ECTOPARASITES OF STRIPED MULLET (Mugil cephalus L.) IN
BRACKISH AND FRESHWATER HABITATS

By

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Mugil cephalus (striped mullet) from freshwater (Crystal River) and brackish (Seahorse Key) sites in Florida were examined for gill and body surface parasites. The parasite fauna of the freshwater mullet consisted almost entirely of the copepod Ergasilus versicolor and the leech Myzobdella lugubris. About 32% of E. versicolor were located at the distal tips of the gill filaments, and both prevalence and intensity were negatively correlated with fish length. The remainder were located proximally between hemibranchs, apparently the first time use of this attachment site has been reported, and intensity was positively correlated with fish length. Intensity of M. lugubris was negatively correlated with fish length.

The fauna of brackish water mullet was more diverse. The copepods E. versicolor, E. lizae, Bomolochus nitidus, and Naobranchia lizae; adult and immature Argulus spp.; and the monogenetic trematode Metamicrocotyla macracantha were commonly encountered. The leech Malmiana philoherma (?) was found irregularly in the nostrils of mullet, and several additional species of copepods were rarely collected. Ergasilus versicolor were found at the distal tips of gill

filaments, not between hemibranchs. Intensity of E. versicolor was positively correlated and intensity of E. lizae was negatively correlated with host length.

Subsamples of mullet from both study sites were examined for nematodes (Contracaecum sp. ?). Prevalence and intensity were significantly greater at the brackish site, although definitive hosts (piscivorous birds) were common at both locations. Intensity was positively correlated with host length at the brackish but not the freshwater location. The kidney was the preferred site of infection at both locations.

Experimental translocations of mullet demonstrated that E. versicolor does not move from filament tips to the proximal area between hemibranchs or vice versa as the salinity changes. At each study site, E. versicolor apparently attaches at the location typical of that site/salinity and remains there through salinity changes. Each parasite species responded differently to salinity changes encountered when held at the alternate study site.

Differences between study sites in ectoparasite diversity, attachment sites of E. versicolor, infection values of Contracaecum sp. (?), sex ratios, and length distributions suggest that in Crystal River a group of larger mullet, primarily females, may reside semi-permanently. There seems to be little intermingling of even smaller mullet between brackish and freshwater areas except during the spawning season. The results of this study may be applicable to mariculture and to mullet management policies.

INTRODUCTION

Mugil cephalus L. (striped mullet) is one of the most widespread and abundant inshore teleosts (Odum, 1970), occurring in the coastal waters of all seas between 42°N and 42°S (Hoesel and Moore, 1977) and in salinities from 0 ppt. (parts per thousand) (Collins, 1981) to 75 ppt. (Simmons, 1957). It supports a valuable commercial fishery in the southeastern U.S., especially in Florida where over 30 million pounds were landed in 1981 (Collins, in press). In many parts of the world this species is important in mariculture (Paperna and Overstreet, 1981; Tang, 1970). Striped mullet spawn at sea, and while they are not truly catadromous, adults do regularly ascend freshwater rivers (Shireman, 1975; Collins, 1981). How long they remain in freshwater habitats is not known. Tagging studies in Florida have concluded that only three loosely knit populations of striped mullet exist along the gulf coast. Also, conversations with commercial mullet fishermen indicate that most believe mullet make only brief excursions into freshwater, soon returning to intermingle with the mullet in salt (brackish) water. However, some information suggests that groups of striped mullet inhabiting freshwater areas may be at least partially isolated because they exhibit different size distributions and sex ratios than fish collected in brackish water (Shireman, 1975; Collins, 1981).

While striped mullet have been included as a host in many general surveys of fish parasites in the U.S. (Wilson, 1936; Pearse, 1952; Causey, 1955), detailed knowledge of their parasite fauna is still limited to a few regions despite the world-wide distribution of M. cephalus. Much of the information has been derived from captive fish in culture operations (Paperna and Overstreet, 1981). In the U.S., works concerning the ecology of striped mullet and their parasites are very limited, the most notable being studies by Rawson (1973) and Skinner (1975), neither of which dealt with freshwater habitats, and a review by Paperna and Overstreet (1981). Most other reports of the ectoparasites of M. cephalus in the U.S. have been only taxonomic records from relatively small samples.

The paucity of ecologically oriented studies of striped mullet parasites is unfortunate. Such studies are imperative in the prevention of parasite epizootics in mono- and polycultural operations involving mullet (Rawson, 1973) and may be valuable in forming mullet management policies since parasites may be used as indicators of diet and migratory behavior (Paperna and Overstreet, 1981). In addition, migratory fishes and their parasites provide excellent opportunities for ecologists to study the effects of changing environments on organisms, especially in anadromous species (Noble, 1960). The present study was an investigation into the occurrence and ecology of the ectoparasites of striped mullet and how the parasite fauna differs between freshwater and brackish habitats. Differences in parasite fauna were then analyzed to provide inferences regarding the length of time mullet remain in a freshwater habitat.

MATERIALS AND METHODS

Collection and Maintenance of Fish Samples

Striped mullet were collected at Seahorse Key (SK) and Crystal River (CR), Florida, at irregular intervals (Tables 1-3) from July to October 1982 and February to November 1983 with castnet (2.54 cm. square mesh) and trammel net (3.18 cm. square mesh gillnet with 15.24 cm. square mesh double walls). Attempts to catch at least ten mullet per sample were not always successful. In 1982 all mullet were immediately placed in plastic bags and held on ice until necropsy. In 1983 usually at least five mullet per sample were put on ice immediately as "controls" while the rest, designated "experimental fish," were held alive in covered, aerated tanks (61 x 46 x 46 cm.) aboard the boat. In experiments designated to monitor the changes in parasite fauna of mullet introduced to a different habitat, some of these experimental mullet were placed in cages at the location where they were caught. Others were transported by road to the other study site, acclimated to the new salinity (0 ppt. at CR, 22-31 ppt. at KS), and placed in cages. In addition, a few mullet from both sites were sacrificed immediately after transport and acclimation.

Salinities in the transport tanks were adjusted by adding water from the study site at which the mullet were to be acclimated. This was accomplished by allowing water from a 6 l. container to trickle into

Table 1. Number of infested hosts and intensities of commonly encountered parasites for each Crystal River Collection.

Date	# Fish	<u>Ergasilus versicolor--</u> distal tips		<u>Ergasilus versicolor--</u> between hemibranchs		<u>Myzobdella</u> <u>lugubris</u>	
		# Infested	Intensity	# Infested	Intensity	# Infested	Intensity
82-09-10	9	4	13.3	9	48.0	3	1.7
82-09-24	17	11	3.7	17	29.3	14	3.7
82-10-29	5	5	13.2	5	27.4	5	5.4
82-02-25(a)	10	10	48.3	10	16.7	9	5.7
83-06-18	12	11	17.3	12	26.6	11	1.9
83-06-24(b)	2	2	44.5	2	18.0	0	---
83-06-28	10	10	7.5	9	28.9	9	1.8
83-07-14	10	8	10.0	10	19.5	6	3.7
83-08-15	8	7	13.3	8	22.6	7	5.6
83-09-03	10	7	5.1	10	28.4	2	6.5

(a) 2 fish with total of 4 E. lizae; one of these also infested with 1 M. macracantha.

(b) 1 fish with one M. philoherma in nostril.

Table 2. Number of infested hosts and intensities of commonly encountered arthropod parasites for each Seahorse key collection. A = No. fish infested; B = Mean intensity.

