)	0.2(26)
61-80				0.2(5)	0(9)	0(1)	1.0(1)	0.1(16)
41-60		31.0(8)	1.6(9)	1.9(10)				10.8(27)
21-40		2.2(14)	0.5(6)					1.1(20)
0-20	0(18)	0(1)						0(19)
Total	0(18)	11.7(23)	1.1(15)	1.3(15)	0(15)	0.2(15)	0.9(15)	2.8(116)
				Lecithaster leiostomi				
101-120						4.0(3)	4.4(5)	4.3(8)
81-100					0(6)	2.3(11)	8.7(9)	4.0(26)
61-80				0(5)	0(9)	4.0(1)	11.0(1)	0.9(16)
41-60		0(8)	0(9)	0(10)				0(27)
21-40		0.4(14)	0(6)					0.2(20)
0-20	0(18)	0(1)						0(19)
Total	0(18)	0.2(23)	0(15)	0(15)	0(15)	2.1(15)	7.4(15)	1.3(116)
Fish Mean Length	17.4 ± 1.3	33.6 ± 11.4	42.0 ± 5.5	57.6 ± 9.4	80.2 ± 7.3	92.6 ± 10.6	97.3 ± 7.3	

Table 3. Abundance of parasites (mean number per host) from *Leiostomus xanthurus* from Pamlico Sound (numbers of hosts examined in parentheses).

Fish Length	Feb	Mar	May	Jun	Jul	Aug	Sep	Oct	Nov	Total
					Diplomonorchis leiostomi					
81-100					1.5(2)	0(3)	2.7(3)		14.8(5)	6.5(13)
61-80				26.5(2)	1.7(7)	2.4(7)	0.8(12)	0(15)	568.7(10)	109.0(53)
41-60			22.5(4)	14.9(13)	2.7(6)	7.0(5)				12.0(28)
21-40		2.5(13)	25.5(11)							13.1(24)
0-20	0.1(15)	0.3(7)								0.2(22)
Total	0.1(15)	1.8(20)	24.7(15)	16.5(15)	2.1(15)	3.5(15)	1.1(15)	0(15)	384.1(15)	46.5(140)
					Ergasilus lizae					
81-100					6.5(2)	42.3(3)	7.0(3)		2.6(5)	13.2(13)
61-80				1.0(2)	1.7(7)	34.6(7)	5.3(12)	0.3(15)	2.2(10)	6.5(53)
41-60			0(4)	0.3(13)	0.2(6)	2.0(5)				0.5(28)
21-40		0(13)	0(11)							0(24)
0-20	0(15)	0(7)								0(22)
Total	0(15)	0(20)	0(15)	0.4(15)	1.6(15)	25.3(15)	5.6(15)	0.3(15)	2.3(15)	3.8(140)

Table 3 (cont.)

					Lacistorhynchus sp.					
81-100					15.0(2)	0(3)	0(3)		4.0(5)	3.8(13)
61-80				0(2)	22.7(7)	0(7)	1.0(12)	0(15)	0(10)	3.2(53)
41-60			0(4)	0(13)	1.0(6)	0(5)				0.2(28)
21-40		0(13)	0(11)							0(24)
0-20	0(15)	0(7)								0(22)
Total	0(15)	0(20)	0(15)	0(15)	13.7(15)	0(15)	0.8(15)	0(15)	1.3(15)	1.6(140)
					Spirocamallanus cricotus					
81-100					0(2)	0(3)	0.3(3)		2.4(5)	1.0(13)
61-80				0(2)	0(7)	0(7)	0.8(12)	6.6(15)	0.6(10)	2.2(53)
41-60			0(4)	0(13)	0(6)	0(5)				0(28)
21-40		0(13)	0(11)							0(24)
0-20	0(15)	0(7)								0(22)
Total	0(15)	0(20)	0(15)	0(15)	0(15)	0(15)	0.7(15)	6.6(15)	1.2(15)	0.9(140)
Fish Mean	16.1 ±	20.6 ±	38.0 ±	55.0 ±	69.0 ±	69.0 ±	75.8 ±	70.0 ±	80.0 ±	
Length	1.0	2.5	6.0	5.3	14.3	13.5	6.8	3.6	9.6	

Table 4. Abundance of parasites (mean number per host) from Micropogonius undulatus from Chesapeake Bay (numbers of hosts examined in parentheses).

Fish Length	Oct	Nov	Jan	Mar	Apr	May	Jul	Total
			Diplomonorchis leiostomi					
81-100							0(2)	0(2)
61-80		1.0(2)	11.0(4)	0(2)	0(2)	0(2)	0(7)	2.4(19)
41-60	0(1)	6.5(4)	3.0(5)	0.7(6)	0(5)	0.3(3)	0.7(7)	1.7(31)
21-40	0(8)	0(7)	0(6)	0.1(7)	0.3(6)			0.1(34)
0-20	0(6)	0(4)			0(1)	0(6)		0(17)
Total	0(15)	1.6(17)	3.9(15)	0.3(15)	0.1(14)	0.1(11)	0.3(16)	1.0(103)
			Macrovalvitrematoides micropogoni					
81-100							1.0(2)	1.0(2)
61-80		0.5(2)	0.8(4)	0(2)	0.5(2)	0(2)	0(7)	0.3(19)
41-60	0(1)	1.3(4)	0(5)	0.3(6)	0.2(5)	0(3)	0.1(7)	0.3(31)
21-40	0.5(8)	0.6(7)	0(6)	0(7)	0(6)			0.2(34)
0-20	0(6)	0(4)			0(1)	0(6)		0(17)
Total	0.3(15)	0.6(17)	0.2(15)	0.1(15)	0.1(14)	0(11)	0.2(16)	0.2(103)

Table 4 (cont.)

				Dollfusentis chandleri				
81-100							0(2)	0(2)
61-80		0(2)	3.0(4)	1.5(2)	0.5(2)	0(2)	0.4(7)	1.0(19)
41-60	0(1)	0(4)	0.3(5)	0.7(6)	0.2(5)	0(3)	0.3(7)	0.1(31)
21-40	0(8)	0.1(7)	0(6)	0.1(7)	0(6)			<0.1(34)
0-20	0(6)	0(4)			0(1)	0(6)		0(17)
Total	0(15)	0.1(17)	1.1(15)	0.4(15)	0(14)	0.1(11)	0.3(16)	0.2(103)
				Scolex polymorphus unilocularis				
81-100							0(2)	0(2)
61-80		0(2)	0.3(4)	0(2)	0(2)	0(2)	0(7)	<0.1(19)
41-60	0(1)	0(4)	0.4(5)	0.8(6)	0.2(5)	0(3)	0(7)	<0.1(31)
21-40	0(8)	0(7)	0(6)	0(7)	0.2(6)			<0.1(34)
0-20	0.2(6)	0(4)			0(1)	0.2(6)		0.1(17)
Total	0.1(15)	0(17)	0.2(15)	0.3(15)	0.1(14)	0.1(11)	0(16)	0.1(103)
Fish Mean	26.2 ±	35.6 ±	46.5 ±	43.8 ±	40.4 ±	38.0 ±	66.3 ±	
Length	9.9	16.9	16.6	10.9	13.7	22.6	14.3	

Table 5. Abundance of parasites (mean numbers per host) from *Micropogonius undulatus* from Pamlico Sound (numbers of hosts examined in parentheses).

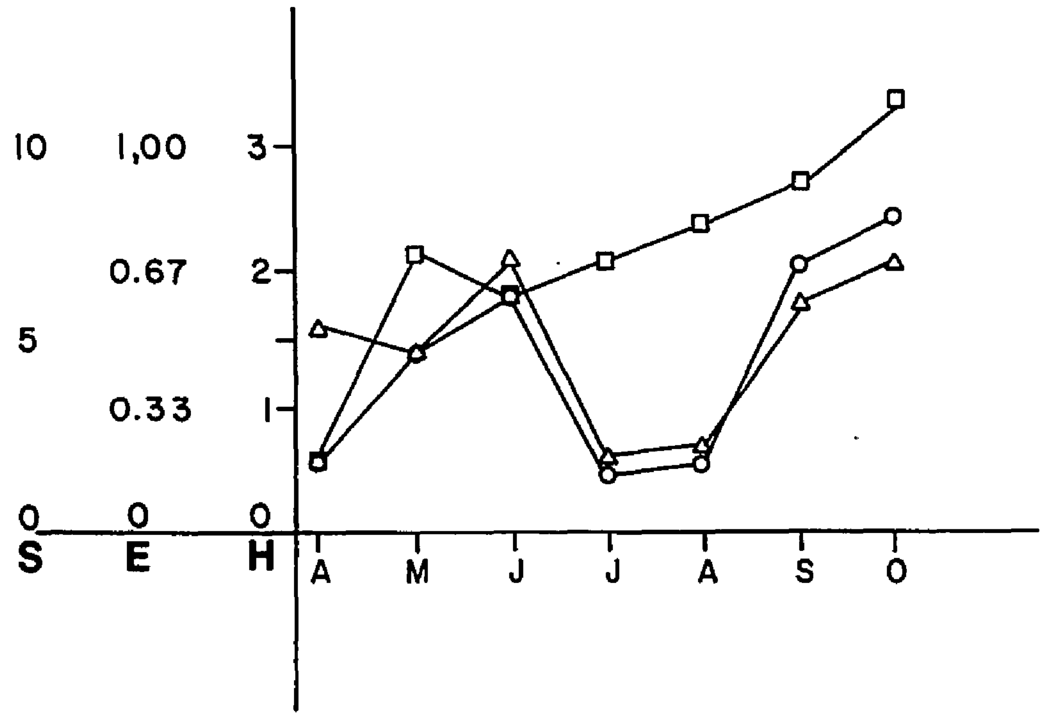
Fish Length	Sep	Nov	Mar	May	Jun	Jul	Aug	Oct	Nov	Total
					Diplomonorchis leiostomi					
101-125						152.3(4)		0(1)	246.0(12)	209.5(17)
81-100						66.0(3)	61.1(7)	1.1(10)	24.3(3)	30.9(23)
61-80					27.9(8)	45.6(5)	64.4(7)			45.1(20)
41-60			29.0(2)		18.9(7)	25.0(3)	16.0(1)			20.4(13)
21-40	0(5)	5.5(4)	18.9(8)	22.2(12)						15.3(29)
0-20	0(10)	0.2(11)		2.0(3)						0.3(24)
Total	0(15)	1.6(15)	20.9(10)	18.1(15)	23.7(15)	74.0(15)	59.7(15)	1.0(11)	201.7(15)	46.3(127)
					Lobatostoma ringens					
101-125						2.5(4)		2.0(1)	2.4(12)	2.4(17)
81-100						0(3)	0.3(7)	3.6(10)	0(3)	1.7(23)
61-80					0.4(8)	0(5)	0.1(7)			0.2(20)
41-60			0(2)		0(7)	0(3)	0(1)			0(13)
21-40	0(5)	0(4)	0(8)	0(12)						0(29)
0-20	0(10)	0(11)		0(3)						0(24)
Total	0(15)	0(15)	0(10)	0(15)	0.2(15)	0.7(15)	0.2(15)	3.5(11)	1.9(15)	0.4(127)

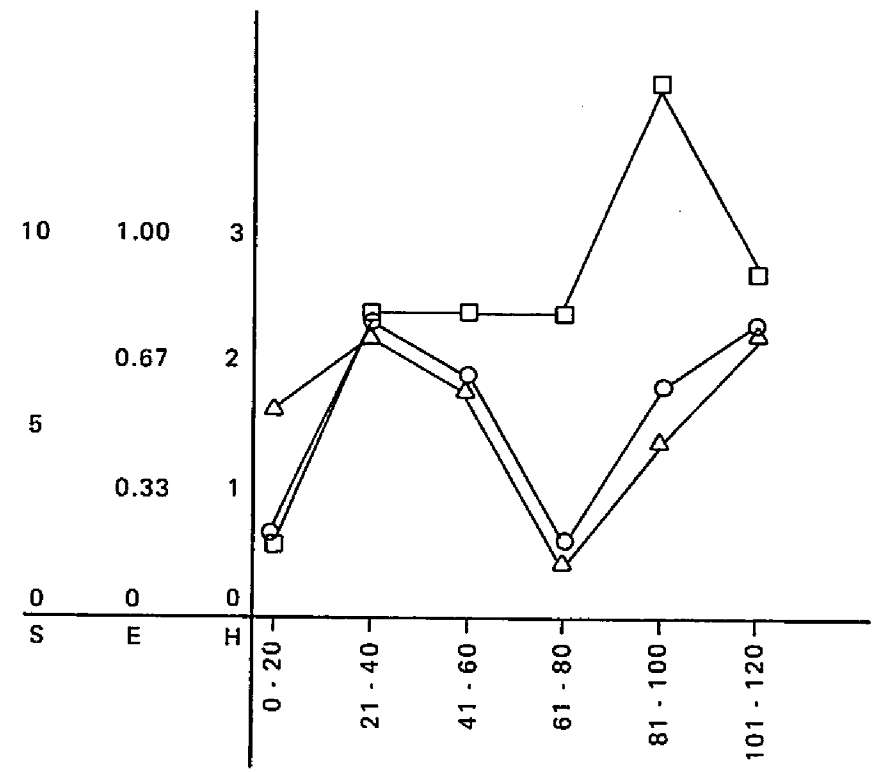
					<u>Macrovalvitrematoides</u> <u>micropogoni</u>					
101-125						1.3(4)		0(1)	0.3(12)	0.4(17)
81-100						0.3(3)	0.1(7)	0.1(10)	0(3)	0.1(23)
61-80					0.3(8)	0.8(5)	0.1(7)			0.4(20)
41-60	0(5)		0(2)		0.1(7)	0(3)	0(1)			<0.1(13)
21-40	0(10)	0(4)	0.4(8)	0.3(12)						0.2(29)
0-20	0(15)	0(11)		0(3)						0(24)
Total	0(15)	0.3(10)	0.2(15)	0.2(15)	0.5(15)	0.1(15)	0.1(11)	0.2(15)	0.2(127)	
					<u>Scolex</u> <u>polymorphus</u> (Type 1)					
101-125						0(4)		0(1)	0(12)	0(17)
81-100						0(3)	0(7)	0(10)	0(3)	0(23)
61-80					0(8)	0(5)	0(7)			0(20)
41-60	0(5)		1.5(2)		0(7)	0(3)	0(1)			0.2(13)
21-40	0.4(10)	0.5(4)	1.4(8)	0(12)						0.5(29)
0-20	0.3(15)	0.6(11)		0(3)						0.4(24)
Total	20.4 ±	0.5(15)	1.4(10)	0(15)	0(15)	0(15)	0(15)	0(11)	0(15)	0.2(127)
Fish Mean	5.9	19.3 ±	37.8 ±	27.1 ±	58.2 ±	81.9 ±	78.3 ±	91.8 ±	106.0 ±	
Length	5.3	3.9	5.9	10.1	20.5	9.3	7.3	10.4		

parasite species present were considered to be minor components of the parasite community of croaker.

In spot collected from Chesapeake Bay (Figure 2) species richness (S), and thus species diversity (H), of component communities of parasites increased from the 0-20 to the 21-40 mm size class, whereas species evenness (E) increased only slightly. Species richness (S) was then stable except for the 81-100 mm size class, which had considerably higher values. The decline in S in fish greater than 100 mm was most likely due to small sample size examined. Evenness and H decreased slightly in the 41-60 mm size class because of increased abundance of D. leiostomi, Zoogonus rubellus, and Lepocreadium setiferoides, decreased greatly in the 61-80 mm size class as numbers of D. leiostomi increased and numbers of Z. rubellus and L. setiferoides decreased, then increased as the dominance of D. leiostomi decreased. When diversity values were compared on a monthly basis the same pattern was apparent except S did not decline at the end of the sampling period due to small sample size. In spot from Pamlico Sound (Figure 3) S increased with host size from postlarvae (0-20 mm) until it reached a plateau in the 61-80 mm size class. A large decrease in E in the 21-40 mm size class was caused by the increased abundance of D. leiostomi. Species evenness (E) and diversity (H) increased slightly through the 61-80 mm size class as numbers of other species increased. A sharp decrease in the occurrence of D. leiostomi and increased numbers of other species resulted in an increase of H and E in 81-100 mm size class. A much more sporadic pattern was apparent when monthly values were examined; however, decreased values for H and E in March, May, and November also resulted from the presence of large numbers of D. leiostomi.

Figure 2. Diversity parameters calculated at the component community level for parasites of spot collected in the Chesapeake Bay. Figure a. Parasite communities examined by month. Figure b. Parasite communities examined by size. (H and circle, diversity; S and square, species richness; E and triangle, species evenness).


10
1,00
3
0.67
2
5
0.33
1
0
0
0
S
E
H
A
M
J
J
A
S
O


10
1.00
3
0.67
2
5
0.33
1
0
0
0
S
E
H
0 - 20
21 - 40
41 - 60
61 - 80
81 - 100
101 - 120

In croaker from Chesapeake Bay (Figure 4) S increased to a peak in the 41-60 mm size class, then decreased slightly in the 61-80 mm size class due to the absence of Absonifibula bychowsky and Hysterothylacium sp. (Figure 4). The great decline of S in 81-100 mm fish was undoubtedly because of the small sample size. Diversity (H) followed the same trend as S. Evenness was relatively stable with a slight decrease in the 61-80 mm size class as the abundance of Dollfusentis chandleri and D. leiostomi increased. A much more sporadic pattern in diversity parameters appeared when monthly values were examined.

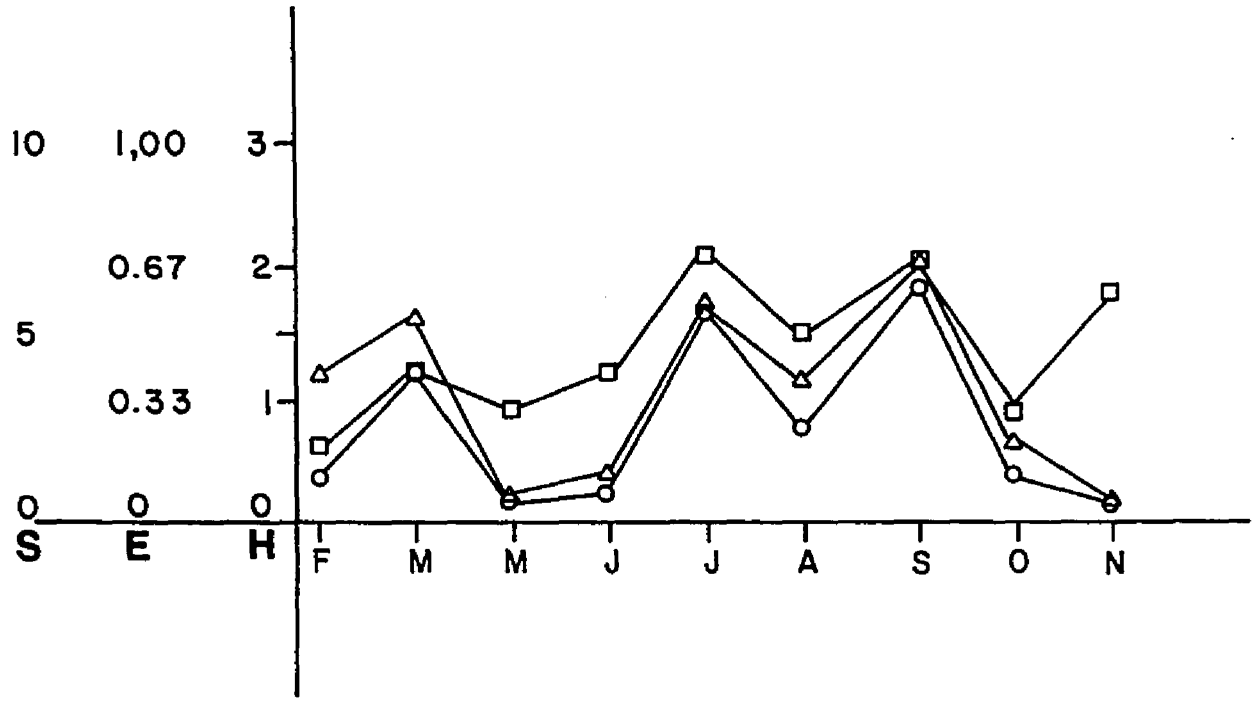
Mean standard lengths of croaker collected in Chesapeake Bay (Table 4) did not continue to increase past January, but decreased into May. In addition, the large standard deviation around the mean standard length indicated that fish varied greatly in size. This recruitment pattern not only resulted in decreased parasite species richness, but also decreased numbers of D. leiostomi, which influenced species evenness and diversity greatly from March through June. Since fish were recruited over a long season it proved more valuable to examine parasite community changes by host size than by month.