Date	# Fish	<u>Ergasilus</u> <u>versicolor</u>		<u>Ergasilus</u> <u>lilae</u>		<u>Bomolochus</u> <u>nifidus</u>		<u>Naobranchia</u> <u>lilae</u>		<u>Argulid</u> <u>(Adult)</u>		<u>Argulid</u> <u>(Immat.)</u>	
		A	B	A	B	A	B	A	B	A	B	A	B
82-07-19	8	8	42.1	6	3.5	3	4.0	4	2.5	3	1.7	1	1.0
82-09-03	9	9	23.4	9	19.9	6	2.5	2	1.0	2	1.0	1	1.0
82-09-17	11	11	22.4	10	9.3	4	1.8	3	4.7	3	2.0	1	1.0
82-09-29	10	10	13.5	7	6.7	4	2.8	3	1.7	5	2.0	0	---
82-10-17	5	5	18.0	5	5.6	2	2.5	3	1.3	1	1.0	1	1.0
82-10-20	9	9	16.2	9	13.4	4	2.5	3	6.3	2	1.0	3	1.3
83-04-30(a)	10	10	25.3	10	9.0	3	1.0	2	1.3	0	---	2	1.0
83-05-14	2	2	24.0	2	3.5	1	1.0	0	---	0	---	0	---
83-06-10	10	10	65.9	10	10.6	3	2.3	4	2.0	0	---	5	3.0
83-07-08	6	6	46.8	6	8.7	4	3.5	1	1.0	3	1.3	2	1.0
83-07-25	10	10	56.3	9	6.6	3	2.0	2	1.5	2	1.0	6	1.7
83-08-09	5	5	69.4	3	3.7	5	2.6	2	8.5	0	---	1	2.0
83-10-17	5	5	43.0	5	7.4	3	2.7	1	1.0	0	---	1	2.0
83-11-02	5	5	37.2	5	2.2	3	4.3	1	2.0	0	---	1	1.0

(a) 1 fish with 4 E. versicolor between hemibranchs.

Table 3. Number of infested hosts and intensities of leeches and monogenetic trematodes for each Seahorse Key collection.

Date	# Fish	<u>Metamicrocotyla macracantha</u>		<u>Malmiana philoherma (?)</u>	
		# Infested	Intensity	# Infested	Intensity
82-07-18	8	3	1.0		
82-09-03	9	2	1.5		
82-09-17	11	6	2.8		
82-09-29	10	4	2.3		
82-10-17	5	3	2.3		
82-10-20	9	4	2.3	5	1.0
83-04-30(a)	10	5	2.0	0	---
83-05-14	2	2	10.0	0	---
83-06-10	10	2	1.5	4	3.0
83-07-08	6	1	1.0	1	1.0
83-07-25	10	2	1.0	1	1.0
83-08-09	5	1	1.0	0	---
83-10-17	5	2	1.0	1	1.0
83-11-02	5	1	1.0	0	---

(a) 1 fish with 5 M. lugubris.

the tank at a rate of 6 l. per 25 min. with a pause of from 10 to 60 min. each time the salinity in the tank changed by 4 ppt. as determined by refractometer. Total acclimation times of 4, 8, or 12 hrs. were used to determine if the rate of salinity change affected parasites or hosts. Caged fish were held from one to forty days. Additionally, a similar series of experiments lasting up to 26 days was run using an indoor tank with CR mullet held in filtered sea water (30 ppt.) and SK mullet in filtered CR water (0 ppt.). These experiments eliminated reinfestation as a factor while addressing the effects of salinity changes on parasite behavior. Also, an experiment was carried out to determine whether certain parasites abandon dead hosts, in which 5 dead CR mullet were held in an aerated aquarium for 6 hrs. and the distribution of their ectoparasites was compared to that of control fish that were necropsied immediately after death.

Laboratory Analysis

In the laboratory standard length (SL) was measured, gills from both sides were removed and preserved in 70% EtOH, and the body surface, mouth, and inner opercle surfaces (and nostrils of most fish) were examined under magnification. Subsamples of non-experimental mullet were chosen at random to examine for nematodes in the liver and kidney. The preserved gills were inspected with the aid of a dissecting microscope. The sites of attached parasites were noted by subdividing the gills (Figure 1). Three dorso-ventral sections (dorsal, medial, ventral) and three filament areas (proximal, medial, distal) were designated for each of three major regions (lateral

Figure 1. A. Diagrammatic representation of a mullet left gill arch, lateral view.
B. Dorsal view of a cross-section along line a-b in Figure 1A.
(Approximately 2 times life size.)

surface, medial surface, and between hemibranchs) for a total of 28 sections per arch when the gill rakers are also included. In order to determine the existence of a pathological response to ergasilid parasites, gill filaments were sectioned and stained with the standard hematoxylin and eosin. Histological preparations were made and evaluated by Dr. Claus Buergelt (Univ. of Florida).

Statistical Tests

All data were recorded on computer for analysis, and all statistical tests were non-parametric (Siegel, 1956). The Spearman Rank test was used to test for correlations of parasite intensity (number per parasitized fish) and prevalence (percent of parasitized fish in the sample) with host length and with the salinity at SK on the date of collection. Contingency Chi-square tests were employed to determine the significance of attachment site preferences by the parasites. Kolmogorov-Smirnov and Mann-Whitney tests were used in comparisons of intensity and prevalence between study sites and between experimental fish and controls, respectively. For all statistical tests, if p were greater than .05 the difference is stated to be not significant. Pooling of experimental fish was often necessary due to small sample sizes.

Identification of Parasites

Identification of many fish parasites, even to genus, can be difficult, especially considering the frequent taxonomic changes that

occur. Several keys and descriptions were utilized including Sawyer et al. (1975) for leeches, and Schell (1970) and Hargis (1956) for monogenetic trematodes. Preliminary identifications of ergasilid copepods were based on works by Roberts (1969, 1970) and Johnson and Rogers (1972, 1973). All final identifications of copepods were made by Dr. Ju-shey Ho (Univ. of California at Long Beach) and Dr. Robert F. Cressey (U.S. National Museum). Dr. Robin M. Overstreet (Gulf Coast Research Laboratory) provided identifications of leeches and monogenetic trematodes. Crustacean parasites were preserved and shipped in glycerin-ethanol, and leeches and monogeneans were fixed in hot aceto-formol-ethanol and shipped in 70% ethanol.

Study Sites

Collections were made at two locations, Crystal River and Seahorse Key. Crystal River flows generally westward into the Gulf of Mexico, has a total length of approximately 9 km., and is primarily spring-fed. All sampling was done in the vicinity of the springs where the salinity was 0 ppt. and the water temperature was $23 \pm 2^{\circ}\text{C}$ at 2 m. The area is tidally influenced, and the substrate is sandy mud with some rock outcroppings. The dominant submergent vegetation is Hydrilla sp., which often fills the entire water column, but substantial patches of Vallisneria sp. also occur.

Seahorse Key is a small island north of Crystal River about 4 km. offshore. Salinities commonly range from 12-32 ppt., but remained at 22-31 ppt. during the study. Extensive beds of

Thalassia testudinum surround the island, and two small mangrove-lined tidal creeks flow into the cove on the north face of the island where collections were made. Oyster bars are also common on the north face of the island. The substrate varies from sand in the areas of T. testudinum to fine mud in most of the cove. Water temperature varied drastically depending on location and time of day, but the maximum measured during collecting operations was 30.0°C. The estuarine nature of this section of Florida's gulf coast is maintained by freshwater input from several rivers, including the Homossassa, Crystal, Withlacoochee, Waccassassa, and Suwanee Rivers in the 60 km. section around the study sites. Thus, while collections were not made in the immediate vicinity of the mouth of Crystal River, the habitat at Seahorse Key is not dissimilar.

Experimental Equipment

Mullet were transported by road between sites and acclimated in 61 x 46 x 46 cm. Nalgene tanks containing approximately 50 l. of water and 3-4 fish. Each tank was aerated by a recirculating system consisting of a 12v 1890 l./hr. submersible bilge pump that removed water from the bottom of the tank and sprayed it onto the surface through a perforated plastic tube.

Experimental cages were constructed from 2.5 cm. poultry mesh (chicken wire) with a frame of cypress strips. The dimensions were 183 x 91 x 61 cm., and the cages were weighted to keep them on the bottom. (One cage was constructed of 1.9 cm. mesh nylon netting

stretched over a frame of 1.9 cm. O.D. PVC pipe, but this cage was discarded after a preliminary trial due to excessive algal growth on the netting.) A maximum of five fish at a time was held in each cage.

The 305 x 610 x 91 cm. indoor concrete tank had a four-corner airlift-powered subsand filter system. Filtration rate was increased by the addition of a 1134 l./hr. pump, which removed water from beneath the sand and sprayed it onto the water surface, thus also increasing aeration. In addition, two floss and charcoal filters (46 x 46 x 46 cm.), which were powered by another 1134 l./hr. pump, filtered water that was pumped directly from the water column. Before a new group of mullet was introduced, the tank was drained, the sides were scrubbed, and all surfaces including the sand were flamed with a propane torch to kill any parasites remaining from the previous group. A maximum of ten mullet was kept in the tank at one time.

RESULTS

Non-Experimental Mullet

Of 198 non-experimental mullet necropsied, 105 were from SK and 93 from CR. No individual was completely free of ectoparasites. Table 4 contains the prevalence and intensities of commonly encountered parasites from the two study sites and Tables 5 and 6 the prevalence and intensity in host length classes.

Phylum Arthropoda

Ergasilus versicolor. This parasite was the most numerous at both study sites and was always found on the gill filaments. Prevalence was 100% at both sites, and intensity varied from 2-217 with a mean of 35.0 at SK and from 3-139 with a mean of 40.1 at CR. At both sites the anterior arches were preferred and intensity significantly decreased from anterior (arch 1) to posterior (arch 4) (Chi-square: $p < .001$) (Table 7). Differences in the characteristics of infestation between study sites were noted. At SK all E. versicolor were found near the tips (distal portion) of the gill filaments (except on one fish), but at CR only about 32% were on the distal portion of the filaments. The majority were located between hemibranchs on the proximal portion of the filaments and were not visible without

Table 4. Prevalence and intensity of commonly encountered parasites and their correlation with host standard length (SL) at both study sites.

Location	Parasite	Prev. (%)	Mean Intensity	(Std. Error)	Correl.: SL with Prev.	Correl.: SL with Intensity
SK	<u>Ergasilus versicolor</u>	100	30.5	(3.4)	---	+, $p < .01$
	<u>Ergasilus lizae</u>	90.5	9.1	(1.0)	n.s.	-, $p < .05$
	<u>Bomolochus nitidus</u>	45.7	2.6	(0.27)	n.s.	n.s.
	<u>Naobranchia lizae</u>	30.5	2.8	(0.49)	n.s.	n.s.
	Argulids					
	Immature	22.9	1.8	(0.22)	n.s.	n.s.
	Adult	21.0	1.5	(0.21)	n.s.	n.s.
	<u>Metamicrocotyla macracantha</u>	36.2	2.3	(0.47)	n.s.	n.s.
	<u>Malmiana philoherma</u>	19.4	1.7	(0.31)	---	---
	Nematode larvae (<u>Contracaecum</u> sp. ?)	100 (liver) (kidney)	4.5 5.5	(0.52) (0.57)	---	+, $p < .01$ +, $p < .05$

Table 4. continued

Location	Parasite	Prev. (%)	Mean Intensity	(Std. Error)	Correl.: SL with Prev.	Correl.: SL with Intensity
CR	<u>Ergasilus versicolor</u> (Total)	100	40.1	(2.6)	---	n.s.
	<u>Ergasilus versicolor</u> (distal filaments)	81.7	15.8	(2.7)	-, $p < .01$	-, $p < .01$
	<u>Ergasilus versicolor</u> (between hemibr.)	98.9	27.4	(2.1)	---	+, $p < .01$
	<u>Myzobdella lugubris</u>	69.9	3.9	(0.57)	n.s.	-, $p < .05$
	Nematode larvae (<u>Contracaecum</u> sp. ?)	86.4	(liver) 1.6 (kidney) 2.5	(0.15) (0.23)	n.s. n.s.	n.s. n.s.

Table 5. Prevalence and intensity of commonly encountered parasites in each length class of Seahorse Key mullet. P = % prevalence; I = Intensity. (Length in mm. SL.)

Parasite	Length					
	<241	241-260	261-280	281-300	301-320	>320
<u>Ergasilus</u> <u>versicolor</u>	P: 100 I: 28.7	100 24.5	100 32.3	100 51.1	100 79.0	100 41.4
<u>Ergasilus</u> <u>lizeae</u>	P: 100 I: 12.3	93.8 10.0	87.5 7.6	92.9 6.9	60.0 4.7	80.0 6.9
<u>Bomolochus</u> <u>nitidus</u>	P: 40.0 I: 2.3	53.1 2.2	41.7 3.7	42.9 3.3	40.0 1.5	50.0 1.8
<u>Naobranchia</u> <u>lizeae</u>	P: 30.0 I: 4.3	31.3 2.1	29.2 2.9	28.6 1.8	40.0 2.0	20.0 2.0
<u>Argulids</u> <u>Adults</u>	P: 10.0 I: 2.5	28.1 1.1	8.3 2.0	28.6 1.8	20.0 2.0	30.0 1.7
<u>Immature</u>	P: 10.0 I: 1.0	12.5 1.8	22.2 1.4	25.7 1.4	60.0 3.7	20.0 1.5
<u>Metamicrocotyla</u> <u>macracantha</u>	P: 20.0 I: 2.8	34.4 2.6	41.7 2.4	57.1 1.1	20.0 1.0	40.0 2.5
<u>No. fish:</u>	20	32	24	14	5	10

Table 6. Prevalence and intensity of commonly encountered parasites in each length class of Crystal River mullet. (Length in mm. SL.)

Length	No. Fish	Ergasilus versicolor				Myzobdella lugubris			
		(Distal Tips)		(Between Hemibranchs)					
		Prevalence	Intensity	Prevalence	Intensity	Prevalence	Intensity	Prevalence	Intensity
<241	5	100	28.8	100	14.8	60.0	13.0		
241-260	8	100	52.5	100	14.0	87.5	4.6		
261-280	27	88.9	15.9	100	22.8	57.1	3.9		
281-300	16	81.3	8.2	100	28.3	66.7	4.7		
301-320	12	83.3	7.0	100	25.5	92.8	2.3		
321-340	12	66.7	4.4	100	37.9	72.7	4.3		
341-360	8	50.0	8.3	100	40.6	66.7	2.3		
>361	4	75.0	4.0	100	34.0	60.0	1.0		

Table 7. Intensity per gill arch of commonly encountered gill parasites from both study sites. (Parasites loose in containers were not included.)