In croaker from Pamlico Sound (Figure 5) the increase in species richness (S) in the 21-40 mm size class can be attributed to the appearance of M. micropogoni and four minor components of the parasite community. Species richness decreased in the 41-60 mm size class due to the absence of the same four minor parasites. Species evenness and, thus, species diversity (H), decreased greatly and remained low in larger fish because D. leiostomi dominated all other species in these size classes. The slight increase of E and H in the 81-100 mm size class resulted from a slight decrease in prevalence of D. leiostomi and the presence of two additional species. Even though S remained the same in the 100-125 mm size class a dramatic increase in mean intensity of D. leiostomi depressed both E and H. A similar pattern was apparent when monthly values were examined.

Size of hosts appeared to have had a stronger influence on diversity indices than season, therefore size was used to calculate mean diversity indices at the infracommunity level. Mean diversity indices calculated for parasite infracommunities of spot from Chesapeake Bay followed the same patterns as those at the component community level, but magnitudes were lower (Table 6). The highest average numbers of parasites occurred in fishes 41-80 mm long. Mean species richness calculated for parasite infracommunities of spot from Pamlico Sound followed the same trends, but magnitudes were lower; however, H and E continued to increase with increased size of fishes (Table 7). The highest numbers of parasites occurred in hosts 61-80 mm long. Few large spot had 0 or 1 parasite species. Large ranges and standard deviation values indicated that there was much variation in these parasite infracommunities.

Mean diversity indices calculated for parasite infracommunities of croaker from Chesapeake Bay followed trends similar to those at the component community level, but magnitudes were lower (Table 8). The small sample size of 81-100 mm length fish did not lead to a decline in S and H as it did at the component community level (Figure 4). The largest numbers of parasites occurred in the 61-80 mm size class. Mean diversity indices calculated at the infracommunity level for croaker from Pamlico Sound (Table 9) did not have the same pattern as those calculated at the component community level. Mean species richness values increased with host size throughout their range. Mean values of evenness were low but

Figure 3. Diversity parameters calculated at the component community level for parasites of spot collected in the Pamlico Sound. Figure a. Parasite communities examined by month. Figure b. Parasite communities examined by size. (abbreviations are as in figure 2).


10
1,00
3
0.67
2
5
0.33
1
0
0
0
S
E
H
F
M
M
J
J
A
S
O
N

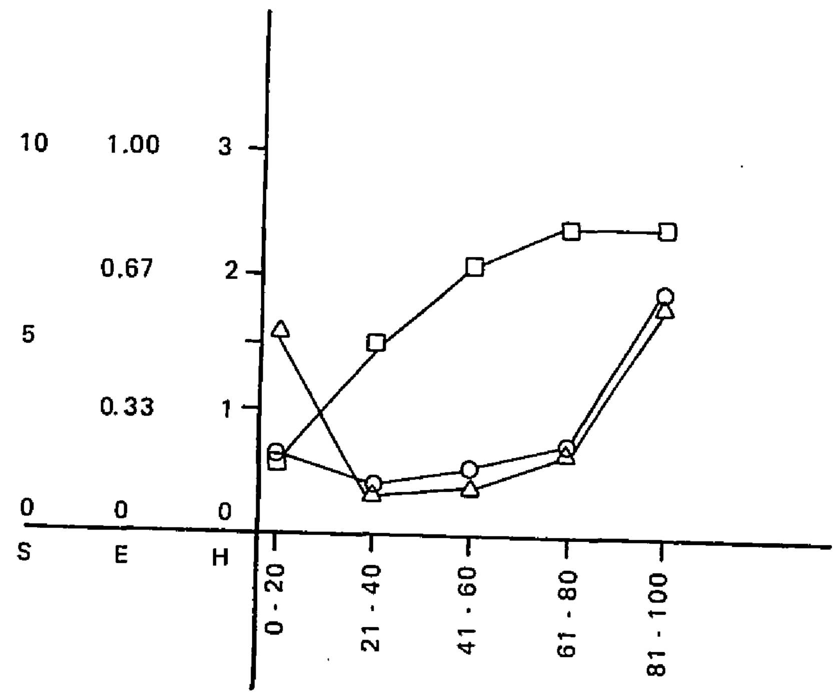
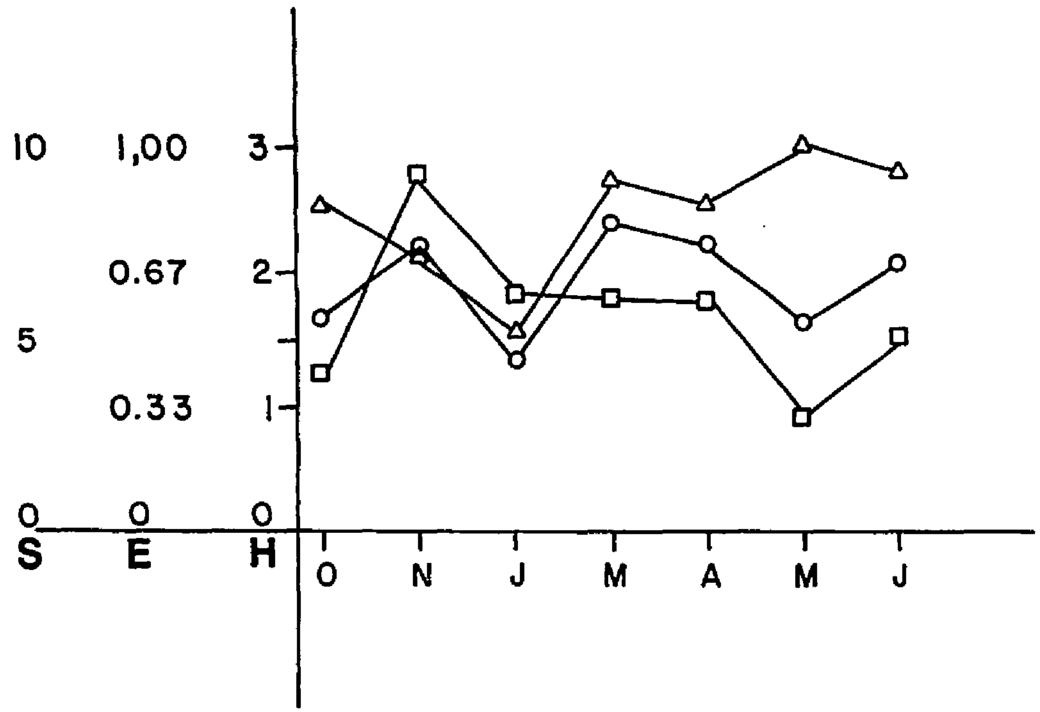

10
1.00
3
0.67
2
5
0.33
1
0
0
0
S
E
H
0 - 20
21 - 40
41 - 60
61 - 80
81 - 100

Figure 4. Diversity parameters calculated at the component community level for parasites of croaker collected in the Chesapeake Bay. Figure a. Parasite communities examined by month. Figure b. Parasite communities examined by size. (abbreviations are as in figure 2).


10
1,00
3
0.67
2
5
0.33
1
0
0
0
S
E
H
O
N
J
M
A
M
J

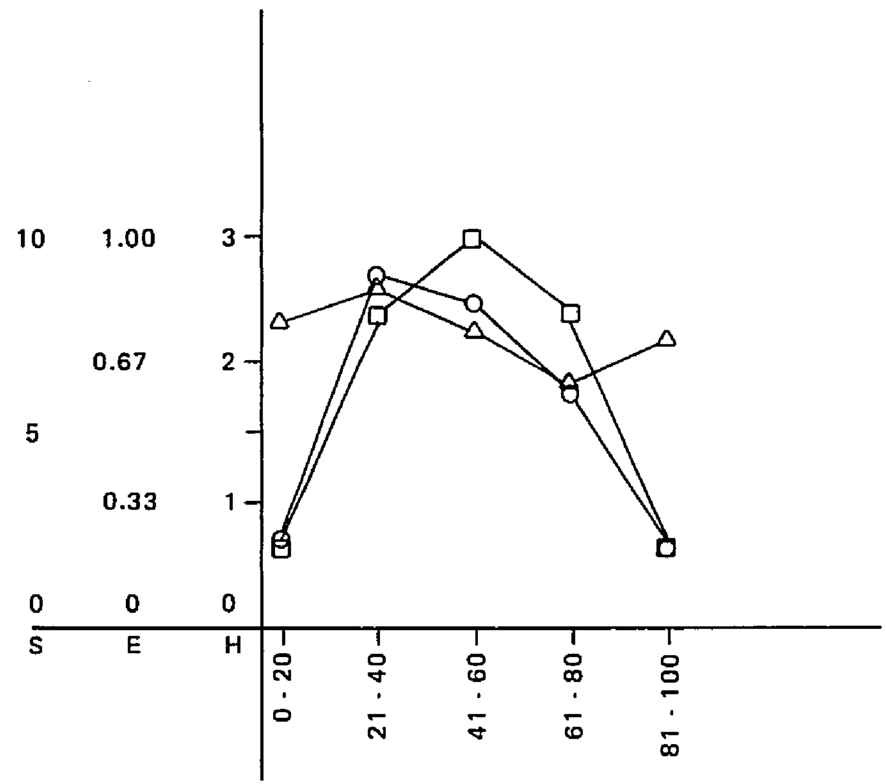
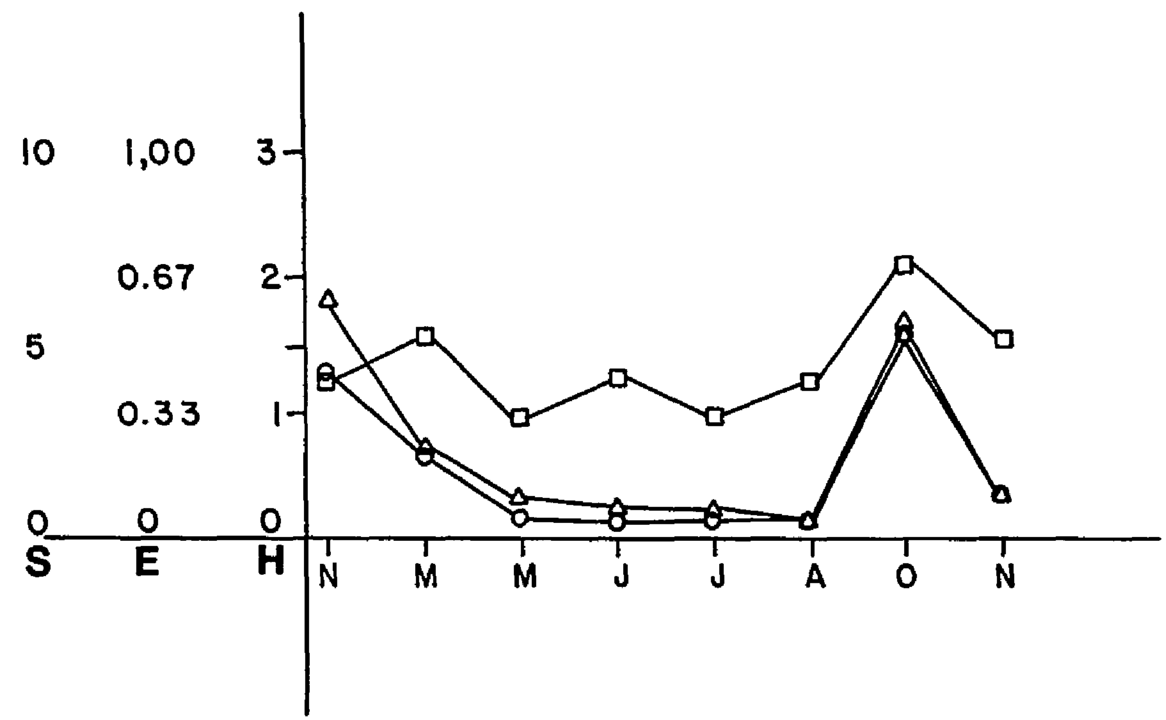
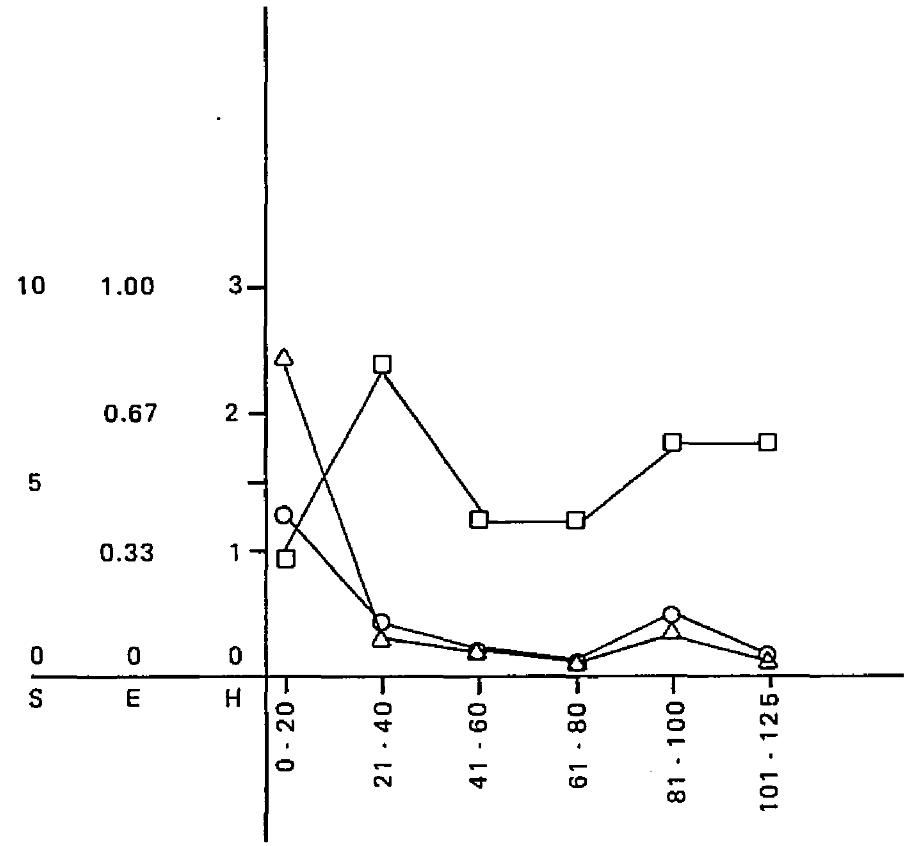

10
1.00
3
0.67
2
5
0.33
1
0
0
0
S
E
H
0 - 20
21 - 40
41 - 60
61 - 80
81 - 100

Figure 5. Diversity parameters calculated at the component community level for parasites of croaker collected in the Pamloco Cound. Figure a. Parasite communities examined by month. Figure b. Parasite communities examined by size (abbreviations are as in Figure 2).


10
1,00
3
0.67
2
5
0.33
1
0
0
0
S
E
H
N
M
M
J
J
A
O
N



10
1.00
3
0.67
2
5
0.33
1
0
0
0
S
E
H
0 - 20
21 - 40
41 - 60
61 - 80
81 - 100
101 - 125

increased slightly in larger fish. Diversity followed the same pattern, showing that H was dominated by effects of E as it was at the component community level (Figure 5). The largest numbers of parasites occurred in the 61-80 and 101-120 mm size classes. Few large individual croaker had 0 or 1 parasite species. Range and standard deviation values indicate considerable variation in parasite infracommunities among croaker as there was in spot.

TABLE 6. Diversity parameters of Parasite Infracommunities of Leiostomus xanthurus from Chesapeake Bay by length (S, species richness; H, diversity; E, species evenness).

Size (mm)	Sample Size		S	H	E	Mean No. of Parasites	% of Hosts with 0 or 1 sp.
0-20	18	$\bar{X}$	0.28	0	0	0.4	100
		SD	0.46	0	0	0.1	
		Range	0-1	0	0	1-3	
21-40	21	$\bar{X}$	1.85	0.71	0.60	5.3	38
		SD	0.93	0.50	0.42	6.0	
		Range	0-3	0-1.33	0-1	0-26	
41-60	27	$\bar{X}$	2.26	0.76	0.53	29.4	22
		SD	1.16	0.54	0.35	36.5	
		Range	0-4	0-1.49	0-0.97	0-139	
61-80	17	$\bar{X}$	1.94	0.35	0.29	29.8	35
		SD	1.24	0.46	0.34	35.2	
		Range	0-6	0-1.58	0-0.99	6-124	
81-100	27	$\bar{X}$	3.81	1.44	0.76	22.1	0
		SD	1.5	0.60	0.22	20.8	
		Range	0-6	0-2.41	0-0.99	2-89	
101-120	7	$\bar{X}$	4.14	1.38	0.78	15.9	14
		SD	1.57	0.62	0.10	9.3	
		Range	0-6	0-2.20	0-0.95	7-29	

TABLE 7. Diversity parameters of Parasite Infracommunities of Leiostomus xanthurus from Pamlico Sound by length (S, species richness; H, diversity; E, species evenness).

Size (mm)	Sample Size		S	H	E	Mean No. of Parasites	% of Hosts with 0 or 1 sp.
0-20	22	$\bar{X}$	0.68	0.05	0.05	1.5	96
		SD	0.57	0.21	0.21	1.7	
		Range	0-2	0-1	0-1	0-7	
21-40	24	$\bar{X}$	1.33	0.29	0.29	13.9	63
		SD	0.56	0.42	0.42	14.0	
		Range	0-2	0-1	0-1	0-46	
41-60	28	$\bar{X}$	1.21	0.23	0.22	13.5	71
		SD	0.62	0.37	0.37	18.6	
		Range	1-2	0-1	0-0.91	0-77	
61-80	51	$\bar{X}$	2.07	0.50	0.37	118.5	37
		SD	1.19	0.54	0.38	359.6	
		Range	1-5	0-1.74	0-1	0-2111	
81-100	13	$\bar{X}$	2.33	0.62	0.48	24.3	23
		SD	1.41	0.59	0.34	32.3	
		Range	1-5	0-1.67	0-0.96	1-95	

TABLE 8. Diversity parameters of Parasite Infracommunities of Micropogonias undulatus from Chesapeake Bay by length (S, species richness; H, diversity; E, species evenness).

Size (mm)	Sample Size		S	H	E	Mean No. of Parasites	% of Hosts with 0 or 1 sp.
0-20	17	$\bar{X}$	0.24	0	0	0.2	100
		SD	0.44	0	0	0.4	
		Range	0-1	0	0	0-1	
21-40	34	$\bar{X}$	0.50	0.16	0.11	0.7	88
		SD	0.93	0.46	0.31	1.2	
		Range	0-3	0-1.57	0-0.99	0-4	
41-60	32	$\bar{X}$	1.23	0.41	0.32	3.19	63
		SD	1.2	0.61	0.45	5.75	
		Range	0-4	0-1.64	0-1	0-30	
61-80	20	$\bar{X}$	1.05	0.32	0.25	3.75	65
		SD	1.13	0.51	0.39	7.11	
		Range	0-3	0-149	0-0.94	0-14	
81-100	2	$\bar{X}$	1	0.46	0.46	1.5	50
		SD	1.41	0.64	0.64	2.12	
		Range	0-2	0-0.91	0-0.91	0-3	

TABLE 9. Diversity parameters of Parasite Infracommunities of *Micropogonias undulatus* from Pamlico Sound by length (S, species richness; H, diversity; E, species evenness).

Size (mm)	Sample Size		S	H	E	Mean No. of Parasites	% of Hosts with 0 or 1 sp.
0-20	24	$\bar{X}$	0.46	0.08	0.08	0.8	88
		SD	0.66	0.27	0.27	1.3	
		Range	0-2	0-0.91	0-0.91	1-4	
21-40	31	$\bar{X}$	1.24	0.19	0.13	16	71
		SD	0.99	0.38	0.26	17.9	
		Range	0-4	0-1.49	0-0.94	0-76	
41-60	13	$\bar{X}$	1.23	0.11	0.11	22.5	77
		SD	0.44	0.24	0.24	13.5	
		Range	1-2	0-0.72	0-0.72	3-48	
61-80	19	$\bar{X}$	1.45	0.11	0.10	45.7	63
		SD	0.60	0.19	0.17	56.6	
		Range	1-3	0-0.64	0-0.64	4-252	
81-100	23	$\bar{X}$	1.57	0.28	0.24	32.9	52
		SD	0.66	0.44	0.35	33.4	
		Range	1-3	0-1.57	0-1	1-106	
101-120	17	$\bar{X}$	2.41	0.30	0.24	183.1	6
		SD	0.71	0.34	0.28	216.4	
		Range	1-4	0-1.09	0-0.91	3-890	

Comparison of the Parasite Communities of *Leiostomus xanthurus* and *Micropogonias undulatus* from the Two Estuaries

Of the 28 parasite species found in spot and croaker from the two estuaries, 12 (43%) occurred in both hosts (Table 1). Jaccard's Index of species overlap indicated moderate levels of shared parasite species within each host species in different estuaries and between host species in the same estuary (Figure 6). Comparisons between spot and croaker taken from different estuaries showed low proportions of shared species. When the 16 parasites not in both host species were excluded, only 25% of the parasites of spot were shared between estuaries and only 21% of the parasites of croaker were shared between estuaries. However, spot and croaker from Chesapeake Bay shared 89% of their parasites while those from Pamlico Sound shared 75%. When the unshared species were excluded when calculating Jaccard's Index, spot and croaker taken from the same estuary shared most of the remaining species; other comparisons showed low proportions of shared species (Figure 7).

Percentage similarity values indicated a different pattern, with highest similarities between the parasite faunas of croaker and spot from different estuaries. The parasite faunas of spot and croaker from Pamlico Sound were also very similar. Other comparisons between host and estuaries were somewhat lower (Figure 8). The high levels all appeared to be due to the strong domination of the parasite faunas by *D. leiostomi*.

Figure 6. Values of Jaccard's Index of species overlap between component parasite communities of spot and croaker collected in the two estuaries (MUCB, croaker from Chesapeake Bay; MUPS, croaker from Pamlico Sound; LXCB, spot from Chesapeake Bay; LXPS, spot from Pamlico Sound).

	MUCB	MUPS	LXCB	LXPS
MUCB		30	38	13
MUPS			12	30
LXCB				38
LXPS				

Figure 7. Values of Jaccard's Index of species overlap between component parasite communities of spot and croaker collected in the two estuaries including only those species that occurred in both hosts (abbreviations are as in figure 6).

	MUCB	MUPS	LXCB	LXPS
MUCB		21	89	23
MUPS			20	55
LXCB				21
LXPS				

Food Habits of Spot and Croaker In Relation to Estuary Collected

Young-of-the-year spot (0-20 mm) in Chesapeake Bay fed mostly on copepods and a few gammarid amphipods (Table 10). Juveniles (21-60 mm) preyed more on benthic organisms such as crustaceans and nematodes. Larger fish fed on a wide range of benthic organisms including pelecypods, polychaetes, fish, and additional crustaceans, and rarely had empty gastrointestinal tracts. Young-of-the-year spot (0-20 mm) in Pamlico Sound fed on a variety of prey including copepods, other crustaceans, nematodes and polychaetes (Table 10). Pelecypods, insect larvae, and some fish constituted a large portion of prey taken in larger fishes. None of these spot had empty gastrointestinal tracts.

Small croaker (0-20 mm) in Chesapeake Bay fed mostly on copepods, gammarids, and mysids (Table 11). Juveniles depended more on gammarids, mysids, and polychaetes and less on copepods with increased size. Small croaker (0-20 mm) in Pamlico Sound fed mostly on copepods, mysids, and some polychaetes (Table 11). With increased size juveniles ingested more pelecypods, insect larvae, and teleosts and fewer copepods. The presence of polychaetes and mysids in gut contents increased, then decreased as host Figure 7. Values of Jaccard's Index of species overlap between component parasite communities of spot and croaker collected in the two estuaries including only those species that occurred in both hosts (abbreviations are as in figure 6). size increased. As their sizes increased fewer individual croakers were found with empty guts.

Application of Jaccard's Index of species overlap indicated relatively high levels of shared prey species (Figure 9). However, levels of prey species overlap (Figure 9) were not significantly correlated with either levels of parasite species overlap (Figure 6) or percentage parasite similarity (Figure 8). Spot collected in Pamlico Sound had high levels of species overlap with both spot from Chesapeake Bay and croaker from Pamlico Sound. Croaker from Chesapeake Bay had lower species overlap in all comparisons and that may be attributed to their smaller size.

Figure 8. Values of Percent Similarity between component parasite communities of spot and croaker collected in the two estuaries (exponents indicate number of shared species in each comparison; abbreviations are as in figure 6).

	MUCB	MUPS	LXCB	LXPS
MUCB		59.1^{6}	71.4^{8}	85.0^{3}
MUPS			90.3^{3}	95.6^{6}
LXCB				68.4^{8}
LXPS				

Figure 9. Values of Jaccard's Index of species overlap between prey items of spot and croaker collected in the two estuaries (abbreviations are as in figure 6).

	MUCB	MUPS	LXCB	LXPS
MUCB		67	70	60
MUPS			80	89
LXCB				90
LXPS				

TABLE 10. Percent occurrence of prey in the gastrointestinal tract of *Leiostomus xanthurus* from Chesapeake Bay and Pamlico Sound.

Length of Fish (mm SL)	0-20		21-40		41-60		61-80		81-100		>100	
Area	CB	PS	CB	PS	CB	PS	CB	PS	CB	PS	CB	PS
Number of Fish	18	22	21	24	27	28	17	51	27	13	7	0
Cirripedia	0	0	4.8	4.2	3.7	0	5.9	0	0	0	14.3	-
Copepoda	44.4	86.4	0	66.7	37.0	78.6	76.5	60.8	70.4	69.2	71.4	-
Gammaridea	5.6	4.5	0	0	0	0	17.6	0	18.5	0	14.3	-
Isopoda	0	0	0	0	0	0	11.8	0	11.1	0	14.3	-
Mysidacea	0	9.1	4.8	4.2	0	21.4	5.9	15.7	11.1	23.1	28.6	-
Insecta	0	0	0	0	0	28.6	0	13.7	3.7	46.2	0	-
Nematoda	0	40.9	0	62.5	22.2	7.1	82.4	64.7	66.7	23.1	71.4	-
Pelecypoda	0	0	0	0	0	10.7	5.9	9.8	0	69.2	0	-
Polychaeta	0	9.1	0	62.5	0	60.7	29.4	35.3	74.1	38.5	85.7	-
Teleostei	0	0	0	0	0	0	0	0	7.4	7.7	28.6	-
Miscellaneous	0	13.1	14.3	0	22.2	17.9	17.6	78.4	11.1	61.5	14.3	-
Empty	50.0	0	76.2	0	3.7	0	0	0	7.4	0	0	-

TABLE 11. Percent occurrence of prey in the gastrointestinal tract of *Micropogonias undulatus* from Chesapeake Bay and Pamlico Sound.

Length of Fish (mm SL)	0-20		21-40		41-60		61-80		81-100		>100	
Area	CB	PS	CB	PS	CB	PS	CB	PS	CB	PS	CB	PS
Number of Fish	15	24	34	31	32	13	20	19	2	23	0	17
Copepoda	26.7	50.0	50.0	25.0	37.5	61.5	15.0	47.4	0	21.7	-	0
Gammaridea	13.3	0	29.4	4.2	65.6	0	45.0	0	50.0	4.3	-	17.6
Isopoda	0	0	0	0	0	0	5.0	0	0	0	-	5.9
Mysidacea	13.3	20.8	29.4	79.2	65.6	53.8	45.0	63.2	50.0	56.5	-	41.2
Insecta	0	0	2.9	0	9.4	7.7	0	31.6	0	21.7	-	29.4
Nematoda	0	0	0	4.2	0	0	10.0	0	50.0	4.3	-	0
Pelecypoda	0	0	0	8.3	0	23.1	0	73.7	0	65.2	-	76.5
Polychaeta	0	8.3	2.9	22.6	9.4	38.5	10.0	26.3	50.0	30.4	-	11.8
Teleostei	0	0	0	4.2	0	0	0	0	0	4.3	-	17.6
Miscellaneous	0	0	0	8.3	0	23.1	0	15.8	0	60.9	-	41.2
Empty	53.3	25.0	20.6	8.3	6.3	7.7	10.0	0	0	0	-	0

DISCUSSION

Comparison of parasites in Leiostomus xanthurus from the Two Estuaries

The parasite communities in spot in the two estuaries were quite different; however, *D. leiostomi* dominated the parasite communities of both areas at particular times of the year. In Chesapeake Bay it was most abundant in July, August, and September, whereas in Pamlico Sound peak abundance occurred during May, June, and November. The occurrence of this digenean earlier in the year in Pamlico Sound may reflect the presence of larger sized hosts in May and June that could have consumed infected intermediate hosts. The greater abundance of *D. leiostomi* in Pamlico Sound (Table 3) resulted mainly from the large numbers of this parasite in the November sample. A November sample from Chesapeake Bay was not available for comparison because most spot had left the estuary by that time. The presence of *D. leiostomi* in postlarvae (0-20 mm) and the larger number of this parasite in juveniles (21-40 mm) from Pamlico Sound then juveniles from Chesapeake Bay may have resulted from a larger number of infected intermediate hosts present there than in Chesapeake Bay.

Population fluctuation of intermediate hosts may account for the differences found between the two estuaries in those parasites with indirect life cycles. The lower salinity regime in Pamlico Sound may affect the distribution of parasites and their intermediate hosts. Fish appeared to have fed on slightly different prey items. Fish from Pamlico Sound fed more on pelecypods, insects, polychaetes, and mysids and less on cirripedes, gammarids, and isopods.

Species richness increased rapidly between the 0-20 and 21-60 mm size classes in both estuaries reflecting the radical change in diet as postlarvae switched from a pelagic diet of mostly copepods to a more benthic diet. The continued increase in S can be accounted for partially by the increase in the number of intermediate host species consumed and partially by the presence of several parasite species with direct life cycles.

Comparison of *Micropogonias undulatus* from the Two Estuarine Systems

The parasite communities of croaker were quite different in the two estuaries. The absence of larger fish in samples from Chesapeake Bay probably accounted for some of the differences observed. Mean standard lengths of croaker from Chesapeake Bay decreased from January through May. There are several explanations for this apparent negative growth. (1) Croaker is a "protracted spawner"; therefore, postlarvae and juveniles entering the bay from fall through spring occurred in samples along with older fish. (2) The winter of 1984-1985 was relatively cold and many of the larvae died that had entered the Bay in fall and early winter. Dead fish were evident in trawls during January and February. Those surviving the colder water temperatures of that winter may have experienced reduced growth rates during the cold temperatures (Chao and Musick 1977). (3) Older fish tend to move up into fresher waters making them unavailable for sampling at the mouth of the York River (Chao and Musick 1977). Although samples were collected along most of the York River, larger individuals were not found. Only two fish larger than 80 mm were captured and they were from the James River.

Diplomonorchis leiostomi was much more abundant in fish from Pamlico Sound than from Chesapeake Bay. The larger size of the hosts collected in Pamlico Sound could have been responsible for the greater overall abundance; however, both prevalence and mean intensity were also much greater in similar size classes of fish (Tables 6, 8). Diplomonorchis leiostomi was more abundant than all other parasites in fish from Pamlico Sound, resulting in low evenness and diversity values for the assemblage (Figures 3 and 5). In contrast, D. leiostomi occurred in much lower numbers in Chesapeake Bay resulting in E being relatively stable and at higher levels. In this case S was much more important in affecting levels of H than E (Figures 2 and 4). Scolex polymorphus unilocularis individuals occurred in croaker from both areas, and had similar distributions among individual hosts. They occurred mainly in fish 0-60 mm with lower abundance in the larger fish (Table 8). Macrovalvitrematoides micropogoni did not occur in fish less than 20 mm from either estuary and their numbers were low in the 21-40 mm size class (Tables 6, 8). Abundance was greater in larger fish. Only one individual of D. chandleri was found in fish from Pamlico Sound, whereas it was a significant component of the parasite fauna in Chesapeake Bay.

The apparent absence of the aspidocotylean L. ringens in Chesapeake Bay may have resulted from the lack of larger hosts for examination. All of the L. ringens recovered from Pamlico Sound occurred in fish larger than 60 mm (Table 8). The presence of L. ringens in fish larger than 60 mm correlated well with the increased prevalence of pelecypods in their diet (Table 11). The clam Donax roemeri protracta is an intermediate host of Lobatostoma ringens. This pelecypod inhabits high-energy, high-salinity beaches (Hendrix and Overstreet 1977). The presence of L.

ringens in young-of-the-year croaker in the low-energy, low-salinity waters of Pamlico Sound suggests that there may be an alternative intermediate host there unless juvenile croaker migrate the long distance required to leave Pamlico Sound, become infected, and then return.

Comparison of the parasite faunas of *Leiostomus xanthurus* and *Micropogonias undulatus* from the Two Estuaries

Only the monogenean *Heteraxinoides xanthophilis*, the myxozoan *Kudoa branchiata*, and possibly the leech *Aestabdella leiostomi* occurred exclusively in spot; only the monogeneans *M. micropogoni* and *A. bychowsky* were specific to croaker. Monogeneans as a group are generally more host specific than other metazoan parasites, especially digeneans. The leech *A. leiostomi* is a newly-described species belonging to a taxon that is generally not host specific; therefore, it eventually may be found on other hosts. The copepod *Paraergasilus* sp. has been collected from adult spot and croaker (see following chapter). The digeneans *Lecithaster leiostomi* and *Parahemiurus merus*, and the copepod *E. lizae* have been reported from several marine teleosts but not from croaker (Overstreet 1973; Johnson and Rogers 1973; Yamaguti 1971). The trematodes *Lecithaster confusus* (Linton 1940; Overstreet 1973), *Lecithochirium microstomum* (Yamaguti 1971), and *L. ringens* (Hendrix and Overstreet 1977) have not been previously reported from spot. The nonspecificity of these parasites in closely related and/or sympatric hosts suggests that their absence in one or the other of these hosts may be ecologically and not physiologically based, i.e. the hosts may be feeding on different intermediate hosts. The leech *Myzobdella lugubris*, which has a direct life cycle, and the nematode *Goezia* sp. have been found infecting croaker previously (Deardorff and Overstreet 1980; Sawyer et al. 1975), but were found infecting only spot during this study. The digenean *O. vitellosus* has been reported from spot previously, but was found only in croaker during this study. The species that have been reported from both hosts, but were absent in one or the other in this study, were minor components of their parasite communities. They might have actually been found in both host species had a greater number of fish been examined.

Jaccard's Index of Species Overlap indicated that the relatively high similarity of spot or croaker with their conspecific counterparts between estuaries shown in Figure 6 resulted from host specific parasites being present. In contrast, spot and croaker parasite communities from the same estuary had high similarity (Figure 7). All of the species that did occur in both hosts have indirect life cycles suggesting that the availability of intermediate hosts as prey was important. The estuary of residence was evidently as important as host species in determining parasite community structure.

Percentage similarity indices, which account quantitatively for the number of individuals of shared species, show different trends than when species overlap was compared. The presence of large numbers of the common species *D. leiostomi* had a dominating influence on indices resulting in all comparisons having high similarity. The parasite faunas of croaker from Chesapeake Bay, which were small individuals and, thus, had few *D. leiostomi*, were not very similar to those of croaker from Pamlico Sound and spot from Chesapeake Bay. The parasite faunas of croaker from Chesapeake Bay appeared more similar to those of spot from Pamlico Sound because the small number of shared species resulted in *D. leiostomi* having a strong influence on similarity. The large numbers of *D. leiostomi* and few shared species between spot from Chesapeake Bay and croaker from Pamlico Sound also resulted in an apparent high similarity. Spot and croaker from Pamlico Sound had a large number of shared species and numbers of each species were similar resulting in a high index of similarity. Spot from the two estuaries had low similarity of parasite faunas even though 8 species were shared. Some species occurred in large numbers in one estuary while others were more common in the other estuary, suggesting that the numbers of intermediate hosts were not consistant between estuaries.

Though many parasites occurred in both hosts from Chesapeake Bay most were much more abundant in one host than the other. Ascocotyle sp., D. leiostomi, L. setiferoides, and Z. rubellus were all more abundant in spot, whereas A. manteri and both tetraphyllidean metacestodes were more abundant in croaker. Both L. setiferoides and Z. rubellus share the same first intermediate host, Ilyanassa obsoletus, with metacercaria in polychaetes, the second intermediate hosts, which may explain their co-occurrence. Polychaetes were more common in the guts of spot than croaker. The intermediate hosts of A. manteri are unknown. In Chesapeake Bay more specimens of D. chandleri were found in spot than croaker; however, they occurred in the larger size classes (81-120 mm), which were not available in croaker samples. The large abundance of D. chandleri in the larger sized spot suggests that had larger croaker been sampled, they also would have been infected. The prevalence of D. chandleri in its hosts is directly related to the occurrence of its intermediate hosts, gammarideans, in their guts (Tables 10, 11). The numbers of Hysterothylacium sp. were similar in the two hosts, but like D. chandleri may have been more abundant if larger croaker had been available.

Many of the parasites in both hosts from Pamlico Sound were also more abundant in one host than the other. Diplomonorchis leiostomi, Scolex polymorphus unilocularis, Lacistorhynchus sp., S. cricotus, and Myzobdella uruguayensis were all more abundant in spot. Small spot depended more than croaker on copepods in their diets (Tables 10, 11, respectively), which may explain the larger numbers of metacestodes in spot. Except for M. uruguayensis, which has a direct life cycle, D. leiostomi, which uses pelecypods as intermediate hosts, and S. cricotus, which may use decapod shrimp as intermediate hosts, life cycles of the other parasites are unknown, but are generally thought to be indirect. Numbers of Echineibothrium sp. were similar in both hosts.

These differences in the prevalence and intensities of parasites between spot and croaker may be explained by differences in their feeding habits. Although spot and croaker fed on many of the same prey species, larger and more mobile epifaunal prey such as teleosts, mysids, and gammarideans, occurred in croaker (Table 11). Spot depended more on benthic, infaunal prey such as nematodes, copepods, and polychaetes (Table 10). The differences in diet observed between spot and croaker in this study are similar to those reported by Chao and Musick (1977), Overstreet and Heard (1978), Currin (1984), Currin et al. (1984), and Sheridan et al. (1984).

The numbers of parasite species found in the two largest size classes of juvenile spot and croaker in this study (Tables 6, 7, 8, and 9) were similar to the largest numbers found in adult freshwater fishes studied by Kennedy et al. (1986). Estimates of S in this study are inflated relative to those of Kennedy et al. (1986) because all parasites found were included, not just gastrointestinal forms. The great diversity of prey items (Tables 10, 11) probably contributes greatly to the large number of intestinal parasites as was suggested by Kennedy et al. (1986)

for parasite faunas of other hosts. In addition, the presence of the same parasite species in other sympatric hosts may contribute to an interacting compound community (parasites in all hosts within a area) and increase diversity (Stock and Holmes 1987). None of the gut parasites are specific to only spot or croaker, but occur in other sympatric fishes. The presence of sympatric reservoir hosts also probably accounts for the larger number of species present by providing alternate habitats and, thus, sources of infection.