Location	Parasite	Arch			
		I	II	III	IV
Seahorse Key	<u>Ergasilus versicolor</u>	15.0	13.4	5.8	0.7
	<u>Ergasilus lizae</u>	1.3	2.2	2.6	2.1
	<u>Naobranchia lizae</u>	1.0	0.9	0.8	0.1
	Argulids (Immature)	0.6	0.4	0.5	0.3
	<u>Metamicrocotyla macracantha</u>	1.7	0.3	0.2	0.0
Crystal River	<u>Ergasilus versicolor</u> (distal tips)	4.6	5.5	2.3	0.6
	(between hemibranchs)	9.5	7.4	7.1	3.1

completely separating the hemibranchs. The present study appears to be the first record of the use of this attachment site by E. versicolor. While the dorso-ventral distribution of E. versicolor located distally was apparently random, the distribution of those from between hemibranchs was significantly different from random (Chi-square: $p < .001$) with the dorsal and ventral thirds of the arches preferred to the medial third (37.8% from dorsal, 20.3% from medial, and 41.8% from ventral).

There was no significant correlation of intensity of infestation by E. versicolor with salinity at SK, but there was a significant positive correlation of intensity with host standard length (Spearman rank: $p < .01$) (Figure 2). At CR there was a significant negative correlation (Spearman rank: $p < .01$) of length with intensity of E. versicolor from the distal parts of the gill filaments, a positive correlation (Spearman rank: $p < .01$) with E. versicolor from between hemibranchs, and no significant correlation with the categories combined (Tables 4-6, Figure 3). There was also a significant (Spearman rank: $p < .01$) negative correlation at CR of prevalence of E. versicolor from filament tips with host length (Figure 4). Histological sections of filament tips with and without E. versicolor verified that there was a pathogenic response of striped mullet to E. versicolor located on filament tips, but apparently not to those located between hemibranchs. When E. versicolor is attached to the distal portions of the gill filaments, the filaments at and distal to the point of attachment are pale, mucous-covered, and exhibit epithelial hyperplasia.

Ergasilus lizae. Except for two infested CR mullet, E. lizae was collected only at SK. Prevalence was 90.5%, maximum intensity was 56, and mean intensity of infested fish was 9.1. While similar in general

Figure 2. Mean intensity of E. versicolor on Seahorse Key mullet vs. host standard length. Bars indicate standard error.

Figure 3. Mean intensity of E. versicolor from distal tips of gill filaments (●—●) and between hemibranchs (o--o) of Crystal River mullet vs. host standard length. Bars indicate standard error.

Figure 4. Percent prevalence of E. versicolor from distal tips of gill filaments of Crystal River mullet vs. host standard length.

appearance to E. versicolor, this species exhibited a very different microhabitat preference. The preferred sites for E. lizae were on the gill rakers or on the proximal parts of the gill filaments on the lateral and medial surfaces; i.e., never between hemibranchs. Of the total number of E. lizae collected, 43.5% were on the lateral surface and 56.5% on the medial, which represents a significant difference from a random distribution (Chi-square: $p < .01$). Also, the dorsal and ventral thirds of the arches were preferred to the middle third on both lateral and medial surfaces (Chi-square: $p < .001$ in both cases). Arches 2 and 3 were preferred over 1 and 4, and arch 1 was utilized least (Table 7). Intensity of infestation by E. lizae was negatively correlated with host length (Spreaman rank: $p < .05$) (Figure 5), but was not significantly correlated with salinity, and prevalence was not significantly correlated with salinity or host length (Tables 4-5).

Bomolochus nitidus. This copepod was collected only from SK mullet, primarily from the inner surfaces of the opercles but occasionally from the gill rakers or the proximal portions of the filaments. Prevalence was 45.7%, maximum intensity was 14, and the mean intensity of infested fish was 2.6. There was no significant correlation of intensity or prevalence with salinity or host length.

Naobranchia lizae. Occurring only at SK, the prevalence of N. lizae was 29.5%, maximum intensity was 12, and mean intensity was 2.8 per infested fish. This species occurred on the lateral and medial surfaces of all arches, never between hemibranchs. There was no significant correlation between intensity or prevalence and salinity or host length. There was, however, a definite avoidance of arch 4, with a total of 31 removed from arch 1, 28 from arch 2, 26 from arch

Figure 5. Mean intensity of E. lizae on Seahorse Key mullet vs. host standard length. Bars indicate standard error.

3, and only 4 from arch 4 (significant, Chi-square: $p < .001$) (Table 7).

Rarer species. Several other copepods occurred rarely enough to make prevalence and intensity values inappropriate. Also, the identifications of all but the first species in this group are tentative, and all were collected from SK mullet only.

Lernaenicus longiventris--12 specimens from fins, especially caudal;

L. polyceraeus--1 specimen from anal fin;

Caligus sp.--4 specimens from fins and body surface;

Neobrachiella longimana--8 specimens from mouth and base of pectorals.

Argulus spp. While occurring with low prevalence and intensity, argulids were collected regularly from SK mullet, but not at CR. Thirty-three adults were collected from the mouth, fins, and body surface of 22 fish (prevalence = 20.9%) with a mean intensity of 1.5 and a maximum of 4 per fish. Immature argulids, which were translucent and lacking in pigment except the eye spots, were found only on the gill filaments. Forty-one specimens were removed from 24 mullet for a prevalence of 22.9%. The maximum intensity was 3 per fish, and the mean intensity was 1.8. The occurrence of neither adult nor immature argulids was correlated with salinity or host length (Tables 4-5), and there was no apparent arch preference by the immature specimens (Table 7).

Phylum Platyhelminthes

All monogenetic trematodes examined were identified as Metamicrocotyla macracantha, but because the gill arches were preserved before removal of parasites, many individuals were broken and not definitely identifiable. Monogeneans were found only on the gill filaments and, with the exception of one specimen, only on SK mullet. Eighty-eight were removed from 38 SK mullet for a prevalence of 36.2%, maximum intensity of 18, and mean intensity of 2.3 per infested fish. Neither prevalence nor intensity was correlated with host length or salinity. There was a definite preference for the anterior arches, especially arch 1. A total of 65 were removed from arch 1, 13 from arch 2, 9 from arch 3, and 1 from arch 4 (significant, Chi-square: $p < .001$) (Table 5).

Phylum Annelida

Myzobdella lugubris. While occurring on only one SK mullet, this parasite was quite common at CR with 253 removed from 65 fish. Prevalence was 69.9%, maximum intensity was 24, and the mean intensity of infested fish was 3.9. Intensity but not prevalence was negatively correlated with host length (Spearman rank: $p < .05$) (Figure 6). M. lugubris occurred on all external surfaces, in the mouth, and rarely on the gill arches, but the most frequently infested sites were the fins (Tables 4-6).

Malmiana philotherma (?). In October 1982 it was noticed that a leech was partially protruding from a nostril of a SK mullet. Both

Figure 6. Mean intensity of M. lugubris on Crystal River mullet vs. host standard length. Bars indicate standard error.

nostrils were checked carefully on all hosts from that point on; 20 leeches were subsequently observed from 12 of 62 SK mullet and only one from a CR mullet. Prevalence at SK was 19.4%, maximum intensity was 4, and mean intensity was 1.7. This parasite was tentatively identified as Malmiana philoherma. Undamaged specimens were hard to acquire due to difficulties in removing them from the nostrils, the only sites from which this species was recovered.