Like the similarity in species richness, the total number of parasites in individuals of juvenile croaker and spot was similar to that found in freshwater fishes (Kennedy et al. 1986). Again non-gastrointestinal forms (ectoparasites and encysted forms) were included in this analysis; however, the total numbers of these other parasites were relatively low and have only a minor effect on total numbers of parasites. Intra- or interspecific competition may have prevented higher intensities from accumulating in the smaller, less complex intestinal habitat of fish, when compared with many higher vertebrates. Also only young-of-the-year fishes, which have not had a long time to acquire parasites, were considered in this study. Further, estuaries are known to have less diverse faunas than marine systems. Fewer prey species (intermediate hosts) present in these systems probably reduced species richness greatly. Kennedy et al. (1986) also suggested that vagility (movement of host) was important in determining species richness. Although both spot and croaker spawn offshore, a relatively long distance from the juvenile nursery grounds, juveniles do not appear to diversify their diets until after reaching the estuarine nursery areas. In contrast, adult fish make annual migrations over great distances, which allows them access to a wider range of prey (intermediate hosts) and, thus, parasites. Therefore, adult fishes would be expected to have not only more parasite species, but higher abundances.

In summary, the parasite communities of juvenile spot and croaker changed with size, season, and geographical area. A total of 21 parasitic species occurred in juvenile spot and 19 occurred in juvenile croaker from Chesapeake Bay and Pamlico Sound. More parasitic species were acquired as juveniles diversified their diets and fed on more intermediate host species. As juveniles grew they were also exposed to infective larvae of parasites with direct lifecycles over longer periods of time. However, equibility and, thus, diversity were depressed due to large numbers of D. leiostomi that dominated the parasite communities of both species. Although spot and croaker shared eight and six parasites, respectively, between estuaries, many of these nonspecific parasites (generalists) were more common in both spot and croaker from one estuary than the other. All of the species occurring in both hosts have indirect life cycles suggesting that the availability of certain intermediate hosts as prey was important. The estuary of residence was clearly as important as host species identity in determining parasite community structure.

Community Ecology and Abundance of the Parasites of Adult Leiostomus xanthurus and Micropogonias undulatus (Sciaenidae) in the Cape Hatteras Region

INTRODUCTION

Kennedy et al. (1986) stated that both birds and mammals have a richer parasite fauna and many more parasites per host than freshwater fishes. They attributed these differences to the greater input of food needed to support an endothermic metabolism in the higher vertebrates, a greater breadth of diet in those endotherms, a greater vagility (movement of host) relative to prey (intermediate hosts) especially in birds, and a larger, more complex gut in many higher vertebrates, which provides additional microhabitats for parasites. Although Kennedy et al. (1986) hypothesized that marine fishes should have greater species-richness and numbers of parasites per host than freshwater fishes because of their greater vagility and wider breadth of diet, no adequate data were available to examine this hypothesis. More recently, Holmes (in press) reported that parasite communities of marine reef-dwelling rockfishes of the genus Sebastes have greater species-richness than freshwater fishes.

There has been an ongoing controversy in community ecology research as to whether species within a community are patterned and predictable or "random" and unpredictable. To test Caswell's (1978) and Hanski's (1982) concept that communities consist of dominant, predictable "core" species surrounded by subordinate, unpredictable, "satellite" species in parasite communities, Bush and Holmes (1986) examined helminths in the lesser scaup duck, Aythya affinis (Eyton). They concluded that helminth patterns in the lesser scaup support Caswell's and Hanski's concepts. They also concluded that much of the predictability found in parasite communities of lesser scaup resulted from their specialized diet, consisting mostly of two species of gammarid amphipods. Each species of amphipod supported a suite of parasitic species that infected lesser scaup. Stock and Holmes (1987) came to a similar conclusion after they examined helminth patterns in four species of grebes. However, they also concluded that this pattern varied in other closely related and ecologically similar hosts due not only to host specificity, but to differences in diet. Holmes (in press) concluded that the parasite dominance hierarchy was less predictable in the marine fish Sebastes nebulosus than in the aquatic birds he studied. He attributed these differences to the diverse diet associated with this species of fish.

Since adult spot and croaker migrate over relatively long distances and feed on a variety of food items, they are ideal hosts for investigating whether marine fishes have the rich parasite faunas postulated by Kennedy et al. (1986). In addition, these hosts are closely related, feed on many of the same food items, and therefore share many parasites allowing investigation of the ways in which diversity parameters vary with area and season in closely related hosts. These characteristics of spot and croaker also make them good hosts for investigating parameters affecting the predictability of parasite communities in specific hosts.

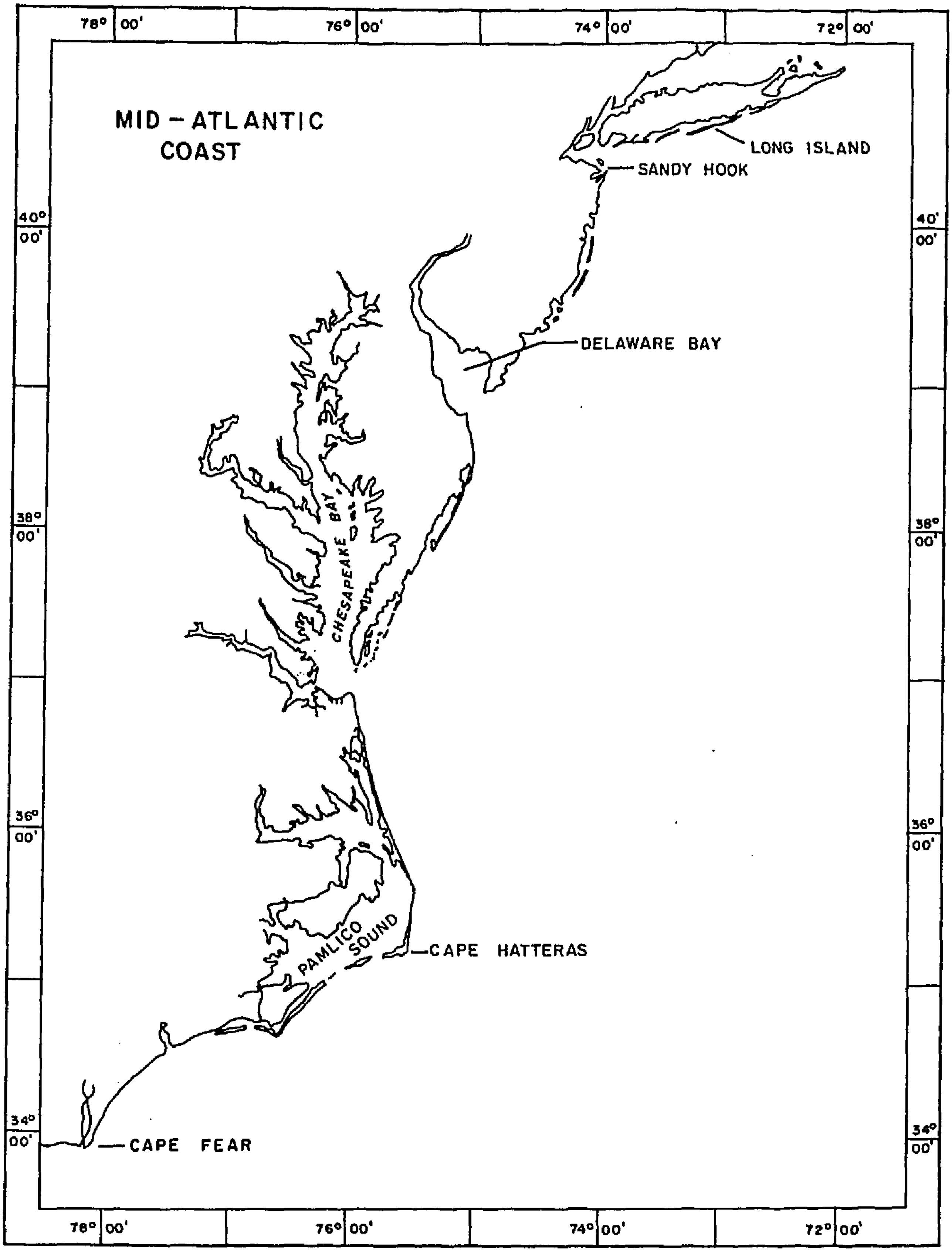
Because spot and croaker are closely related, have similar life histories, have an overlapping diet, and therefore share many parasite species, the parasite communities of these adult hosts were investigated to examine several ecological hypotheses. (1) Since Cape Hatteras is considered a "faunal break" for the Atlantic coast, the parasite communities of adult spot and croaker should be distinct in these geographic areas. (2) Since season has an effect on the abundances of many organisms (potential intermediate hosts), seasonal differences in parasite communities should be detectable. (3) The diverse diet of spot and croaker should result in parasite communities that are richer than those of freshwater fishes. (4) Diverse diets of spot and croaker should result in parasite communities that are less predictable than other vertebrates with more specific diets.

METHODS AND MATERIALS

Spot and croaker were collected with a 13 meter Yankee Trawl aboard the R/V Albatross IV during the Spring (February 27 - March 16, 1984) and Fall (September 12 - 30, 1983) Ground Fish Trawl Surveys of the National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole, Massachusetts. Forty-nine spot and 55 croaker were collected between Cape Fear ($32^{o}50'$N) and Cape Hatteras, North Carolina ($35^{o}13'$N), in the Spring (SHS); 44 spot and 47 croaker were collected between Cape Fear and Cape Hatteras in the Fall (SHF); and 48 spot and 54 croaker were collected between Cape Hatteras and Delaware Bay (39^{o}N) in the Fall (NHF) (Figure 1). Fish were not available north of Cape Hatteras in the Spring. Standard length (SL) of fishes ranged from 100- 230 mm (mean = 137 mm) for spot and 127-253 mm (mean = 174 mm) for croaker. Some fish were examined for parasites immediately after capture, a few were fixed in 10% neutral-buffered formalin, but most were frozen immediately after capture for later examination. The following sites in each host were examined for metazoan parasites: eyes, skin, muscle, gills, nares, mouth, stomach, pyloric caecae, intestine, rectum, liver, gall bladder, swim bladder, kidney, and mesentery. Preparation of parasites follow methods outlined in Chapter I. Ecological terms follow Margolis et al., 1982. Abundance refers to the mean number of parasites per individual host in a sample.

Following parasite identification, the data were subjected to several statistical analyses using SAS (1985) statistical packages. Parasite intensities (numbers of individual parasite species per host) were transformed using natural logarithms to meet criteria of Least Squares

Figure 1. Regions north and south of Cape Hatteras from which adult spot and croaker were collected.


MID-ATLANTIC COAST
LONG ISLAND
SANDY HOOK
DELAWARE BAY
CHESAPEAKE BAY
PAMLICO SOUND
CAPE HATTERAS
CAPE FEAR
78° 00'
76° 00'
74° 00'
72° 00'
40° 00'
38° 00'
36° 00'
34° 00'

Linear Regression and Chi Square Goodness of Fit Test. Least Squares Linear Regression (Sokal and Rohlf, 1969) was used to determine if parasite intensities were associated with host standard length (SL), Kendall's Tau B Correlation was used to determine if species-richness and the total number of parasites within individual hosts was associated with SL, Chi-square was used to test for overdispersion in the distribution of each parasite species (Bliss and Fisher, 1953), and Wilcoxon scores of ranked sums (Snedecor and Cochran, 1980) were used to test for differences in parasite intensities between sexes of the two hosts and intensities, prevalences, abundances, and diversity parameters within and between hosts. Principle Component Analysis was used to determine if there were patterns within and between parasite communities of spot and croaker based on their parasite distributions. Principle Component Analysis was also used to determine if there were patterns within and between diets of spot and croaker based on food found in their gastrointestinal tracts. Fager's recurrent group analysis (Fager and McGowan, 1965) was used to examine presence-absence data for regular co-occurring groups of species. Since common and rare species cannot be combined in Fager's recurrent group analysis (Holmes and Bush, 1986), criteria provided by Fager (1957) and Rottman (1978) were used to determine which parasites could be included in the analyses. Spearman's rank correlation was used to test relationships between parasite prevalence and mean intensity, to examine concordance of intensities of parasites within recurrent groups, and to determine if intensities of the common parasites were positively associated in all individuals of each host.

RESULTS

Twenty-three species of metazoan parasites were recorded from spot (Table 1) and 26 from croaker (Table 2). Individual spot harbored a mean of 6 parasitic species (S.D. = 1.9; range = 1-12) and a mean of 142 individual parasites (S.D. = 187.1; range = 3-1062). Individual croaker harbored a mean of 7 parasite species (S.D. = 2.3; range = 2- 14) and a mean of 150 individual parasites (S.D. = 444.2; range = 4- 5044). Of the 33 parasitic species found, 17 occurred in both spot and croaker. No significant differences in intensity of parasites occurred between sexes of either spot or croaker.

Although mean intensity of some parasites of spot and croaker did increase significantly with host length (Tables 3, 4, respectively), the regression coefficients were generally quite low. Only the digenean *Apocreadium manteri* and the psuedophyllidean from spot and the copepod *Clavella inversa* from croaker, had significant regression coefficients. Similar trends occurred in both fishes when parasite intensities were compared with host-length separately in the three collections. Both species-richness and the total number of parasites increased significantly with host length in spot ($r^2 = 0.19$, $P < 0.001$ and $r^2 = 0.34$, $P < 0.001$, respectively), whereas in croaker species- richness increased, but the total number of parasites did not increase with host length ($r^2 = 0.41$, $P < 0.001$ and $r^2 = 0.03$, $P > 0.05$, respectively). All parasitic species in both hosts had a significantly large variance to mean ratio indicating that individuals were overdispersed (clumped) among hosts, i.e. most of the parasites occurred in a few individual hosts.

The abundance of 13 parasitic species in spot was significantly different in the three collections (Table 5). The common digenean Diplomonorchis leiostomi from SHS (South of Cape Hatteras, North Carolina, in the Spring) and SHF (South of Cape Hatteras in the Fall) was significantly less abundant than those from NHF (North of Cape Hatteras in the Fall). The encapsulated trypanorhynch metacestodes Lacistorhynchus sp., Nybelinia sp., and the larval nematode Hysterothylacium sp. were significantly more abundant in SHF than in SHS and NHF. Abundance of the digenean Lecithaster leiostomi from SHS was not significantly different from that in SHF and NHF, but SHF had a significantly higher abundance than NHF. Abundance of the monogenean Heteraxinoides xanthophilis from SHS was not significantly different, from that in SHF and NHF, but SHS had significantly more individuals than NHF. The abundances of ten species including the common tetraphyllidean metacestode Scolex polymorphus unilocularis (this is a group name which most likely represents several species of metacestodes) were not significantly different among the three collections.

The abundance of 15 parasitic species in croaker was significantly different in the three collections (Table 6). Hysterothylacium sp. and the monogenean Macrovalvitrematoides micropogoni were all significantly more abundant in SHS than in SHF and NHF. The most common parasite, S. polymorphus unilocularis, was significantly more abundant in SHF than in SHS and NHF. Abundances of the monogenean Neopterinotrematoides avaginata were significantly different in all three collections. The abundances of

Table 1. Population parameters of parasites from Leiostomus xanthurus (n = 141).

Parasite	Prevalence	Mean Intensity	Range	Abundance	Variance	k
Digenea						
Cardicola sp.	0.7	1.0	1	<0.1	<0.1	-
Apocreadium manteri Overstreet, 1970	4.3	4.2	1-7	0.2	1.0	0.05
Diplomonorchis leiostomi Hopkins, 1941	95.0	112.9	1-1030	107.3	31812.5	0.36
Zoogonus rubellus (Olsson, 1868) Odhner, 1902	5.7	11.6	1-40	0.7	16.4	0.03
Lepocreadium setiferoides (Miller and Northup, 1926) Martin, 1938	12.8	5.3	1-29	0.7	8.5	0.06
Opecoeloides fimbriatus (Linton, 1934) Sogandares and Hutton, 1959	7.8	2.9	1-17	0.2	2.2	0.02

Table 1 (cont.)

O. vitellosus (Linton, 1900) von Wickler, 1946	62.4	4.9	1-31	3.1	27.5	0.39
Parahemiurus merus (Linton, 1910) Manter, 1940	19.9	3.8	1-11	0.7	4.5	0.13
Lecithaster leiostomi Overstreet, 1970	29.1	12.3	1-80	3.6	117.6	0.11
Aponurus pyriformis (Linton, 1910) Overstreet, 1970	27.7	2.3	1-9	0.6	2.1	0.24
Ascocotyle sp.	31.9	8.8	1-51	2.8	79.4	0.10
Monogenea						
Heteraxinoides xanthophilis (Hargis, 1956) Yamaguti, 1963	38.3	2.0	1-6	0.8	1.8	0.64
Cestoda						
Scolex polymorphus unilocularis*	89.4	13.8	1-465	12.4	1667.4	0.09
Psuedophyllidea	3.5	1.2	1-2	<0.1	<0.1	0.08

Table 1 (cont.)

Lacistorhynchus sp. (Rudolphi, 1819) Diesing, 1850	25.5	4.9	1-30	1.2	17.1	0.09
Nybelinia sp.	11.3	3.7	1-24	0.4	5.8	0.03
Nematoda						
Hysterothylacium sp.	53.9	8.5	1-70	4.6	115.6	0.19
Capillaria sp.	22.7	2.7	1-8	0.6	1.9	0.28
Acanthocephala						
Dollfusentis chandleri Golvan, 1969	22.7	1.5	1-8	0.3	0.8	0.18
Serrasentis sagittifer (Linton, 1889) Golvan, 1969	5.7	1.0	1	0.1	0.1	-
Copepoda						
Ergasilus lizae Krøyer, 1863	12.8	9.2	1-33	1.2	21.0	0.07
Paraergasilus sp.	14.2	4.5	1-33	0.6	11.0	0.03
Lernaeenicus radiatus (LeSueur, 1824) Wilson 1917	1.4	1.0	1	<0.1	<0.1	-

* Group name

Table 2. Population parameters of parasites from *Micropogonias undulatus* (n = 156).

Parasite	Prevalence	Mean Intensity	Range	Abundance	Variance	k
Digenea						
Cardicola sp.	2.6	1.5	1-3	<0.1	<0.1	1.29
Diplomonorchis leiostomi	53.2	23.8	1-529	12.6	2912.7	0.05
Lepocreadium setiferoides	10.3	20.9	1-164	21.4	22963.2	0.02
Opecoeloides fimbriatus	34.6	6.5	1-27	2.3	24.9	0.23
O. vitellosus	59.6	6.7	1-44	4.0	46.5	0.38
Lecithochirium microstomum Chandler, 1935	16.7	2.1	1-6	0.5	4.0	0.07
Aponurus pyriformis	13.5	2.1	1-12	0.3	1.3	0.09
Ascocotyle sp.	24.4	31.4	1-200	12.1	3364.1	0.04
Stephanostomum tenue (Linton, 1898) Linton, 1934	3.2	1.6	1-3	<0.1	0.1	0.05
Aspidocotylea						
Lobatostoma ringens (Linton, 1907) Eckmann, 1932	21.2	3.1	1-20	0.7	5.2	0.11

Table 2 (cont.)

Monogenea						
Macrovalvitrematoides micropogoni (Pearse, 1949) Yamaguti, 1963	64.1	4.2	1-28	2.7	16.5	0.53
Neopterinotrematoides avaginata?	66.7	6.2	1-39	4.1	46.5	0.40
Cestoda						
Scolex polymorphus unilocularis*	85.3	102.2	1-5000	87.2	194004.0	0.04
Psuedophyllidea	17.9	3.6	1-15	0.6	4.1	0.10
Lacistorhynchus sp.	67.9	19.4	1-100	13.2	39158.8	0.44
Nybelinia sp.	46.8	13.2	1-158	46.5	14429.1	0.15
Nematoda						
Hysterothylacium sp.	67.3	5.6	1-27	3.7	23.4	0.70
H. fortalezae Klein, 1973	1.9	1.3	1-2	<0.1	<0.1	-
Hysterothylacium MD Deardorff and Overstreet, 1981	1.9	1.0	1	<0.1	<0.1	-
Capillaria sp.	16.7	3.0	1-17	0.6	3.9	0.11
Spirocamallanus cricotus Fusco and Overstreet, 1978	0.6	1.0	1	<0.1	<0.1	-

Table 2 (cont.)

Acanthocephala						
Dollfusentis chandleri	23.7	2.2	1-10	0.5	2.0	0.17
Serrasentis sagittifer	12.8	2.1	1-7	0.3	0.9	0.15
Copepoda						
Paraergasilus sp.	4.5	10.6	1-29	0.5	9.1	0.03
Lernaeenicus radiatus	9.6	1.5	1-5	1.4	256.3	0.01
Clavella inversa Wilson, 1913	6.4	2.1	1-8	0.1	0.6	0.02

* Group name

Table 3. Parasite intensity regressed against standard length of *Leiostomus xanthurus*.

Parasite	Slope	ln y-intercept	Reg Coef	Significance	n
Apocreadium manteri	0.04	-5.09	0.46	ns	6
Diplomonorchis leiostomi	0.02	1.77	0.05	*	134
Zoogonus rubellus	-0.02	5.36	0.06	ns	8
Lepocreadium setiferoides	0	1.71	0.01	ns	18
Opecoeloides fimbriatus	0.01	-0.44	0.07	ns	11
O. vitellosus	0.01	-0.11	0.10	**	88
Parahemiurus merus	0.01	-0.19	0.05	ns	28
Lecisthaster leiostomi	0.02	-0.79	0.13	*	41
Aponurus pyriformis	0.01	-0.37	0.17	**	39
Ascocotyle sp.	-0.02	4.60	0.13	*	45
Heteraxinoides xanthophilis	-0.01	1.71	0.06	ns	54
Scolex polymorphus unilocularis	0	2.05	0	ns	126
Psuedophyllidea	0.01	-0.29	0.95	**	5
Lacistorhynchus sp.	0.01	-0.67	0.08	ns	36
Nybelinia sp.	0.02	-0.99	0.10	ns	16

Table 3 (cont.)

Hysterothylacium sp.	0.03	-2.68	0.27	***	76
Capillaria sp.	0	1.19	0	ns	32
Dollfusentis chandleri	0.01	0.10	0.11	ns	32
Serrasentis sagittifer	0	0.69	0	ns	8
Ergasilus lizae	-0.02	4.02	0.11	ns	18
Paraergasilus sp.	-0.01	2.07	0.02	ns	20

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

Table 4. Parasite intensity regressed against standard length of _Micropogonias_ _undulatus._

Parasite	Slope	ln y-intercept	Reg Coef	Significance	n
Cardicola sp.	0.01	-0.27	0.22	ns	4
Diplomonorchis _leiostomi_	0	2.52	0	ns	83
Lepocreadium _setiferoides_	0.02	-1.28	0.17	ns	16
Opecoeloides _fimbriatus_	0	1.11	0.01	ns	54
_O._ _vitellosus_	0.01	0.33	0.05	*	93
Lecithochirium _microstomum_	0	0.32	0.09	ns	26
Aponurus _pyriformis_	0.01	-0.65	0.14	ns	21
Ascocotyle sp.	0.01	-0.06	0.02	ns	38
Stephanostomum _tenue_	-0.01	1.96	0.06	ns	5
Lobatostoma _ringens_	0	1.72	0.03	ns	33
Macrovalvitrematoides _micropogoni_	0.01	0.40	0.04	*	100
Neopterinotrematoides _avaginata_	0.01	0.32	0.06	*	104
Scolex _polymorphus_ _unilocularis_	0.01	0.49	0.05	*	133
Psuedophyllidea	0.01	0.46	0.04	ns	28
Lacistorhynchus sp.	0.02	-0.69	0.12	***	106

Table 4 (cont.)

Nybelinia sp.	0.01	-0.17	0.06	*	73
Hysterothylacium sp.	0	1.47	0	ns	105
Capillaria sp.	0	0.38	0.04	ns	26
Dollfusentis chandleri	0	1.36	0.14	ns	37
Serrasentis sagittifer	0	1.09	0	ns	20
Paraergasilus sp.	0.01	0.09	0.15	ns	7
Clavella inversa	0.02	-1.88	0.28	ns	10
Lernaeenicus radiatus	0	0.05	0.20	ns	15

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

Table 5. Mean abundance of parasites from *Leiostomus xanthurus* in each area followed by range in parentheses and then frequency (values with same letter are not significantly different).

Parasite	Spring South of Cape Hatteras	Fall South of Cape Hatteras	Fall North of Cape Hatteras	Significance
Cardicola sp.	0 A	0 A	<0.1 (0-1) 1 A	ns
Apocreadium manteri	0 A	0.1 (6) 1 A	0.4 (0-7) 5 B	*
Diplomonorchis leiostomi	31.1 (0-104) 15 A	49.5 (0-305) 38 A	238.1 (5-1030) 48 B	***
Zoogonus rubellus	0 A	0 A	1.9 (0-40) 8 B	***
Lepocreadium setiferoides	0.6 (0-7) 8 A	0.1 (0-2) 2 A	1.3 (0-29) 8 A	ns
Opecoeloides fimbriatus	<0.1 (0-1) 2 A	0.5 (0-17) 14 A	0.2 (0-4) 5 A	ns
O. vitellosus	1.7 (0-13) 28 A	4.1 (0-27) 30 A	3.6 (0-31) 30 B	ns
Parahemiurus merus	0.1 (0-1) 3 A	0.1 (0-1) 5 A	2.0 (0-11) 20 B	***
Lecisthaster leiostomi	2.5 (0-24) 19 AB	7.3 (0-80) 14 B	1.2 (0-28) 8 A	*
Aponurus pyriformis	0.4 (0-3) 15 A	1.5 (0-9) 20 B	0.1 (0-2) 4 A	***
Ascocotyle sp.	5.2 (0-51) 23 A	1.2 (0-44) 5 B	1.8 (0-37) 17 B	***
Heteraxinoides xanthophilis	1.2 (0-6) 20 B	0.7 (0-3) 22 AB	0.4 (0-3) 12 A	*
Scolex polymorphus	12.2 (0-116) 45 A	15.9 (0-465) 39 A	9.2 (0-69) 42 A	ns
Psuedophyllidea	0.1 (0-1) 4 A	<0.1 (0-2) 1 A	0 A	ns

Table 5 (cont.)

Lacistorhynchus sp.	0.3 (0-4) 10 A	2.9 (0-30) 21 B	0.7 (0-25) 5 A	***
Nybelinia sp.	0.1 (0-1) 3 A	1.2 (0-24) 10 B	0.1 (0-1) 3 A	**
Hysterothylacium sp.	1.7 (0-7) 21 A	10.4 (0-51) 42 B	2.2 (0-70) 30 A	***
Capillaria sp.	0.2 (0-5) 3 A	0.3 (0-8) 5 A	1.4 (0-5) 24 B	***
Dollfusentis chandleri	0.4 (0-8) 11 A	0.3 (0-4) 10 A	0.3 (0-3) 11 A	ns
Serrasentis sagittifer	0.1 (0-1) 3 A	0.1 (0-1) 4 A	<0.1 (0-1) 1 A	ns
Ergasilus lizae	2.8 (0-33) 14 A	0.1 (0-2) 2 B	0.5 (0-21) 2 B	***
Paraergasilus sp.	0.8 (0-20) 8 A	1.1 (0-33) 9 A	0.1 (0-1) 3 A	ns
Lernaeenicus radiatus	0 A	<0.1 (0-1) 1 A	<0.1 (0-1) 1 A	ns

* = $P < 0.05$.

** = $P < 0.01$.

*** = $P < 0.001$.

Table 6. Mean abundance of parasites from Micropogonias undulatus in each area followed by range in parentheses and then frequency (values with same letter are not significantly different).

Parasite	Spring South of Cape Hatteras	Fall South of Cape Hatteras	Fall North of Cape Hatteras	Significance
Cardicola sp.	<0.1 (0-1) 2 A	0.1 (0-3) 2 A	0 A	ns
Diplomonorchis leiostomi	5.4 (0-96) 38 A	28.2 (0-529) 25 A	5.9 (0-60) 20 B	ns
Lepocreadium setiferoides	0 A	0.1 (0-2) 4 A	6.1 (0-164) 12 B	***
Opecoeloides fimbriatus	1.2 (0-14) 17 A	5.2 (0-27) 25 B	0.8 (0-13) 12 A	***
O. vitellosus	3.3 (0-18) 38 A	4.1 (0-44) 22 A	4.6 (0-34) 33 A	ns
Lecithochirium microstomum	0.2 (0-3) 7 A	0.9 (0-6) 7 A	0.6 (0-6) 12 A	ns
Aponurus pyriformis	0.7 (0-12) 17 A	<0.1 (0-1) 2 B	0.1 (0-3) 2 B	***
Ascocotyle sp.	10.4 (0-200) 19 A	6.0(0-200) 7 A	6.3 (0-200) 12 A	ns
Stephanostomum tenue	<0.1 (0-1) 1 A	0 A	0.1 (0-3) 4 A	ns
Lobatostoma ringens	0.4 (0-7) 7 A	1.3 (0-20) 17 B	0.4 (0-6) 9 A	*
Macrovalvitrematoides micropogoni	4.5 (0-28) 46 A	1.3 (0-7) 28 B	2.0 (0-20) 26 B	***
Neopterinotrematoides avaginata	8.6 (0-39) 51 A	2.2 (0-25) 32 B	1.3 (0-19) 21 C	***
Scolex polymorphus	162.8 (0-5000) 55 A	8.7 (0-60) 32 B	78.5 (0-1850) 46 A	***
Psuedophyllidea	1.8 (0-15) 25 A	<0.1 (0-1) 1 B	<0.1 (0-1) 2 B	***

Table 6 (cont.)

Lacistorhynchus sp.	13.3 (0-91) 44 A	12.8 (0-89) 29 A	11.4 (0-100) 33 A	ns
Nybelinia sp.	1.8 (0-15) 27 A	2.0 (0-30) 17 A	9.8 (0-158) 29 B	*
Hysterothylacium sp.	6.3 (0-27) 51 A	2.8 (0-24) 26 B	1.9 (0-19) 28 B	***
H. foraltazae	0 A	0.1 (0-2) 3 B	0 A	*
Hysterothylacium MD	<0.1 (0-1) 2 A	0 A	<0.1 (0-1) 1 A	ns
Capillaria sp.	0 A	0.2 (0-1) 2 A	1.4 (0-17) 21 B	***
Spirocamallanus cricotus	0 A	<0.1 (0-1) 1 A	0 A	ns
Dollfusentis chandleri	<0.1 (0-1) 2 A	0.9 (0-10) 15 B	0.7 (0-9) 20 B	***
Serrasentis sagittifer	<0.1 (0-7) 9 A	0.1 (0-2) 6 A	0.1 (0-4) 5 A	ns
Paraergasilus sp.	0 A	1.4 (0-29) 6 B	0.1 (7-7) 1 A	**
Lernaeenicus radiatus	0.2 (0-2) 9 A	<0.1 (0-1) 1 A	0.2 (0-5) 5 A	ns
Clavella inversa	0.4 (0-8) 9 A	<0.1 (0-1) 1 B	0 B	***

* = $P < 0.05$.

** = $P < 0.01$.

*** = $P < 0.001$.

11 species including the common digeneans D. leiostomi and Ascocotyle sp. were not significantly different among the three collections.

Prevalence and intensity of parasites were also compared between spot and croaker (Tables 1 and 2). Both prevalence and intensity of D. leiostomi were significantly higher in spot than croaker. The prevalence and intensity of the digenean Opecoeloides fimbriatus, Lacistorhynchus sp., and Nybelinia sp. were significantly higher in croaker than spot. The digenean Aponurus pyriformis had similar intensities in both hosts, but a significantly higher prevalence in spot. The psuedophyllidean plerocercoid, the encysted acanthocephalan Serrasentis sagittifer, and the copepod Lernaeenicus radiatus had similar intensities in both hosts, but significantly higher prevalence in croaker. Scolex polymorphus unilocularis and the encysted metacercaria of Ascocotyle sp. had similar prevalences in both hosts, but they had significantly higher intensities in croaker. The copepod Paraergasilus sp. had a significantly higher prevalence in spot than croaker and a significantly higher intensity in croaker than spot. There was not a significant difference in intensity or prevalence between hosts for the digeneans Lepocreadium setiferoides and Cardicola sp., the nematode Capillaria sp., and the acanthocephalan Dollfusentis chandleri.

Results of principle component analysis (PCA) revealed that the first three principle components accounted for 48.3% of the variance in parasite distributions of spot (Figure 2). Principle component I accounted for 23.6% of the variance. Four parasites, A. pyriformis, Lacistorhynchus sp., Nybelinia sp., and Hysterothylacium sp., contributed the most to the loadings on this principle component and were most abundant SHF. Principle component II accounted for 13.1% of the variance. Two parasites, D. leiostomi and P. merus, contributed the most to the loadings on this principle component and were most abundant NHF. Ergasilus lizae had a negative loading for this principle component and was least abundant NHF. Principle component III accounted for 11.7% of the variance. Two parasites, L. leiostomi and Ascocotyle sp., contributed most to the loadings of this principle component. Ascocotyle sp. was abundant SHS and L. leiostomi was most abundant SHS and SHF. Spot from all three collections overlapped to some extent, but most spot from each collection formed distinct clusters. The parasites of spot from SHS and NHF were the most similar both within and between collections, whereas spot from SHF were aggregated loosely and associated with principle component I (Figure 2).

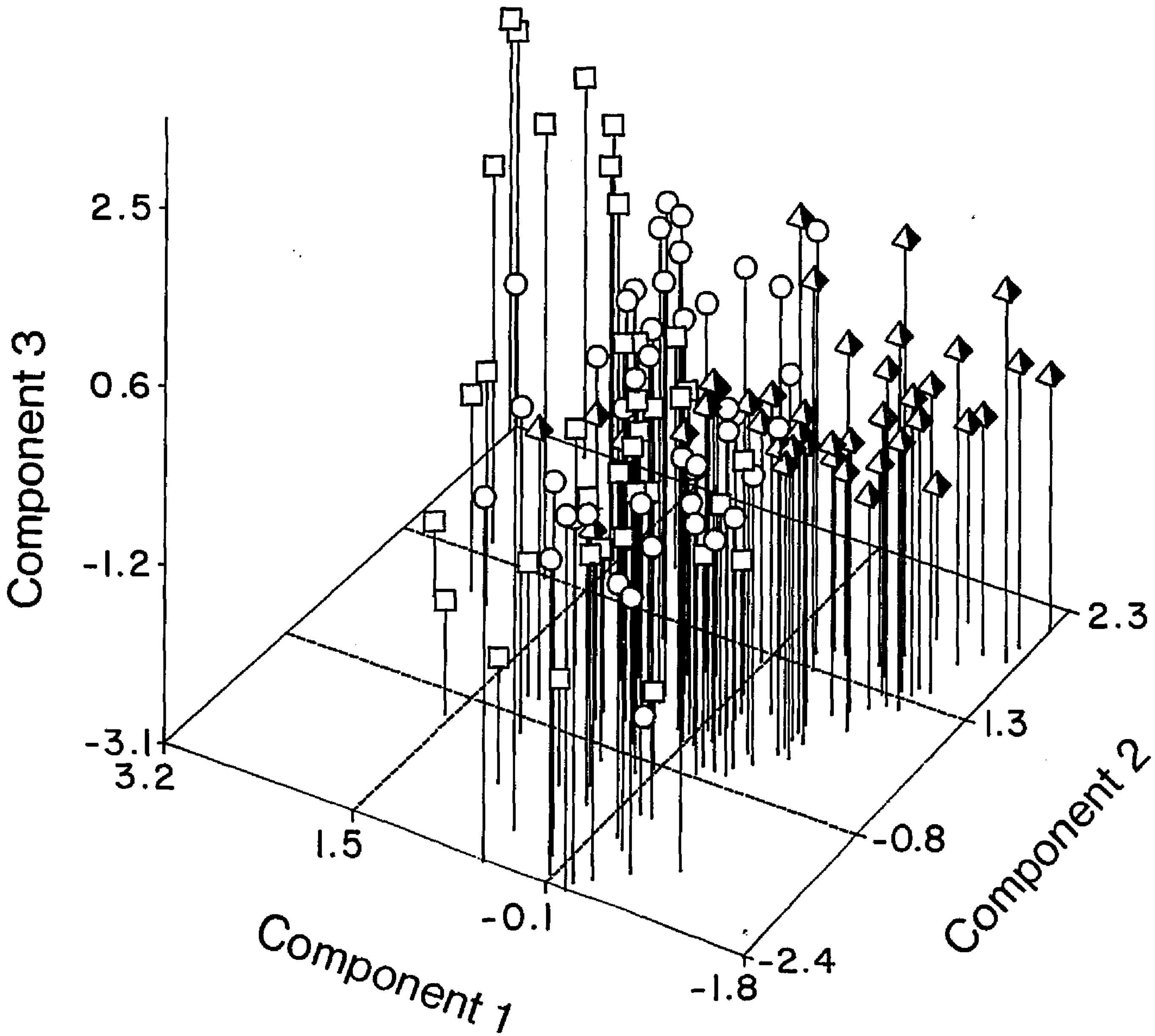
Results of PCA revealed that the first three principle components accounted for 41.5% of the variance in parasite distributions of croaker (Figure 3). Principle component I accounted for 19.6% of the variance. Six parasites, A. pyriformis, M. micropogoni, N. avaginata, S. polymorphus unilocularis, the psuedophyllidean metacestode, and Hysterothylacium sp., contributed the most to the loadings on this principle component and were most abundant SHS. Principle component II accounted for 12.0% of the variance. Two parasites, D. leiostomi and Paraergasilus sp., contributed the most to the loadings on this principle component. These parasites were most abundant SHF. Nybelinia sp. had a negative loading for this principle component and was most abundant NHF. Principle component III accounted for 9.8% of the variance. Capillaria sp. contributed the most to the loadings on this principle component and was most abundant NHF. Parasite infracommunities of croaker collected from SHS and NHF were less variable than those collected SHF. Croaker parasite distributions from

SHF and NHF overlapped greatly and croaker from SHS were for the most part separate from other collections.

Principle component analysis was also used to examine possible patterns of parasite distributions between spot and croaker (Figure 4). The first three components accounted for only 30.2% of the variance. Principle component I accounted for 14.6% of the variance. Four parasites, Lacistorhynchus sp., Nybelinia sp., Hysterothylacium sp., and the psuedophyllidean metacestode, contributed the most to the loadings of the principle component. They were all more abundant in croaker than spot. Diplomonorchis leiostomi had a negative loading for this component and was much more abundant in spot than croaker. Principle component II accounted for 8.5% of the variance. Two parasites, D. leiostomi and Paraergasilus sp., contributed the most to the loadings of this principle component. Principle component III accounted for 7.6% of the variance. Two monogeneans of croaker, M. micropogoni and N. avaginata, contributed the most to the loadings of this principle component. Spot and croaker were grouped tightly in two separate areas of Figure 4.

A similar analysis was executed using only the 10 parasites that occurred in at least 20 individual spot and also in 20 individual croaker to determine if distributions of shared parasitic species were different between hosts (Figure 5). In this case the first three principle components accounted for 46.3% of the variance. Principle component I accounted for most (44.7%) of the variance associated with the first three components. Four parasites, O. fimbriatus, Lacistorhynchus sp., Nybelinia sp., and Hysterothylacium sp., contributed the most to the

Figure 2. Distributions of communities of parasites of spot along the first three principle components (circle, south of Cape Hatteras in the spring; square, south of Cape Hatteras in the fall; pyramid, north of Cape Hatteras in the fall).



Component 3
2.5
0.6
-1.2
-3.1
3.2
1.5
-0.1
-1.8
Component 1
-2.4
-0.8
1.3
2.3
Component 2

Figure 3. Distributions of communities of parasites of croaker along the first three principle components (circle, south of Cape Hatteras in the spring; square, south of Cape Hatteras in the fall; pyramid, north of Cape Hatteras in the fall).