Phylum Nematoda

The livers and kidneys of 50 SK mullet were checked for macroscopic nematodes (encysted larvae, probably Contracaecum sp.), producing 202 from the former and 268 from the latter with a prevalence of 100%. Of 66 CR mullet examined, 57 were infected (prevalence = 86.4%) with 123 nematodes removed from the kidneys and 56 from livers. The intensity of infection was significantly greater for SK than for CR mullet (Kolmogorov-Smirnov: $p < .001$). Host length was positively correlated with kidney (Spearman rank: $p < .01$) and liver (Spearman rank: $p < .05$) infection intensities for SK fish but with neither for CR mullet. Intensity was not related to host sex at either study site, and the kidney was preferred over the liver as the site of infection at both locations (Chi-square: $p < .01$) (Table 8). Figure 7 illustrates for both study sites the changes in total mean intensity with host length.

Experimental Mullet

Seventy-five mullet from SK and 35 from CR were collected and held alive. Data were collected from 54 SK fish and 27 CR fish, and

Figure 7. Mean intensity of encysted nematodes (Contracaecum sp. ?) in Crystal River (o--o) and Seahorse Key (●—●) mullet vs. host standard length. Bars indicate standard error.

Table 8. Total nematodes (Contracaecum multipapillatum ?) per infection site and host sex for both study locations.

Location	Host Sex	No. Hosts	Liver	Kidney
Seahorse Key	Female	23	113	169
	Male	27	89	99
Crystal River	Female	43	39	82
	Male	23	17	41

the rest either escaped, died, or were removed from cages by vandals. Of the mullet caught at SK, 22 were caged at CR, 11 were kept in CR water in an indoor tank, 14 were caged at SK, and 7 were transported and acclimated to 0 ppt. but then sacrificed. Of the mullet collected at CR, 8 were caged at SK, 5 were caged at CR, 9 were held in brackish (30 ppt.) water in an indoor tank, and 5 were sacrificed and then held in an aerated aquarium for 6 hours.

SK Mullet Transported and Acclimated Only

No effects on any parasites due to the transport and acclimation procedure were apparent (Table 9). Ergasilus lizae, E. versicolor, L. longiventris, B. nitidus, M. philotherma, M. macracantha, and immature argulids were all present on one or more of these seven mullet and were all in good condition and at sites on the body listed previously for SK mullet. While intensities of parasites were lower on experimental fish than on controls, none of the differences were statistically significant.

SK Mullet Caged at SK

Despite being caged at a location where the water depth was less than 6 inches on low spring tides, the water temperature highly variable, and D.O. levels often low, these 14 fish remained the healthiest-looking of all caged mullet. All parasites remained in the expected locations and there was no significant difference in intensity of any parasite between pooled experimental fish and

Table 9. Intensity of and number of fish infested by commonly encountered parasites on Seahorse Key mullet sacrificed after acclimation and transport (Experimental) and necropsied immediately (Control).

	Control	Experimental
No. Fish:	22	7
<u>Ergasilus versicolor</u>		
No. Infested:	22	7
Intensity:	56.9	23.0
<u>Ergasilus lizae</u>		
No. Infested:	21	6
Intensity:	8.1	6.7
<u>Bomolochus nitidus</u>		
No. Infested	7	4
Intensity:	2.0	1.8
<u>Naobranchia lizae</u>		
No. Infested:	6	0
Intensity:	1.7	---
Argulid (immat.)		
No. Infested:	11	2
Intensity:	2.3	1.0
<u>Metamicrocotyla macracantha</u>		
No. Infested:	6	3
Intensity:	4.2	2.3

controls. On only one host were any parasites present in much greater numbers than on control fish caught at the same time and sacrificed immediately; 291 E. versicolor were removed from the distal parts of the filaments of a mullet held for one month, while the maximum number on any control fish caught during that period was 58 (Table 10).

SK Mullet in Indoor Tank of CR Water

Eleven SK mullet were held indoors, one for 7 days, nine for 14 days, and one for 26 days (Table 11). All were in good condition. There was no change in the location of E. versicolor and no statistically significant difference in the numbers of E. versicolor or E. lizae on the pooled experimental mullet compared to 10 control fish collected on the same dates. While monogeneans were absent from the "26 day" mullet, they were present and apparently in good condition on fish held up to 14 days. On the "7 day" fish all E. lizae and N. lizae were in good condition, but on the other experimental fish most E. lizae had lost their egg sacks, and all five N. lizae had empty egg sacks. No B. nitidus were present on experimental mullet, but six of the controls were infested with a total of 21 specimens, a significant difference (Chi-square: $p < .01$) (Table 11).

SK Mullet in CR Cages

Of the 22 SK mullet caged at CR, various numbers were held for 3 days, 7 days, 12 days, 14 days, and 30 days (Table 12). Several of the fish were emaciated and sluggish and many had reddish lesions

Table 10. Intensity of and number of fish infested by parasites commonly encountered on Seahorse Key mullet caged at Seahorse Key.

Days in Cage:	0	7	14	17	30	40
No. Fish:	16	5	5	2	1	1
<u>Ergasilus versicolor</u>						
No. Infested:	16	5	5	2	1	1
Intensity:	33.4	34.4	30.0	50.0	291.0	16.0
<u>Ergasilus lizae</u>						
No. Infested:	16	5	5	2	1	1
Intensity:	8.9	18.6	5.8	11.5	12.0	21.0
<u>Bomolochus nitidus</u>						
No. Infested:	7	2	3	2	0	0
Intensity:	2.4	3.0	1.0	5.0	---	---
<u>Naobranchia lizae</u>						
No. Infested:	3	0	1	0	0	0
Intensity:	1.3	---	1.0	---	---	---
Argulid (adult)						
No. Infested:	3	0	2	2	1	1
Intensity:	1.3	---	1.0	4.5	4.0	1.0
Argulid (immat.)						
No. Infested:	4	0	0	0	0	0
Intensity:	1.0	---	---	---	---	---
<u>Metamicrocotyla macracantha</u>						
No. Infested:	6	2	3	0	1	0
Intensity:	1.8	3.5	2.7	---	4.0	---

Table 11. Intensity of and number of fish infested by parasites commonly encountered on Seahorse Key mullet held in a tank of filtered Crystal River water.

Days in Tank:	0	7	14	26
No. Fish:	10	1	9	1
<hr/>				
<u>Ergasilus versicolor</u> (a)				-
No. Infested:	10	1	9	1
Intensity:	39.8	30.0	29.4	23.0
<hr/>				
<u>Ergasilus lizae</u>				
No. Infested:	10	1	7	1
Intensity:	4.8	10.0	7.0	10.0
<hr/>				
<u>Bomolochus nitidus</u>				
No. Infested:	6	0	0	0
Intensity:	3.5	---	---	---
<hr/>				
<u>Naobranchia lizae</u>				
No. Infested:	2	1	3	0
Intensity:	1.5	1.0	1.7	---
<hr/>				
Argulid (immat.)				
No. Infested:	2	0	0	0
Intensity:	1.5	---	---	---
<hr/>				
<u>Metamicrocotyla macracantha</u>				
No. Infested:	3	1	2	0
Intensity:	1.0	5.0	1.0	---

(a) all E. versicolor were at distal tips of filaments.

Table 12. Intensity of and number of fish infested by parasites commonly encountered on Seahorse Key mullet caged at Crystal River.