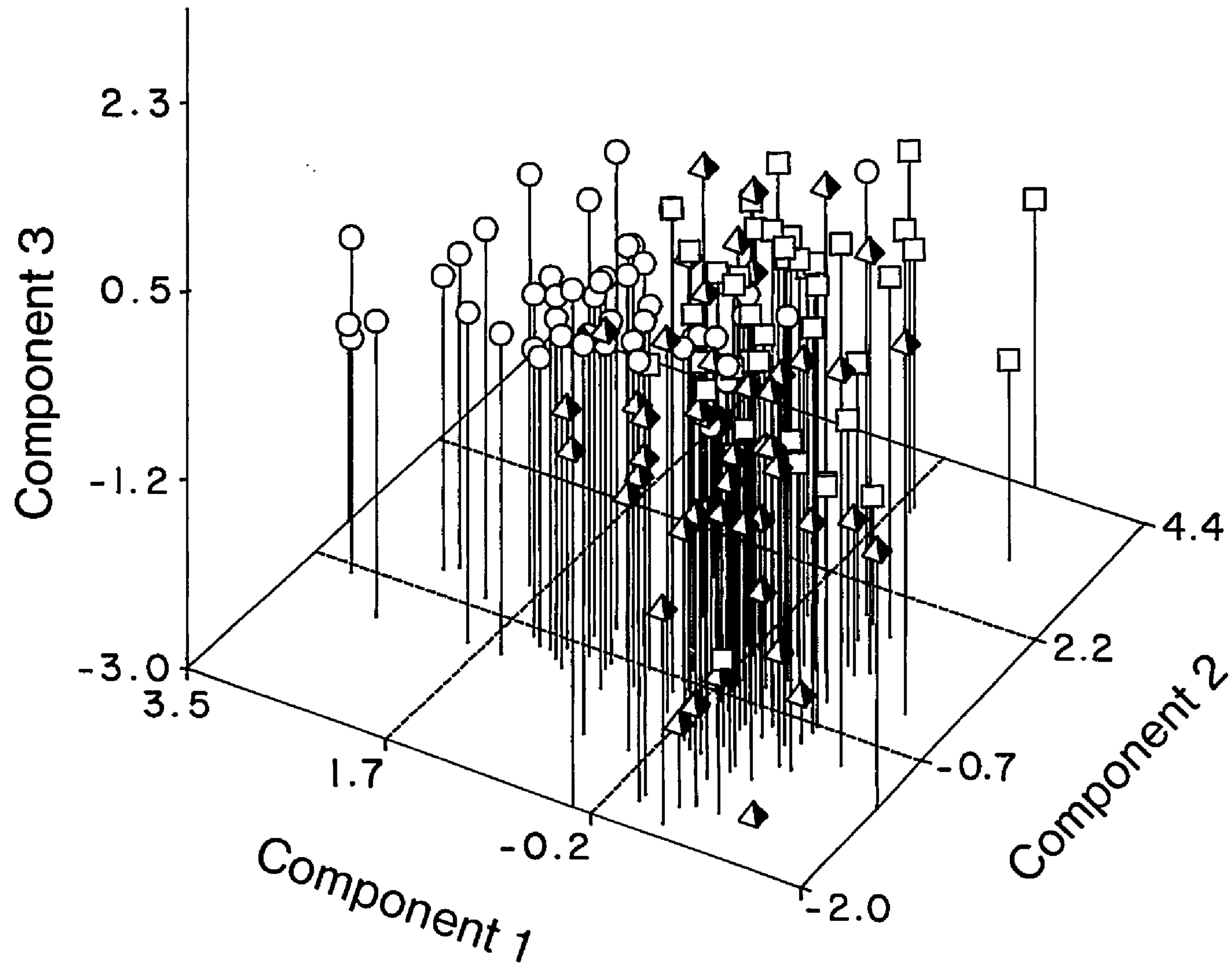

Component 3
2.3
0.5
-1.2
-3.0
3.5
1.7
-0.2
-2.0
Component 1
-0.7
2.2
4.4
Component 2

Figure 4. Distributions of communities of parasites of spot and croaker along the first three principle components (circle, croaker; pyramid, spot).

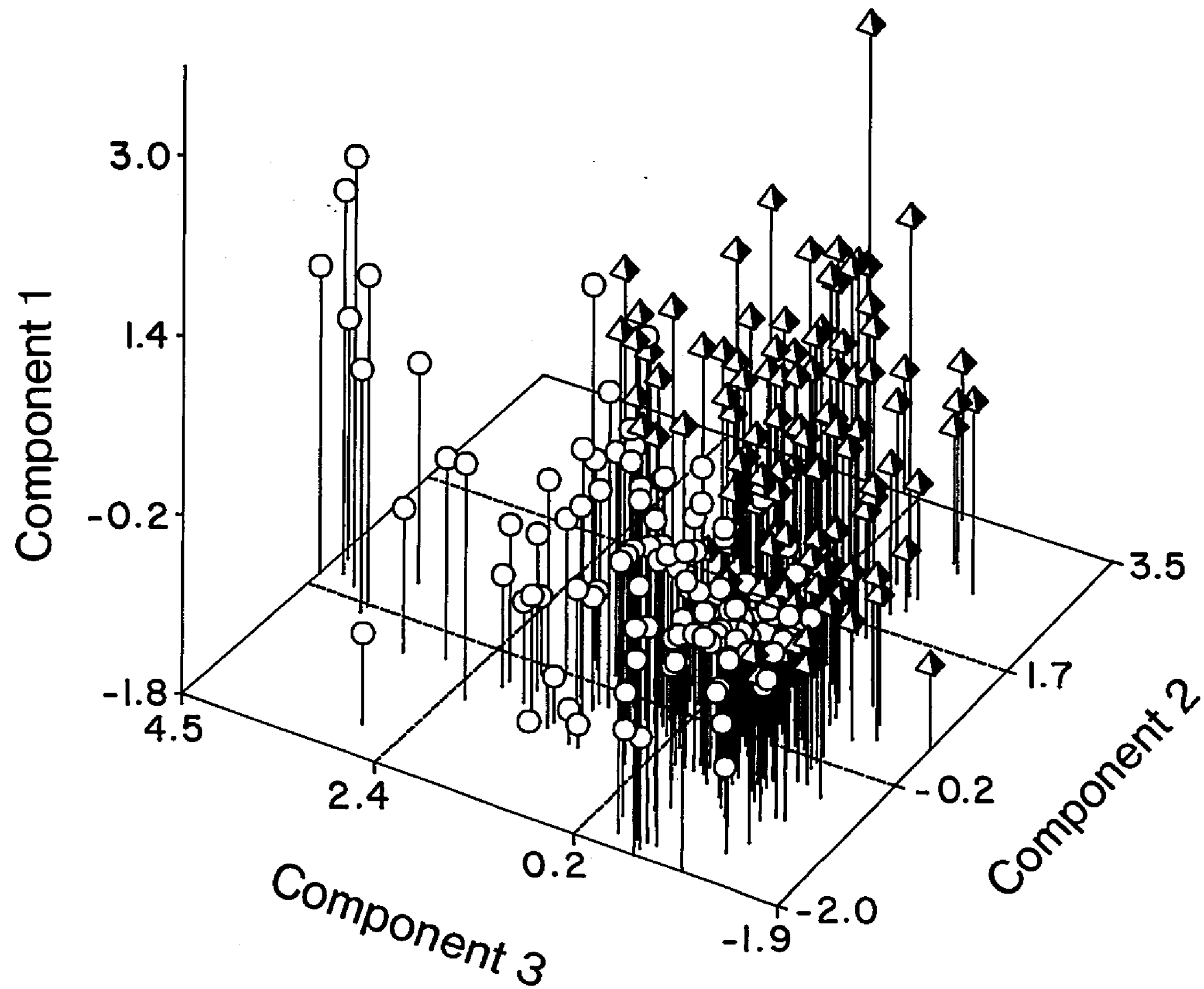

Component 1
3.0
1.4
-0.2
-1.8
4.5
2.4
0.2
-1.9
Component 3
3.5
1.7
-0.2
-2.0
Component 2

Figure 5. Distributions of communities of parasites of spot and croaker, excluding those parasitic species that did not occur in both hosts, along the first three principle components (circle, croaker; pyramid, spot).

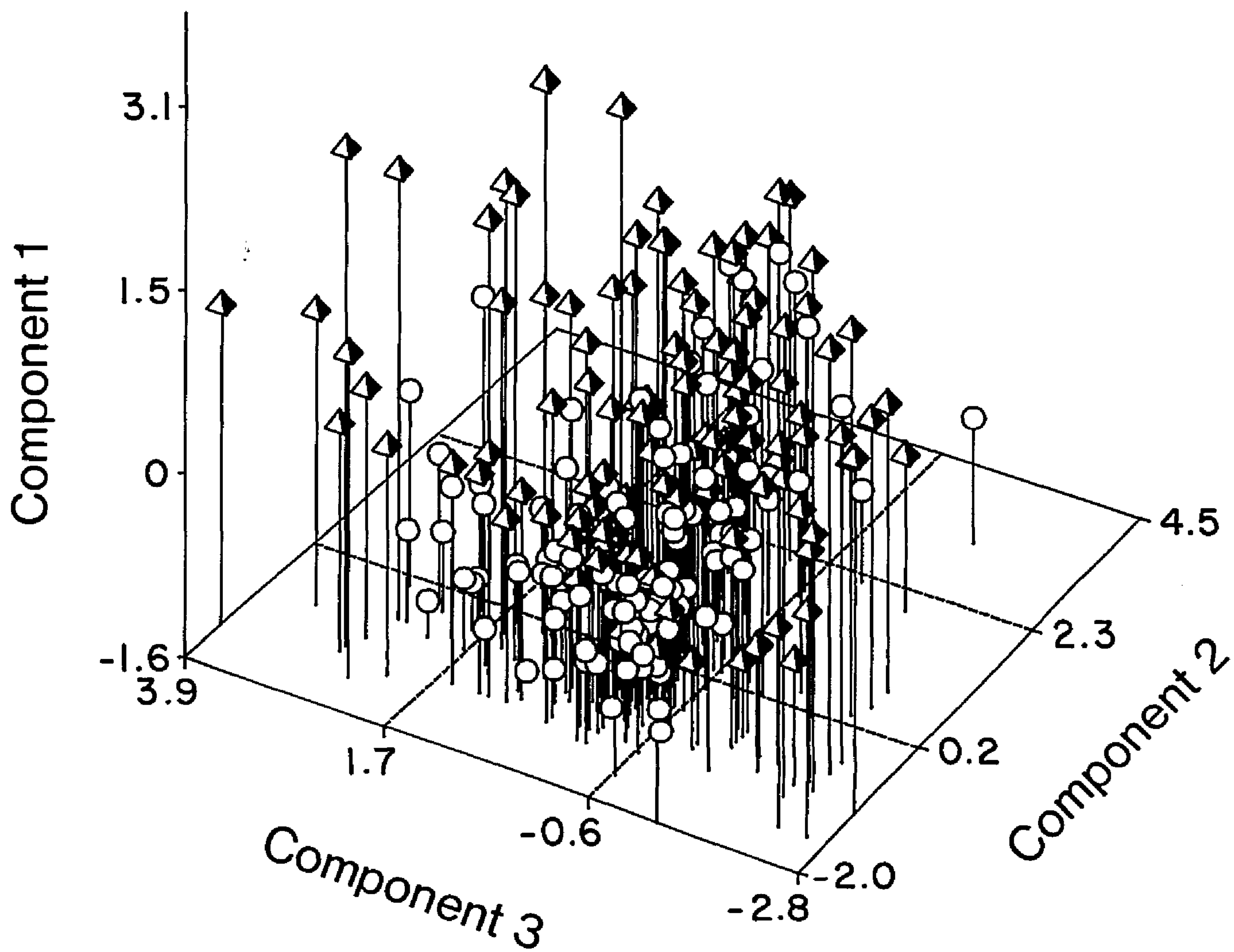
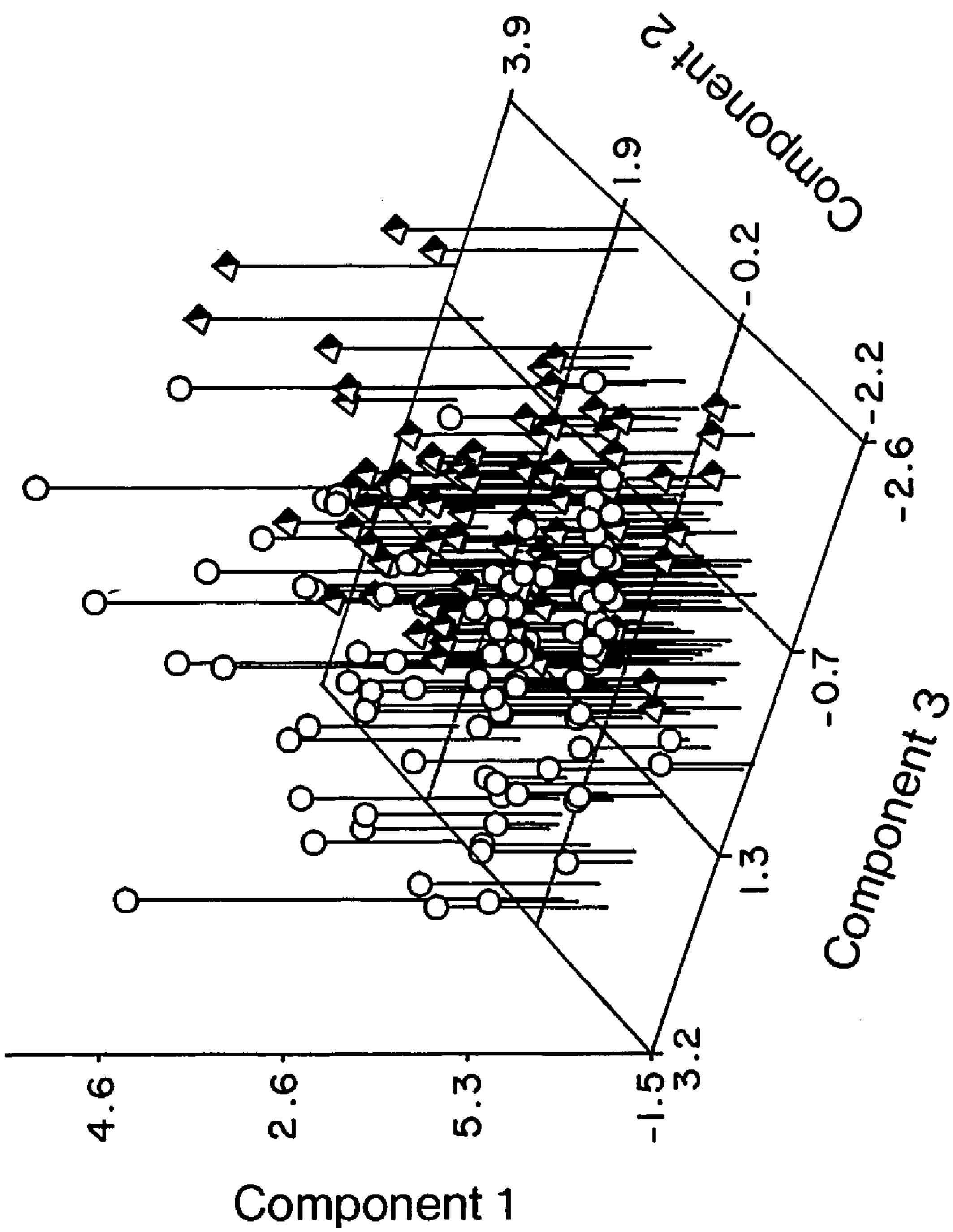

Component 1
3.1
1.5
0
-1.6
3.9
1.7
-0.6
-2.8
Component 3
-2.0
0.2
2.3
4.5
Component 2

Figure 6. Distributions of prey items of spot and croaker along the first three principle components (circle, croaker; pyramid, spot).


Component 1
4.6
2.6
5.3
-1.5
3.2
Component 2
3.9
1.9
-0.2
-2.2
Component 3
-2.6
-0.7
1.3

loadings of this principle component. Individual spot and croaker overlapped much more than when all parasites were included, but a host specific pattern still existed.

Principle component analysis was used to examine possible patterns of prey item distribution between spot and croaker (Figure 6). Principle component I accounted for 11.8% of the variance. Principle component II accounted for 7.3% of the variance. Principle component III accounted for 7.1% of the variance. Although some overlap occurred in the diets of spot and croaker, there diets appeared to be quite distinct (Figure 6) (Table 7). Spot tended to feed more on infaunal prey such as copepods, clams, nematodes and foraminiferans, which were associated with principle component I, whereas croaker fed on more epibenthic mobile prey such as crabs and shrimp, which were associated with principle component II. Prey items that were fed upon by both hosts in similar numbers such as gammarideans and polychaetes were associated with principle component III.

When diversity parameters were calculated for all individual fish using all parasitic species (Table 8) croaker had significantly higher species-richness, species diversity and species evenness of parasitic species than spot. The difference in the number of parasites in the two fishes was not significant. When diversity parameters of spot were compared in the three collections, no significant difference appeared in the numbers of parasites, species diversity, and species evenness. Species-richness was significantly higher in SHF. In croaker numbers of parasites, diversity, and richness were all significantly higher in SHS, whereas evenness was significantly lower. No difference occurred in species-richness in the three collections.

Diversity parameters were also calculated only for the gastrointestinal helminths of spot and croaker (Table 9) for comparison with the parasitic faunas of other host taxa represented in the literature. Spot had significantly higher species-richness and numbers of gut helminths than croaker. Diversity and evenness were not significantly different in the two fish species.

A significant correlation (Spearman rank correlation $r = 0.58$, $P < 0.001$) occurred between prevalence and mean intensity of parasites from spot; parasites with the highest intensities were also the most prevalent. When frequency of occurrence was compared with the number of parasitic species (Figure 7), three groups of parasites were identified. The two most abundant species (D. leiostomi and Scolex polymorphus unilocularis) represent "core" species and accounted for 84.4% of all individual parasites. The 12 uncommon species represent "satellite" species and accounted for 2.9% of all individual parasites. The 9 other species accounted for 12.7% of all individual parasites and are considered "secondary" species following terminology of Bush and Holmes (1986). When frequency of occurrence was compared among collections (Table 5) the parasite dominance hierarchy varied to some extent. In SHS, most of the species followed the same trends as when all spot were grouped, except that Capillaria sp. was a "satellite" species and the copepod Ergasilus lizae was a "secondary" species. In SHF Hysterothylacium sp. was a "core" species, Capillaria sp. and Ascocotyle sp. were "satellite" species, and Nybelinia sp. and O. fimbriatus were "secondary" species. In NHF A. pyriformis and Lacistorhynchus sp. were "satellite" species, the digenean

Table 7. Percent occurrence of prey in the gastrointestinal tract of adult spot and croaker.

Prey	Spot	Croaker
n=	137	136
Foraminifera	11.8	0
Ectoprocta	1.5	0
Cladocera	13.9	0.7
Cumacea	15.4	0
Cirripedia	0.7	2.1
Copepoda	69.1	5.8
Caprellidea	0	1.5
Gammaridea	43.4	40.1
Isopoda	1.5	5.1
Mysidacea	22.8	20.4
Decapoda (shrimp)	18.4	38.0
Decapoda (crabs)	3.6	34.3
Kinorhyncha	3.6	0
Nematoda	22.8	2.9
Pelecypoda	74.3	29.2
Gastropoda	13.9	5.1
Cephalopoda	0	2.1
Polychaeta	47.8	48.2
Sipuncula	5.1	0
Echinoidea	22.8	15.3
Ophiuroidea	2.2	11.7
Teleostei	2.9	20.4

Table 8. Summary of *Leiostomus xanthurus* and *Micropogonias undulatus* metazoan parasite diversity parameters (SHS, south of Cape Hatteras in the spring; SHF, south of Cape Hatteras in the fall; NHF, north of Cape Hatteras in the fall).

Host		Area	No. parasite species (S)	No. of parasites	Shannon-Wiener Index (H)	Evenness (E)	% samples with 0 or 1 parasite species
Leiostomus	Mean	All	6.0	142.1	1.40	0.56	1
xanthurus	SD		1.9	187.1	0.69	0.25	
	Range		1-12	3-1062	0-2.88	0.06-1.00	
		SHS	5.9	61.6	1.64	0.65	0
			1.6	33.9	0.58	0.18	
			3-10	15-174	0.53-2.88	0.27-0.90	
		SHF	6.5	97.4	1.71	0.66	0
			2.3	120.9	0.58	0.21	
			3-12	3-627	0.37-2.58	0.16-1.00	
		NHF	5.7	265.3	0.89	0.36	2
			1.8	256.2	0.63	0.23	
			1-10	16-1062	0-2.7	0.06-0.94	

Table 8 (cont.)

<u>Micropogonias</u>	All	7.3	149.9	1.80	0.65	3
<u>undulatus</u>		2.3	444.2	0.63	0.20	
		2-14	4-5044	0.10-3.22	0.03-0.95	
	SHS	8.7	221.8	1.89	0.62	4
		2.1	670.0	0.66	0.22	
		4-14	11-5044	0.10-2.89	0.03-0.91	
	SHF	6.6	78.7	1.78	0.68	2
		2.0	97.9	0.61	0.20	
		2-12	4-559	0.37-2.65	0.14-0.95	
	NHF	6.6	138.8	1.71	0.66	4
		2.3	318.5	0.62	0.20	
		2-14	7-1932	0.25-3.22	0.08-0.93	

Table 9. Summary of all Leiostomus xanthurus and Micropogonias undulatus gastrointestinal helminth diversity parameters.

Host		No. helminth species (S)	No. of helminths	Shannon-Wiener Index (H)	Evenness (E)	% samples with 0 or 1 parasite species
Leiostomus	Mean	4.2	130.8	1.07	0.55	2
xanthurus	SD	1.4	188.5	0.60	0.28	
	Range	1-9	2-1038	0-2.49	0.03-1.00	
Micropogonias		3.7	111.5	1.07	0.60	3
undulatus		1.31	441.7	0.58	0.27	
		1-8	1-5015	0-2.66	0.01-1.00	

Parahemiurus merus was a "secondary" species and H. xanthophilis and L. leiostomi had reduced numbers, but the two were considered "secondary" species. In general, the dominant species were dominant in all three collections with most changes occurring in the less common species.

Mean intensity and prevalence of parasites from croaker were also significantly correlated ($r = 0.76$, $P < 0.001$). When frequency of occurrence was compared with the number of parasites species (Figure 8), three groups of parasites were identified. The most abundant species, S. polymorphus unilocularis, represented the only "core" species and accounted for 58.2% of all individual parasites. The 19 uncommon species were "satellite" species accounting for 14.9% of all individual parasites. The 6 other species accounted for 26.9% of all individual parasites. When frequency of occurrence was compared among collections (Table 6) the parasite dominance hierarchy changed to some extent. In SHS several species including Hysterothylacium sp., Lacistorhynchus sp., N. avaginata, M. micropogoni, S. polymorphus unilocularis were "core" species and the psuedophyllidean metacestode and Nybelinia sp. were "secondary" species. In SHF S. polymorphus unilocularis was less prevalent so that along with S. polymorphus unilocularis several species including O. vitellosus, O. fimbriatus, D. leiostomi, N. avaginata, M. micropogoni, and Hysterothylacium sp. were the dominant species, but since their prevalence was not as great as "core" species in other collections they should probably be considered "secondary" species. In NHF D. chandleri, Capillaria sp., and Nybelinia sp. were "secondary" species. Though many species had a higher prevalence in certain collections the overall hierarchy of dominance did not vary greatly among collections.

Figure 7. Frequencies of parasites in 141 spot (AD, Apocreadium manteri; AP, Aponurus pyriformis; AS, Ascocotyle sp.; CP, Capillaria sp.; CS, Cardicola sp.; DC, Dollfusentis chandleri; DL, Diplomonorchis leiostomi, EL, Ergasilus lizae; HS, Hysterothylacium sp.; HX, Heteraxinoides xanthophilis; LC, Lacistorhynchus sp.; LL, Lecithaster leiostomi; LS, Lepocreadium setiferoides; LX, Lernaeenicus radiatus; NS, Nybelinia sp.; OF, Opecoeloides fimbriatus; OV, O. vitellosus; PL, psuedophyllidean metacestode; PM, Parahemiurus merus; PN, Paraergasilus sp.; SP, Scolex polymorphus unilocularis; SS, Serrasentis sagittifer; ZR, Zoogonus rubellus).

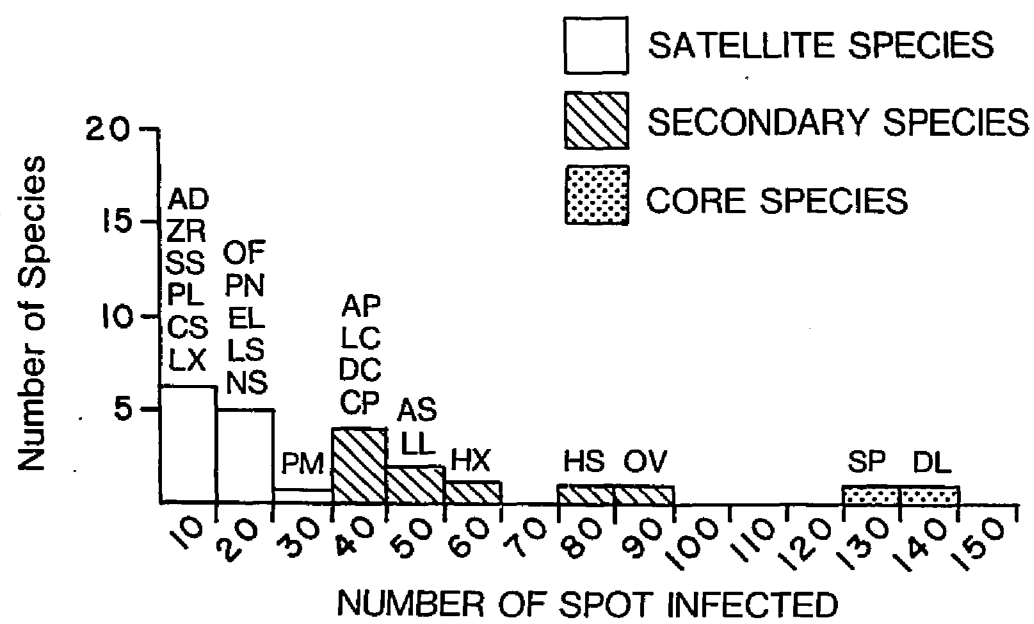
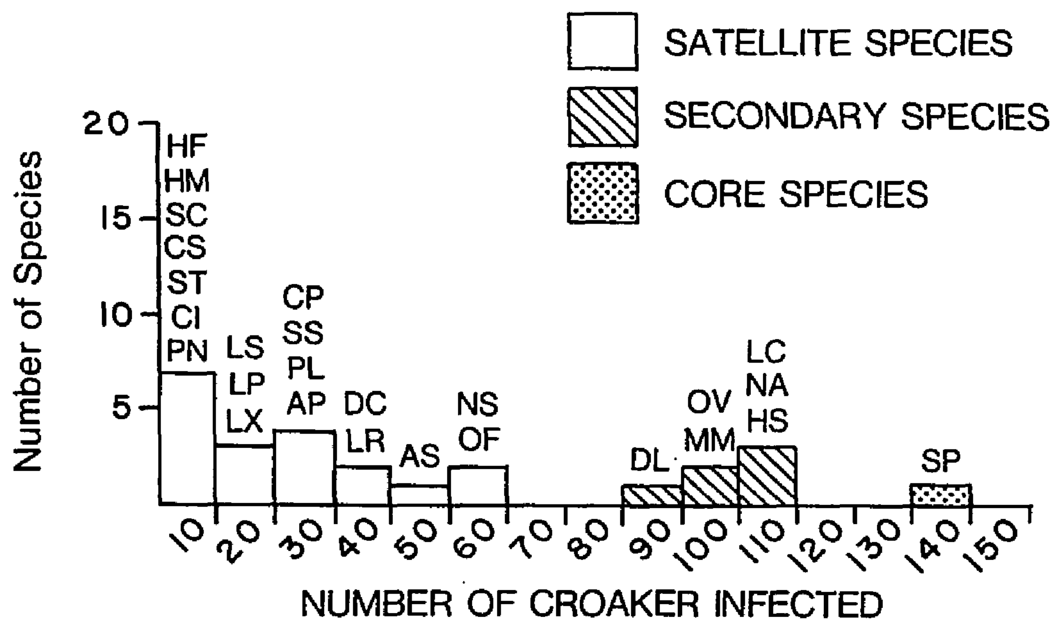

SATELLITE SPECIES
SECONDARY SPECIES
CORE SPECIES
Number of Species
20
15
10
5
AD
ZR
SS
PL
CS
LX
OF
PN
EL
LS
NS
PM
AP
LC
DC
CP
AS
LL
HX
HS OV
SP DL
10 20 30 40 50 60 70 80 90 100 110 120 130 140 150
NUMBER OF SPOT INFECTED

Figure 8. Frequencies of parasites in 156 croaker (AP, *Aponurus pyriformis*; AS, *Ascocotyle* sp.; CI, *Clavella inversa*; CP, *Capillaria* sp.; CS, *Cardicola* sp.; DC, *Dollfusentis chandleri*; DL, *Diplomonorchis leiostomi*, HF, *Hysterothylacium fortalezae*; HM, *Hysterothylacium* MD; HS, *Hysterothylacium* sp.; LC, *Lacistorhynchus* sp.; LP, *Lecithochirium microstomum*; LR, *Lobatostoma ringens*; LS, *Lepocreadium setiferoides*; LX, *Lernaeenicus radiatus*; MM, *Macrovalvitrematoides micropogoni*; NA, *Neopterinotrematoides avaginata*; NS, *Nybelinia* sp.; OF, *Opecoeloides fimbriatus*; OV, *O. vitellosus*; PL, psuedophyllidean metacestode; PN, *Paraergasilus* sp.; SC, *Spirocamallanus cricotus*; SP, *Scolex polymorphus unilocularis*; SS, *Serrasentis sagittifer*; ST, *Stephanostomum tenue*).


SATELLITE SPECIES
SECONDARY SPECIES
CORE SPECIES
Number of Species
20
15
10
5
HF
HM
SC
CS
ST
CI
PN
LS
LP
LX
CP
SS
PL
AP
DC
LR
AS
NS
OF
DL
OV
MM
LC
NA
HS
SP
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
NUMBER OF CROAKER INFECTED

Only the six most common parasites of spot (Table 10) and the eight most common parasites of croaker (Table 11) were examined using Fager's recurrent group analysis. The two "core" and one "secondary" parasitic species of spot were included in the recurrent group. The single "core" species and four "secondary" parasitic species of croaker were included in the recurrent group.

Relative intensities of the parasitic species within the recurrent group were tested to determine if they were concordant. Only hosts which harbored all species within the recurrent group were included in the analysis. Thirty-nine spot met this criteria and 22 of those were collected from SHF. Of the 741 comparisons among spot, 584 had a positive relationship and only 85 were significant. Fifty-four percent had a correlation coefficient (r) greater than 0.7. Only 10 relationships (6%) were significant negative associations. Twenty-seven croaker harbored all species in the recurrent group and 22 of those were collected from SHF. Of the 351 comparisons among croaker 230 showed a positive relationship and 46 were significant. Thirty-seven percent had a correlation coefficient (r) greater than 0.7. Only four relationships (3%) were significantly negative associations.

Table 10. Fager's Recurrent Group Analysis of the common parasites in *Leiostomus xanthurs*.

	Freq	1	2	3	4	5	6
1. *Diplomonorchis leiostomi*	134		0.72	0.61	0.64	0.52	0.54
2. *Scolex polymorphus*	126			0.73	0.62	0.52	0.49
3. *Opecoeloides vitellosus*	88				0.50	0.46	0.36
4. *Hysterothylacium* sp.	76					0.47	0.22
5. *Heteraxinoides xanthophilis*	54						0.28
6. *Ascocotyle* sp.	45						

Table 11. Fager's Recurrent Group Analysis of the common parasites in *Micropogonias undulatus*.

	Freq	1	2	3	4	5	6	7	8
1. *Scolex polymorphus*	135		0.71	0.72	0.74	0.72	0.69	0.65	0.61
2. *Lacistorhynchus* sp.	107			0.78	0.66	0.61	0.61	0.54	0.61
3. *Hysterothylacium* sp.	105				0.73	0.65	0.75	0.51	0.64
4. *Neopterinotrematoides avaginata*	101					0.77	0.58	0.61	0.51
5. *Macrovalvitrematoides micropogoni*	99						0.54	0.52	0.49
6. *Opecoeloides vitellosus*	93							0.45	0.51
7. *Diplomonorchis leiostomi*	83								0.44
8. *Nybelinia* sp.	73								

DISCUSSION

Many of the parasites recovered in this study have been reported previously. Lacistorhynchus sp., Nybelinia sp., and S. sagittifer were reported for the first time from spot. The copepod L. radiatus, Nybelinia sp., N. avaginata, and two larval ascaridoids, which resemble Hysterothylacium M.D. and H. fortalezae, are reported for the first time in croaker. A new species of Paraergasilus (to be described in a separate paper) was observed on juvenile spot collected in both adjacent estuaries (see Chapter I), but not on croaker.

Several species reported in this study including A. pyriformis, Cardicola sp., O. fimbriatus, Nybelinia sp., Capillaria sp., S. tenue, N. avaginata, C. inversa, and S. sagittifer were not found in juvenile fishes collected in the adjoining estuarine systems (see Chapter I). The absence of these species in juvenile fishes from Chesapeake Bay and Pamlico Sound (except N. avaginata and C. inversa, which have direct life cycles) indicates either that their intermediate hosts do not occur in those estuarine systems or that juvenile fish fed on different prey. Salinity could have been a factor limiting the distributions of N. avaginata and C. inversa, as well as other parasites. Also, several species reported in juvenile fishes in these estuaries (see Chapter I) were not recovered offshore, including the myxozoan Kudoa branchiata, the digenean Lecithaster confusus, the monogenean Absonifibula bychowsky, the larval nematode Goezia sp., and two leeches Myzobdella lugubris and M. uruguayensis. All of these species, except Goezia sp., L. confusus and, possibly, K. branchiata, have direct life cycles.

Parasites from adult offshore fishes examined in this study were either more or less abundant than those of juvenile fishes (see Chapter I). Several parasites of spot including, D. leiostomi, L. leiostomi, Ascocotyle sp., H. xanthophilis, A. pyriformis, P. merus, Paraergasilus sp., Hysterothylacium sp., and S. polymorphus unilocularis, were more abundant offshore than in either estuary suggesting that parasites were either accumulating over time (in older hosts) or that more intermediate hosts were available offshore (except for H. xanthophilis, which has a direct life cycle). Zoogonus rubellus and D. chandleri were more abundant in juvenile fish from both estuarine systems than from offshore suggesting that either more intermediate hosts are infected or that the diet of juvenile fish is less diversified and they are specializing more on those intermediate hosts. Several parasites of croaker, including L. microstomum, O. vitellosus, L. ringens, Ascocotyle sp., M. micropogoni, S. polymorphus unilocularis, the psuedophyllidean metacestode, Lacistorhynchus sp., Hysterothylacium sp., and D. chandleri, were more abundant offshore than in either estuary. Greater abundances offshore suggest that these parasites had either been accumulating over time or that a greater number of infected intermediate hosts were available to fishes offshore (except for M. micropogoni, which has a direct life cycle). Lepocreadium setiferoides from spot and croaker and Z. rubellus from spot were more abundant north of Cape Hatteras in both estuarine and offshore environments, whereas D. leiostomi from spot and croaker was more abundant south of Cape Hatteras in both environments. Lobatostoma ringens was more abundant south of Cape Hatteras in both inshore and offshore environments.

Adult spot collected offshore in this study had much greater species-richness, diversity, and total number of individual parasites than juvenile spot collected in adjoining estuaries (see Chapter I). Individual parasitic species collected from juvenile fish were generally less evenly distributed among hosts than those from adult fish collected offshore.

Adult croaker collected offshore in this study had greater species-richness, diversity, and evenness than juvenile croaker collected in adjoining estuaries (see Chapter I). The total number of individual parasites was also much lower in juvenile croaker collected in estuaries, except the largest size class (101-125 mm SL) of juvenile croaker collected in Pamlico Sound in which a few fish harbored large numbers of D. leiostomi. A larger number of juvenile spot and croaker were uninfected than adults.

Host length was associated with intensities of 7 parasitic species in spot and 6 in croaker. Intensities of four adult digeneans of spot and one digenean and the common metacestode S. polymorphus unilocularis from croaker increased with host length suggesting that these parasites either live long enough to accumulate as hosts grow, that larger fish are consuming larger numbers of infected prey during a circumscribed period of time, or both. The two monogeneans of croaker increased in intensity with host length suggesting that they too live long enough to accumulate as croaker grow. The other parasites that increased in intensity with host size were all encysted forms that are able to accumulate over time due to their longevity. The large amount of variation associated with intensity of each parasitic species and host length is reflected in low regression coefficients. Overdispersed (clumped) populations are expressed as negative binomial distributions that are defined by the mean (abundance) and an exponent k which is a measure of dispersion (Table 1 and 2). The more overdispersed a distribution is, the lower the value for k. All the parasites had overdispersed or clumped distributions indicating that factors associated with individual hosts (infracommunity level) were extremely important in determining parasite intensities among hosts. These factors probably relate to individual susceptibility and the availability and distribution of infective stages.

When samples of spot from spring and fall south of Cape Hatteras were compared with those from north of Cape hatteras in the fall, both seasonal and geographical differences in abundances of parasites were apparent (Table 5). Parasite infracommunities of spot collected from south of Cape Hatteras in the spring and north of Cape Hatteras in the fall were less variable and more similar to each other than those collected South of Cape Hatteras in the fall. The occurrence of more diverse habitats south of Cape Hatteras may have resulted in more heterogenous samples of spot, which may explain the greater variability of infracommunities from that area when compared with north of Cape Hatteras. The lower variability in infracommunities collected in the spring may have resulted from fewer infected intermediate host species being present in the spring collections than in those of the fall. The three collections also formed groups that overlapped to some extent; however, differences in abundances of various parasitic species distinguish the three collections. Diversity, evenness, and the numbers of parasites appear to have been relatively homogeneous with season and area (Table 7) suggesting that empty sites within hosts were filled rapidly by available parasitic species. In addition, the 10 parasitic species that showed no differences with season and area contribute to the stability of the component community.

When samples of croaker from spring and fall south of Cape Hatteras were compared with each other and with those from north of Cape hatteras in the fall, both seasonal and geographical differences in abundances of parasites were apparent (Table 6). The component parasite community of croaker collected from north of Cape Hatteras more closely resembled the component community collected south of Cape Hatteras in the fall and was different than that collected in the spring. These similarities were also shown when diversity parameters were examined in the three collections (Table 8). Species-richness was not different in the three collections, but the total number of individual parasites was higher in the spring. Since diversity was greater and evenness was lower in the spring it is likely that the greater abundance of species such as S. polymorphus unilocularis, N. avaginata, and Hysterothylacium sp. had significant influence on the component community of croaker parasites in spring. In croaker collected during this study, season had more of a dominating influence on parasite communities than geographical location. Croaker appear to be more discriminant in their diet than spot, which may have resulted in parasite infracommunities having less variability in the three collections.

Comparison of spot and croaker parasite faunas indicated that their respective parasite component communities were distinct and that similar infracommunity variability existed in both hosts (Figure 4). There were 16 parasitic species that did not occur in both spot and croaker and the fauna exhibited little overlap between species. If those parasites occurring in only one host or the other were removed so that only shared parasitic species were analyzed the component communities of spot and croaker overlapped greatly, but not completely (Figure 5). Clearly, distributions of the shared parasitic species in most of the spot and croaker were somewhat distinct at the infracommunity level.

A few of the individual parasitic species of spot and croaker found in this study, such as Ascocotyle sp., which is infective in low salinity areas, met criteria established by MacKenzie (1983, 1987) and Sindermann (1983) as being good biological tags. Since spot and croaker parasites were examined only at a few sites within the two estuaries the potential usefulness of these parasites as biological tags is unknown. Spot and croaker occurring North of Cape Fear, North Carolina, probably spawn offshore of North Carolina, and therefore individuals of each species may be considered as coming from a single population. Since fishes from both north and south of Cape Hatteras congregate south of Cape Hatteras in late fall through early spring, their respective parasite communities should have been a mix of both collections. In addition, seasonality influenced the parasite communities strongly since some of the parasites are probably short lived.