Days in Cage:	0	3	7	12	14	30
No. Fish:	27	5	7	4	3	3
<u>Ergasilus versicolor</u>						
Between hemibr.						
No. Infested:	0	1	2	2	3	3
Intensity:	---	22.0	22.0	1.5	10.3	5.3
Distal tips						
No. Infested:	27	5	7	4	3	3
Intensity:	46.0	45.6	128.0	135.5	36.0	20.3
<u>Ergasilus lizae</u>						
No. Infested:	24	5	6	1	3	2
Intensity:	7.6	11.2	5.5	6.0	2.3	4.5
<u>Bomolochus nitidus</u>						
No. Infested:	12	0	0	0	0	0
Intensity:	2.3	---	---	---	---	---
<u>Naobranchia lizae</u>						
No. Infested:	9	2	2	0	0	0
Intensity:	3.1	2.0	1.0	---	---	---
Argulid (adult)						
No. Infested:	2	0	0	1	0	0
Intensity:	1.0	---	---	6.0	---	---
Argulid (immat.)						
No. Infested:	12	2	0	0	0	0
Intensity:	2.3	1.0	---	---	---	---
<u>Metamicrocotyla macracantha</u>						
No. Infested:	7	2	2	0	0	0
Intensity:	3.7	2.0	2.5	---	---	---
<u>Myzobdella lugubris</u>						
No. Infested:	0	0	0	2	2	3
Intensity:	---	---	---	5.5	3.5	5.3

where scales were lost. No B. nitidus were present on any of the mullet, including those held for only three days, whereas 48.5% of 33 SK control fish for the period were infested. Similarly, 42.4% of the controls had immature argulids on their gill filaments while none were found on experimental fish held for more than 3 days. Naobranchia lizae and monogeneans were present on fish held up to seven days and appeared to be in good condition, except that the one N. lizae held for seven days had empty egg sacks. Monogeneans and adult argulids occurred irregularly on controls during this period, so no conclusion as to their tolerance to freshwater can be made. Myzobdella lugubris appeared only on fish held 12 days or longer in freshwater with six of 10 fish held for this time period infested with an average of 6 leeches each. Leeches did not occur on the SK controls.

Ergasilus lizae were present on all but four of the experimental fish. While there was no statistically significant difference in intensity on pooled experimental fish compared to controls, many lost their egg sacks. Combining data from cage and indoor tank experiments, the percent of E. lizae with eggs declined from 95.6% for controls to 0% for all fish held six days or longer (Figure 8). There was a negative correlation between percent of E. lizae with egg sacks and number of days in freshwater, significant at $p < .01$ (Spearman rank).

All experimental mullet were infested with E. versicolor on the distal parts of the gill filaments. Intensity was unexpectedly high compared to controls on only two fish, one held 7 days and one 12 days, from which 441 and 426 were removed. There was no statistically significant difference in intensity of E. versicolor on filament tips

Figure 8. Percent of *E. lizae* with eggs vs. number of days
hosts (Seahorse Key mullet) were held in freshwater.

between controls and pooled experimental fish. Ergasilus versicolor began appearing between hemibranchs on mullet held for three days and more in an area surrounded by Hydrilla sp., but of the six mullet held 7 or 12 days at the site where native vegetation (especially Vallisneria sp.) predominated, only one fish was infested by one E. versicolor between hemibranchs.

CR Mullet Sacrificed and Held in Aerated Freshwater

When the parasites of five mullet held in aerated water for 6 hours after death were compared to those of ten controls caught at the same time (Table 13), there were no significant differences in the numbers of E. versicolor between hemibranchs or numbers of M. lugubris. However, the five experimental fish had significantly fewer (Mann-Whitney: $p < .05$) E. versicolor on the distal parts of the filaments than did the controls: 1 E. versicolor from the experimental fish and 36 from the controls.

CR Mullet Caged at CR

Of five CR mullet caged at CR, two were held for 6 days, one for 12 days, and two for 18 days (Table 14). There were no statistically significant changes in the numbers or distributions of E. versicolor between hemibranchs or on distal filaments of the pooled experimental fish compared to 14 controls collected during that time period. However, the number of leeches (M. lugubris) increased with the length of time the mullet were caged. The mean intensity for the

Table 13. Intensity of and number of fish infested by E. versicolor and M. lugubris on Crystal River mullet held in aerated water for 6 hrs. after death (Experimental) and necropsied immediately (Control).

No. Fish:	Control	Experimental
	10	5
<u>Ergasilus versicolor</u>		
Between hemibr.		
No. Infested:	10	5
Intensity:	28.4	21.2
Distal tips		
No. Infested:	7	1
Intensity:	5.1	1.0
<u>Myzobdella lugubris</u>		
No. Infested:	2	3
Intensity:	6.5	1.7

Table 14. Intensity of and number of fish infested by parasites commonly encountered on Crystal River mullet caged at Crystal River.

Days in Cage:	0	6	12	18
No. Fish:	14	2	1	2
<u>Ergasilus versicolor</u>				
Between hemibr.				
No. Infested:	14	2	1	2
Intensity:	25.4	11.5	5.0	80.5
Distal tips				
No. Infested:	13	2	1	2
Intensity:	21.5	6.0	2.0	1.5
<u>Myzobdella lugubris</u>				
No. Infested:	12	2	1	2
Intensity:	1.8	1.0	10.0	22.0

controls was 1.75, while there were an average of 11.20 leeches per experimental fish. The difference in number of leeches between caged and control fish was significant at $p < .01$ (Mann-Whitney).

CR Mullet Caged at SK

Six CR mullet were held at SK for 5 days, one for 7 days, and one for 11 days (Table 15). Infestation by M. lugubris continued through 11 days, and there were no statistically significant changes in the numbers of E. versicolor between hemibranchs or on distal filaments of pooled experimental fish. Infestations by E. lizae, adult argulids, and one immature argulid occurred while the fish were caged.

CR Mullet in Indoor Tank of Brackish (30 ppt.) Water

Of the nine mullet kept in the tank, five were held 11 days and four for 20 days (Table 16). Compared to ten controls from CR, there were no statistically significant changes in the number of E. versicolor on distal filaments or in number of M. lugubris (not tested; perusal of table only), but the mean intensity of E. versicolor between hemibranchs decreased as the length of time in brackish water increased. Mean intensity for controls was 28.4, for fish held 11 days was 16.2, and for fish held 20 days was 3.8. Both groups of experimental mullet had significantly fewer E. versicolor between hemibranchs than controls (Mann-Whitney: 11 days, $p < .05$; 20 days, $p < .001$).

Table 15. Intensity of and number of fish infested by parasites commonly encountered on Crystal River mullet held in cages at Seahorse Key.

Days in Cage:	0	5	7	11
No. Fish:	18	6	1	1
<u>Ergasilus versicolor</u>				
Between hemibr.				
No. Infested:	17	6	1	1
Intensity:	25.9	46.2	4.0	10.0
Distal tips				
No. Infested:	17	6	1	0
Intensity:	9.9	3.0	5.0	---
<u>Myzobdella lugubris</u>				
No. Infested:	15	6	0	1
Intensity:	4.3	6.3	---	4.0
<u>Ergasilus lizae</u>				
No. Infested:	0	4	1	0
Intensity:	---	2.0	1.0	---
Argulid (adult)				
No. Infested:	0	1	1	1
Intensity:	---	2.0	1.0	1.0
Argulid (immat.)				
No. Infested:	0	1	0	0
Intensity:	---	1.0	---	---

Table 16. Intensity of and number of fish infested by parasites commonly encountered on Crystal River mullet held in a tank of filtered water at 30 ppt. salinity.