The number of parasitic species and diversity in adult fish was greater in croaker than spot. Since the total number of individual parasites was similar in both fishes, greater species evenness in croaker can be attributed to the smaller number of individuals of species such as D. leiostomi and larger numbers of individuals of species such as L. setiferoides and Ascocotyle sp. When infracommunity diversity parameters for the gastrointestinal parasites alone were examined, spot had greater species-richness as well as greater numbers of individual helminths, suggesting that they had a more diverse diet and that they fed on more infected intermediate hosts than croaker. The parasitic species of spot were also distributed among the large number of individual parasites in such a way that neither diversity nor evenness were different between fishes. Adults of both spot and croaker harbored 12 gastrointestinal species that made up 52% and 46% of the parasitic species recorded.

Marine fishes tend to have richer helminth communities than freshwater fishes but harbor similar numbers of individual helminths (Holmes, 1989). Values for spot and croaker obtained during this study fit this generalization. In both spot and croaker the mean number of parasitic species was greater than those for freshwater fishes and fewer than those for most birds and mammals (Kennedy et al., 1986). The total number of individual parasites was similar to that of freshwater fishes (Kennedy et al., 1986). Marine benthic fishes do not necessarily have richer helminth faunas than marine pelagic fishes (Holmes, 1989), but the larger variety of prey (intermediate hosts) and the migratory habits of these adult fishes probably contribute to the greater richness and abundance of their parasite communities. The juvenile spot and croaker studied in Chapter I had less time to acquire parasites and inhabited less diverse and more confined habitats in inshore estuaries, which resulted in less diverse parasite communities than offshore fishes.

Spot and croaker contained fewer "core" species than the China rockfish, Sebastes nebulosus Ayres studied by Holmes (1989). The number of their core species were more similar to other marine teleosts (Holmes, 1989). The presence of few "core" species caused low predictability of parasite communities. In addition, most parasites of marine fishes, including those of spot and croaker, are "generalists," in contrast to the specialists occurring in birds (Bush and Holmes, 1986; Stock and Holmes, 1986), which may also cause the lower predictability of the communities of marine fish hosts. Despite the low numbers of "core" species and large number of "generalists" present, similarity appeared relatively high in each collection for each host.

Although the parasite dominance hierarchy in adults of both species did vary slightly between areas and seasons sampled, there appeared to be a predictable group of dominant species that was accompanied by subordinate, less predictable species. In adult spot, D. leiostomi and S. polymorphus uniloculsris dominated all other collections except south of Cape Hatteras in the fall, where Hysterothylacium sp. would have been considered a "core" species had prevalence been the sole factor. Several parasites from croaker collected in the spring could have been considered "core" species based on prevalence alone; however, considering abundance S. polymorphus unilocularis easily dominated all other parasites. Parasites considered "core" species dominated parasite communities of adult croaker collected south of Cape Hatteras in the fall, but their abundances were not as great as "core" species observed in other collections. Scolex polymorphus unilocularis was a "core" species of all three component communities of adult spot and croaker, indicating that it was a "generalist" in regard to host specificity. Since spot and croaker are fed upon by many of the same predators it would be advantageous for a metacestode to infect two such closely related intermediate hosts. Spot and croaker are also intermediate hosts for Lacistorhynchus sp. and Hysterothylacium sp. Diplomonorchis leiostomi was not only a "core" species of spot, it was a "secondary" species of croaker, indicating that it too was a "generalist," even though more common in spot. Opecoeloides vitellosus and several "satellite" species found infecting both hosts were "generalists" with more even distributions among individual fish. Several parasites, most of which were considered "satellite" species, did not occur in both hosts, but were still considered "generalists" because they occurred in other species of sympatric fishes. All of these less common "generalist" species were extremely important contributors to diversity at both the component and infra- community levels (Kennedy et al., 1986). Only the monogeneans were host specific, which agrees with Rohde's (1982) conclusions regarding other monogeneans.

Fager's recurrent group analysis indicated that spot had four and croaker had six regular co-occurring parasitic species. All "core" species as well as a few "secondary" species were included in the recurrent groups. Only 54% of the adult spot harboring all four recurrent group species were concordant ($r > 0.7$), suggesting variability in the relative intensities of those parasites. Since only 28% of the spot harbored all four recurrent group species there also appears to be variability associated with presence-absence of those parasites. Only 14% of the croaker harbored all six recurrent group species and only 37% of those were concordant ($r > 0.7$), suggesting that there was also variability in both intensities and presence- absence of parasites in croaker as well.

Holmes (in press) concluded that a high degree of phylogenetic, ecological, or physiological specificity results in component communities that are restricted subsets of the compound community and that infracommunities are generally "random" samples of the component community. If host specificity is not important, then infracommunities are subsamples of the compound community. Parasite communities of adult spot and croaker fall in between the two extremes. The occurrence of a few "specialists" among a larger number of parasites that, even though they are "generalists," occurred only in one host or other, results in component communities that are restricted subsets of the compound community. There were also a number of parasites that occurred "randomly" in both fishes that contributed to variability making their component communities less distinct and predictable. In general, the component communities of adult spot and croaker were more similar within each host species than between host species suggesting that their communities were relatively predictable and stable for marine fishes. However, the variability in both relative intensities and presence-absence of parasites within communities make them less predictable than those of lesser scaup studied by Holmes et al. (1986). Scaup were more species-specific in diet than spot and croaker, feeding mostly on two species of gammarid amphipods that were intermediate hosts for many of the parasitic species. As a result their parasite faunas were significantly concordant and predictable, whereas the much more diverse diet of spot and croaker resulted in much less predictable parasite communities than those in scaup.

SUMMARY

Twenty-three species of metazoan parasites were recorded from adult spot and 26 from adult croaker. Of the 33 parasitic species found, 17 occurred in both spot and croaker. No significant differences in intensity of parasites occurred between sexes of either spot or croaker. All of the parasites had overdispersed, or clumped, distributions among hosts. Adult spot and croaker collected offshore had much greater species- richness, diversity, and total number of individual parasites than juvenile fishes collected in adjoining estuaries. The juvenile spot and croaker had less time to acquire parasites and inhabited less diverse and more confined habitats in inshore estuaries, which resulted in less diverse parasite communities than offshore fishes. The number of species and diversity of parasites in adult fish was greater in croaker than spot. However, when only gastrointestinal helminths were considered, spot had greater species-richness as well as greater numbers of individual helminths, suggesting that they had a more diverse diet and that they fed on more infected intermediate hosts than croaker. In both adult spot and croaker the mean number of parasitic species was greater than those of freshwater fishes and fewer than those for birds and mammals. The total number of individual parasites was similar to that of freshwater fishes. The opportunistic diet and the migratory habits of both spot and croaker contribute to their diverse parasite faunas. Comparison of adult spot and croaker parasite faunas collected offshore indicated that their respective parasite component communities were distinct and that similar parasite infracommunity variability existed in both hosts and that their

communities were not "random" samples, but restricted subsets of the compound community. Although the parasite dominance hierarchy in adults of both species varied slightly between areas and seasons sampled, there appeared to be a predictable dominant species that was accompanied by subordinate, less predictable species. However, the variability in both relative intensities and presence-absence of parasites within communities resulting from their diverse diets make them less predictable than those of other vertebrates with less diverse diets such as the lesser scaup and more like those of other marine fishes.

GENERAL SUMMARY AND CONCLUSIONS

(1) Species richness increased rapidly in juvenile spot and croaker reflecting the radical change in diet as postlarvae switched from a pelagic diet of mostly copepods to a more diverse benthic diet.

(2) The estuary of residence was clearly as important as host species in determining parasite community structure.

(3) The number of parasitic species and the total number of parasites in individuals of the largest size classes of juvenile spot and croaker were similar to those found in freshwater fishes. In general, estuarine fishes probably have greater numbers of parasitic species than most freshwater fishes because of the more diverse assemblage of prey (potential intermediate hosts) available.

(4) Both adult spot and croaker collected offshore had much greater species-richness, diversity, and total number of individual parasites than juvenile spot and croaker collected in adjoining estuaries. The more diverse offshore habitats provide more potential intermediate hosts than estuarine habitats, and in addition, adult fish have had more time to acquire parasites.

(5) The number of parasitic species and their diversity in adult fish was greater in croaker than spot.

(6) When infracommunity diversity parameters for the gastrointestinal parasites alone were examined, spot had greater species-richness, as well as greater numbers of individual helminths, suggesting that they

had a more diverse diet and that they fed on more infected intermediate hosts than croaker.

(7) Adult spot and croaker collected offshore were similar to most other marine fishes in that they have greater species-richness than freshwater fishes, but similar numbers of individual parasites. Most birds and mammals examined thus far tend to have greater numbers of individual parasites and to have greater numbers of individual parasites and greater species richness.

(8) All parasitic species of adult fishes collected offshore had clumped distributions indicating that factors associated with individual hosts were important in determining parasite intensities among hosts.

(9) The component parasite community of croaker collected from north of Cape Hatteras more closely resembled the component community collected south of Cape Hatteras in the fall and was different than that collected in the spring. Seasonal differences were greater than differences between geographical areas. In contrast, all component communities of spot were distinct from each other, with those collected north of Cape Hatteras in the fall being more similar to those collected south of Cape Hatteras in the spring than to that collected south of Cape Hatteras in the fall.

(10) Although the parasite dominance hierarchy in adult spot and croaker varied slightly between areas and season samples, there appeared to be a predictable group of core species that were accompanied by subordinate, less-predictable species. However, the variability in both relative intensities and presence-absence of parasites within communities resulting from their diverse diets make them less

predictable than those of other vertebrates which have less diverse diets such as the lesser scaup.

(11) Comparison of spot and croaker parasite faunas indicated that 1) their respective parasite component communities were distinct, 2) similar infracommunity variability existed in both hosts, and 3) their communities were not "random" samples, but restricted subsets of the compound community.

(12) Additional studies of parasite communities of various marine and freshwater fishes with different life histories and feeding habits need to be conducted in order to better examine these effects on parasite communities.

LITERATURE CITED

BLISS, C. I. and FISHER, R. A. 1953. Fitting the negative binomial distribution to biological data. Biometrics 9: 176-200.

BUSH, A. O. and J. C. HOLMES. 1986. Intestinal helminths of lesser scaup ducks: Patterns of Association. Canadian Journal Zoology 64:132-141.

CASWELL, H. 1978. Predator-mediated coexistence: a nonequilibrium model. American Naturalist 112:127-154.

CHAO, L. N. and MUSICK, J. A. 1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fisheries Bulletin 75: 657-702.

COLLINS, M. R., MARSHALL, M. J., and LANCIANI, C. A. 1984. The distribution of Poecilancistrium caryophyllum (Trypanorhyncha) plerocercoids in spot, Leiostomus xanthurus Lacepede, and spotted seatrout, Cynoscion nebulosus (Cuvier). Journal Fish Biology 25: 63-68.

CURRIN, B. M., REED, J. P., and MILLER, J. M. 1984. Growth, production, food consumption, and mortality of juvenile spot and croaker: a comparison of tidal and nontidal nursery areas. Estuaries 7: 451-459.

DEARDORFF, T. L. and OVERSTREET, R. M. 1980. Taxonomy and biology of North American species of Goezia (Nematoda: Anisakidae) from fishes, including three new species. Proceedings of the Helminthological Society of Washington 47: 192-217.

DEARDORFF, T. L. and OVERSTREET, R. M. 1981a. Review of Hysterothylacium and Iheringascaris (both previously = Thynnascaris) (Nematoda: Anisakidae) from the Northern Gulf of Mexico. Proceedings of the Biological Society of Washington 93: 1035-1079.

DEARDORFF, T. L. and OVERSTREET, R. M. 1981b. Larval Hysterothylacium (= Thynnascaris) (Nematoda: Anisakidae) from fishes and invertebrates in the Gulf of Mexico. Proceedings of the Helminthological Society of Washington. 48: 113-126.

DEARDORFF, T. L. and OVERSTREET, R. M. 1981c. Raphidascaris camura sp. n., Hysterothylacium eurycheilum (Olsen) comb. n., and comments on Heterotyphlum spaul (Nematoda: Ascaridoidea) in marine fishes. Journal of Parasitology 67: 426-432.

FAGER, E. W. 1957. Determination and analysis of recurrent groups. Ecology 38: 586-595.

FAGER, E. W. and J. A. MCGOWAN. 1963. Zooplankton species groups in the North Pacific. Science 140:453-460.

FUSCO, A. C. and OVERSTREET, R. M. 1978. Spirocamallanus cricotus sp. n. and S. halitrophus sp. n. (Nematoda: Camallanidea) from fishes in the northern Gulf of Mexico. Journal of Parasitology 64: 239-244.

GOLDSTEIN, R. J. 1963. A note on the genus Poecilancistrium Dollfus, 1929 (Cestoda: Trypanorhyncha. Journal of Parasitology 49: 301- 304.

GOVONI, J. J. 1983. Helminth parasites of three larval fishes in the northern Gulf of Mexico. Fisheries Bulletin 81: 895-898.

GROSSLEIN, M. D. and AZAROVITZ, T. R. 1982. Fish Distribution. Mesa New York Bight Atlas Monograph 15, 182 p.

HANSKI, I. 1982. Dynamics of regional distribution: the core and "satellite" species hypothesis. Oikos 38:210-221.

HARGIS, W. J., JR. 1956. Monogenetic trematodes of Gulf of Mexico fishes. Part XI. The family Microcotylidae Taschenberg, 1879. (Continued). Proceedings of the Helminthological Society of Washington 23: 153-162.

HENDRIX, S. S. and OVERSTREET, R. M. 1977. Marine aspidogastrids (Trematoda) from fishes in the northern Gulf of Mexico. Journal of Parasitology 63: 810-817.

HOLMES, J. C. 1989. Helminth communities in marine fishes. _In_ Esch, G. W., A. O. Bush, and J. M. Aho, editors. Parasite Communities: Patterns and Processes. Chapman-Hall, London. (in press)

HOPKINS, S. H. 1941a. New genera and species of the family Monorchiidae (Trematoda), with a discussion of the excretory system. Journal of Parasitology 27: 395-407.

HOPKINS, S. H. 1941b. Excretory systems of _Helicometra_ and _Cymbephallus_ (Trematoda), with remarks on their relationships. Transactions of the American Microscopical Society 60: 41-44.

JOHNSON, S. K.. and ROGERS, W. A. 1973. Distribution of the genus _Ergasilus_ in several Gulf of Mexico drainage basins. Alabama Agricultural Experimental Station Bulletin (Auburn University) No. 445 74pp.

JOY, J. E. 1974. Incidence and intensity of _Spirocamallanus pereirai_ (Nematoda: Camallanidae) infestations in the croaker, _Micropogon undulatus_ (Linneaus) and spot, _Leiostomus xanthurus_ Lacepede, from Texas. Contributions in Marine Science 18: 1-6.

JOY, J. E. 1976. Gill parasites of the spot _Leiostomus xanthurus_ from Clear Lake, Texas. Transactions of the American Microscopical Society 95: 63-68.

JOY, J. E. and PRICE, W. W. 1976. Macrovalvitrematoides micropogoni (Pearse, 1949) (Monogenea: Diclidophoroidea) on the Atlantic croaker, Micropogon undulatus (Linnaeus) from Texas. Proceedings of the Helminthological of Washington 43: 90-91.

KENNEDY, C. R., BUSH, A. O., and AHO, J. M. 1986. Patterns in helminth communities: why are birds and fish different? Parasitology 93: 205-215.

LEONG, T. S. and HOLMES, J. C. 1981. Communities of metazoan parasites in open water fishes of Cold Lake, Alberta. Journal of Fish Biology 18: 693-713.

LINTON, E. 1940. Trematodes from fishes mainly from the Woods Hole region, Massachusetts. Proceedings of the United States National Museum 88: 1-172.

MACKENZIE, K. 1983. Parasites as biological tags in fish population studies. Advances in Applied Biology 7: 251-331.

MACKENZIE, K. 1987. Parasites as indicators of host populations. International Journal of Parasitology 17: 345-352.

MARGOLIS, L., ESCH, G. W., HOLMES, J. C., KURIS, A. M., and SCHAD, G. A. 1982. The use of ecological terms in parasitology. (Report of an ad hoc committee of the American Society of Parasitologists.) Journal of Parasitology 68: 131-133.

OVERSTREET, R. M. 1970. Two new species of Digenea from the spot, Leiostomus xanthurus Lacepede, from the Gulf of Mexico. Journal of Parasitology 56: 1055-1057.

OVERSTREET, R. M. 1973. Some species of Lecithaster Luhe, 1901 (Digenea: Hemiuridae) and related genera from fishes in the northern Gulf of

Mexico. Transactions of the American Microscopical Society 92: 231-240.

OVERSTREET R. M. and HEARD, R. W. 1978. Food of the Atlantic croaker, Micropogonias undulatus, from Mississippi Sound and the Gulf of Mexico. Gulf Research Reports 6: 145-152.

OVERSTREET, R. M. and HOWSE, H. D. 1977. Some parasites and diseases of estuarine fishes in polluted habitats of Mississippi. Annals of the New York Academy of Sciences Sci. 298: 427-462.

ROBERTS, L. S. 1970. Ergasilus (Copepoda: Cyclopoida): revision and key to species in North America. Transactions of the American Microscopical Society 89: 134-161.

ROHDE, K. 1982. Ecology of Marine Parasites. St. Lucia, Queensland, University of Queensland Press.

ROTTMAN, M. L. 1978. Ecology of recurrent groups of pteropods, euphausiids, and chaetognaths in the Gulf of Thailand and the South China Sea. Marine Biology (Berlin) 48: 63-78.

SAS. 1985. SAS user's guide: statistics. Version 5 edition. SAS Institute, Cary, North Carolina, USA.

SAWYER, R. T., LAWLER, A. R., and R. M. OVERSTREET. 1975. Marine leeches of the eastern United States and the Gulf of Mexico with a key to the species. Journal of Natural History 9: 633-667.

SCHLICHT, F. G. and MCFARLAND, W. N. 1967. Incidence of trypanorhynchan plerocercoids in some Texas coast sciaenid fishes. 12: 101-112.

SHERIDAN, P. F., TRIMM, D. L., and BAKER, B. M. 1984. Reproduction and food habits of seven species of northern Gulf of Mexico fishes. Contributions in Marine Science 27: 175-204.

SINDERMANN, C. J. 1983. Parasites as natural tags for marine fish: a review. NAFO Science Council Study 6:63-71.

SNEDECOR, G. W. and W. G. COCHRAN. 1980. Statistical Methods. 7th Ed. The Iowa State Univ. Press, Ames, Iowa, 507 p.

SOKAL, R. R. and F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, California, 726 p.

STOCK, T. M. and HOLMES, J. C. 1987. Host specificity and exchange of intestinal helminths among four species of grebes (Podicipedidae). Canadian Journal of Zoology 65: 669-676.

VOORHEES, J. T. and SCHWARTZ, F. J. 1979. Attachment site, seasonality, and effects of the parasitic copepod Lernaeenicus radiatus on two estuarine fishes in the Cape Fear River, North Carolina. Transactions of the American Microscopical Society 108: 191-196.

WARLEN, S. M. and CHESTER, A. J. 1985. Age, growth, and distribution of larval spot, Leiostomus xanthurus, off North Carolina. Fisheries Bulletin 83: 587-599.

YAMAGUTI, S. 1971. Synopsis of Digenetic Trematodes of Vertebrates. Volumes 1 and 2. Keigaku Publishing Co., Ltd., Tokyo. 1074pp.

VITA

Born February 12, 1954 in Burbank, California. Completed Bachelor's Degree in zoology with strong emphasis in invertebrate biology and fisheries at Humboldt State University, Arcata, California in 1979. Completed Master's Degree in biology with strong emphasis in parasitology and ichthyology at HSU in 1984 while working toward Ph.D. in marine science at the Virginia Institute of Marine Science, College of William and Mary. Started curatorial position at the New York Aquarium, New York Zoological Society in February, 1989.