Days in tank:	0	11	20
No. Fish:	10	5	4
<u>Ergasilus versicolor</u>			
Between hemibr.			
No. Infested:	10	5	4
Intensity:	28.4	16.2	3.8
Distal tips			
No. Infested:	7	4	4
Intensity:	5.1	9.0	2.3
<u>Myzobdella lugubris</u>			
No. Infested:	2	1	0
Intensity:	6.5	1.0	---

DISCUSSION

Experimental Equipment and Techniques

The transport and acclimation containers containing approximately 50 liters of water and aerated by submersible bilge pumps proved quite adequate for handling 3-4 adult mullet at a time, as no fish died during transport or acclimation except when a pump failed. Tanks containing M. cephalus should be completely covered at all times, however, as this fish jumps strongly and accurately. While not statistically tested due to inadequate data, survival through the experimental periods appeared to increase as acclimation time decreased from 12 to 4 hours, suggesting that stress due to captivity in small containers is of greater importance than stress due to rapidly changing salinity, both from freshwater to brackish and vice versa. However, direct transfer from 25 ppt. to 0 ppt. produced 100% mortality of seven mullet in a preliminary experiment.

Because capture of mullet in a trammel net requires that the fish be handled to remove them from the net, fish collected in this manner might be expected to show a greater mortality or at least a greater tendency toward fungal and microbial skin infections than those collected with a castnet and never handled directly. This did not prove to be the case, as there were no apparent differences in the conditions of mullet caught with these nets. It should be noted that

fish that gilled (became entangled by the opercula) in the trammel net were not used. Fish held at SK rarely showed any signs of damage or external infection, even after a month or more of captivity. However, fish held at CR, regardless of their place of origin, often possessed reddened and occasionally necrotic areas on the fins and body after only a few days. This was especially noted at the CR site dominated by Hydrilla sp. and having less water flow and lower D.O. than the shallower site dominated by Vallisneria sp.

The 1.02 cu. m. wire cages proved adequate for holding up to five adult mullet for extended periods (at least one month). Abraded areas around the mouth and caudal fin were occasionally observed at both sites, but became microbially infected only at CR. However, the wire corroded at SK and had to be replaced periodically. For long-term experiments, a non-abrasive and non-corroding mesh, perhaps of plastic, would be highly desirable as long as it did not have a tendency to collect fouling organisms. Esch et al. (1976) held bluegills (Lepomis macrochirus) in cylindrical cages covered with nylon netting to study recruitment of endoparasitic helminths, and while they reported no ill effects due to the cages, the fish were held for only seven days. The single most important factor in improving the productivity of experiments such as these might be the use of an area to which access by the public is restricted, as a significant number of fish and three cages were lost to vandals.

The Parasites

Ergasilus spp.

As the Mugilidae are common and widely distributed, so are ergasilid copepods. Both mugilids and ergasilids occur in habitats from freshwater to marine, and both M. cephalus and Ergasilus spp. have been reported circumglobally from the tropics to the temperate zones (Kabata, 1970; Paperna and Overstreet, 1981; Rivas, 1980). As with the taxonomy of many groups of fish parasites, the taxonomy of Ergasilus spp. has recently been in a state of flux, often making comparisons with older studies inappropriate. It is apparent, however, that both E. versicolor and E. lizae are common parasites of Mugil cephalus. Ergasilus lizae is probably a cosmopolitan species (Roberts, 1970), but valid reports of E. versicolor appear restricted to North America. Ergasilus lizae appears restricted to coastal areas and ranges as far north as Chesapeake Bay in the eastern U.S. (Paperna and Overstreet, 1981), and E. versicolor extends well inland and has been reliably reported from the Mississippi River east to Florida and north at least to Georgia (Johnson and Rogers, 1973).

Widespread ergasilid-induced mortality of fish in the U.S. is apparently rare, although Kelly and Allison (1962) reported an epizootic of E. lizae, later shown to be primarily E. arthrosis by Roberts (1969), on centrarchids in a brackish Alabama lake. In Europe and Asia, however, mass fish kills due to ergasilids, especially E. sieboldi, are not uncommon. In addition, even non-lethal infestations of some fishes can produce a significant decrease in

age-specific weight, condition factor, and commercial value (Kabata, 1970). Heavy infestations occur more frequently in crowded fish culture ponds and have resulted in poor growth and extensive mortalities (Paperna and Overstreet, 1981). Lahav and Sarig (1967) reported an epizootic of E. sieboldi, re-identified as E. lizae according to Paperna and Overstreet (1981), on M. cephalus in brackish Israeli culture ponds, causing emaciation and death and reducing the harvest significantly.

Feeding by ergasilids apparently involves external digestion to partially dissolve gill tissues, which are then ingested with the aid of the mouth appendages and first swimming legs. Recent evidence shows that while some blood is ingested (by E. sieboldi), epithelial cells are the primary diet (Kabata, 1970). The feeding activity together with the mode of attachment (surrounding and gripping a gill filament with modified second antennae) can result in eroded respiratory epithelium, obstructed branchial blood vessels, and epithelial hyperplasia. Although E. lizae, but apparently not E. versicolor, has been shown to have drastic, even lethal, effects on M. cephalus (Lahav and Sarig, 1967), E. versicolor was observed in the present study to produce a pathological response similar to the effects of Sinergasilus major reported by Bauer and Babaev (1964, as cited by Kabata, 1970). Histological sections show epithelial hyperplasia in the area of and distal to the point of attachment. Neither E. versicolor located between hemibranchs nor E. lizae were observed in the present study to induce any apparent pathological response.

E. versicolor. In the northern Gulf of Mexico region, hosts of E. versicolor include the families Lepisosteidae, Catostomidae,

Ictaluridae, and Mugilidae, but saltwater hosts are primarily mugilids, especially M. cephalus (Johnson and Rogers, 1973). Skinner (1975) found a 31% prevalence and maximum intensity of 25 per gill arch for E. mugilis (E. versicolor ?) on M. cephalus from Biscayne Bay, FL, while Rawson (1973) reported that the intensity of E. versicolor peaked at 24 per age class I M. cephalus at Sapelo Is., GA, and although he gave no overall prevalence, it seemed to be about 65%. Rawson also found a positive correlation between intensity and host length, as was found for SK mullet in this study. The prevalence values (100%) found at both CR and SK in the present study are much greater than reported from these two previous investigations. While Rawson's maximum intensity seems quite low, it must be remembered that he was working with age class 0 and I mullet ranging in standard length from 22 to 218 mm. Skinner (1975), on the other hand, looked at mullet ranging from 105 to 436 mm. SL, and while the range in intensities she noted were comparable to those of the present study, the prevalence of 31% stated by Skinner seems inexplicably low. Neither Rawson nor Skinner mentioned checking for ergasilids between gill hemibranchs, and apparently no previous records of E. versicolor using this site exist. If attachment between hemibranchs is preferred by E. versicolor on other host species in freshwater, actual intensity and prevalence values may be greater than has been noted for these hosts.

Why E. versicolor on striped mullet in freshwater most often occur proximally between hemibranchs rather than on the distal ends of the filaments as in brackish water is not known. It is known that

Ergasilus spp. can change positions on the gills, especially on the same filament, and that they even retain their swimming ability (Kabata, 1970). However, the fact that no E. versicolor appeared between hemibranchs on SK mullet held in a tank of filtered CR water for up to 26 days, but did appear after only 5 days on fish caged at CR, suggests that these copepods do not move from the distal filament tips to the proximal region between hemibranchs when their hosts enter freshwater. Rather, E. versicolor that become attached while mullet are in freshwater appear to infest the area between hemibranchs, but those that were attached before the mullet left brackish water remain at the filament tips. There are probably exceptions, however, since even the largest fish, typical of CR but not SK, usually have a few E. versicolor on filament tips nearly a year after their estimated return from the Winter-Spring spawning migration.

Evidence concerning the fate of E. versicolor in the reciprocal situation is inconclusive. The CR mullet that were caged at SK showed no significant differences in the numbers of E. versicolor between hemibranchs or at filament tips compared to controls, but on fish held in an indoor tank of brackish water there was a significant decrease in the numbers between hemibranchs. It is probable that the caged mullet were not held long enough for a change to occur since only one fish was held for the maximum time of 11 days while in the indoor tank five mullet were held for 11 days and four for 20 days. It is possible but considered unlikely that some aspect of the artificial environment of the indoor tank caused the loss of copepods from

between hemibranchs. These missing E. versicolor apparently did not move to the filament tips since there was no significant difference between experimental and control fish in the numbers of copepods at that site. They also probably did not abandon their hosts since E. versicolor between hemibranchs do not leave even dead hosts, according to the results of the experiment in which dead mullet were held for 6 hrs. in aerated water. Thus, accepting the results of the indoor tank and dead host experiments, death from unknown causes seems to be the most likely fate of the copepods lost from between hemibranchs. However, the small sample sizes of this series of experiments prohibit a definite conclusion.

Reasons for the differences in distribution of E. versicolor between the two study sites and the behavior of the copepods during experiments, including the possible mortality of those between hemibranchs of CR fish subjected to brackish water, are not apparent. While it is possible that the differences are due to separate parasite populations with different behavior patterns, physiological tolerances, and site preferences, this seems unlikely due to the probable continual exchange of gravid parasites from one habitat to the other by host migration during the spawning season of the mullet. It seems more probable that the numerous physico-chemical differences between the study sites induce behavioral changes in a single, relatively homogenous parasite population. The most obvious possible reason for the preference for attachment sites between hemibranchs of mullet in freshwater is that being surrounded by gill tissue across which ions are continually lost by the fish provides the

copepods with a higher "salinity" environment than do the distal portions of gill filaments. Since new infestation by E. versicolor occurs at CR, this species is capable of tolerating the freshwater environment there, but their energetic efficiency may be increased by utilizing the less stressful site provided by the area between gill hemibranchs. Whether the distributional differences between study sites are actually determined by temperature, salinity, or some other factor is not known and, until the life cycle of E. versicolor can be completed in the laboratory so that uninfested fish may be experimentally infested, it will be difficult to discern.

Differences in the infestation rates of ergasilids on mugilids in adjacent microhabitats have been previously noted. Raibaut et al. (1975) concluded that in Lake Ischkeul in Tunisia striped mullet are more heavily parasitized by E. nanus in some areas than in others, although the areas were not contrasted. Data from the present study suggest more rapid infestation by E. versicolor at CR in areas densely vegetated by the exotic Hydrilla sp. than in an area less than 100 m. away where the native Vallisneria sp. predominates. The epibiota of Hydrilla sp. comprise a major portion of the diet of mullet in CR (Collins, 1981), providing E. versicolor ample opportunity to infest mullet while they are feeding. No explanations for the differences in infestation values between microhabitats were presented by Raibaut et al. (1975), and none are apparent from the present study.

E. lizae. The results of this study (Table 7) confirm the observations by Rawson (1973) that E. lizae is more common on arches

2 and 3, but Rawson noted a slight preference for the ventral region of the arches while in this study the ventral was second in preference to the dorsal region. In addition, Rawson reported a positive correlation between host length and intensity of E. lizae, the reverse of the correlation found at SK. However, Joy (1976) reported a negative correlation between prevalence and intensity of E. lizae and length of spot (Leiostomus xanthurus) in Texas and hypothesized a resistance to infestation by E. lizae in older fish.

The preference of E. lizae for the proximal portions of the gill filaments found in this study has been previously noted (Rawson, 1973). Paperna and Overstreet (1981) and Lahav and Sarig (1967) included photographs of M. cephalus gills infested by E. lizae in which the parasites were located primarily near the arch, even in hyperinfestations (Lahav and Sarig initially identified their parasites as E. sieboldi). In addition, Lahav and Sarig (1967) described their specimens as being attached to the gill filaments close to the arches, although they found a few immature individuals on the distal parts of the filaments. No previous mention of E. lizae attached to the gill rakers was found, while about 15% were so located in the present study.

Experimental evidence demonstrates why E. lizae is considered a brackish water or coastal species. While this copepod appears to survive quite well in freshwater at CR, after six days no individuals were found to possess egg sacks (Figure 8). No new infestations occurred at CR, but did at SK, so this parasite has probably not been established at CR despite probable frequent introductions by mullet

returning in late Winter-early Spring from spawning migrations. The one sample of CR mullet in which E. lizae occurred was in February when returning spawners might be expected.

Bomolochus nitidus

Bomolochus nitidus, also known as B. concinnus and B. mugilis, according to Paperna and Overstreet (1981), is a common parasite of mullet in the southeastern U.S. and has also been reported from the Pacific coast of Mexico (Causey, 1960). It would seem that this copepod, while appearing on mugilids regularly, usually does not occur in large numbers or with high prevalence. Skinner (1975) found 2 to 25 specimens per fish on 20 of 83 striped mullet examined from Biscayne Bay, FL. In Georgia Rawson (1973) reported this parasite from age class 0 and I mullet with a prevalence in the older group of about 25% and mean intensity of about 1.8. The prevalence (45.7%) found at SK in the present study is greater than in either of these previous investigations.

Bomolochus nitidus appears to be more sensitive to low salinity than most of the other copepods infesting mullet at SK. While some of the other species lost their eggs after introduction of the host to freshwater, B. nitidus seemed to completely disappear within 3 days. This copepod does not possess the powerful grasping appendages of the ergasilids, nor does it embed a portion of itself in its host for attachment. Thus, it may drop off the host even if a brief introduction to freshwater merely weakens rather than kills it. Bangham

(1940) reported Bomolochus sp. from Mugil cephalus in a paper entitled "Parasites of fresh-water fish of southern Florida." Because salinities were not measured at the various collection sites, which included the Everglades, it is likely that some of his "freshwater" parasites were actually from brackish water habitats.

Naobranchia lizae

Naobranchia lizae has been reported from several marine fishes in the southeastern U.S., including striped mullet. As with B. nitidus it seems to occur regularly but with low prevalence and intensity. Skinner (1975) reported from 1 to 8 specimens per fish on 11% of the mullet examined, but Rawson (1973) did not encounter it on Georgia mullet. While considered a marine parasite, N. lizae did not seem extremely sensitive to low salinity. Most specimens were in good condition even after their host had been in freshwater for several days, and the eggs did not disappear until after at least one week. The parasites themselves were still alive after at least two weeks in freshwater. Unlike B. nitidus and the ergasilids, the eggs of N. lizae are not in easily broken sacks attached to a posterior segment of the copepod. Rather they are in lateral wing-like compartments, which remain flaccid and obviously empty, even after the eggs have disappeared. The mechanism by which the eggs were lost is not known, as no holes were visible in the egg compartments.

Argulus spp.

Argulids infested SK mullet at relatively low intensities (maximum of 4 per host) compared to the 100 per host maximum found by Skinner (1975), but with a prevalence greater than reported by Skinner (1975) or Rawson (1973). Neither of these previous studies reported argulids from the mouths of mullet, while this was a common site of infestation at SK. Also, neither reported immature argulids, which were as prevalent as adults in the present study and were found only on the distal portions of gill filaments. While the immature specimens may have occurred on the body surface and been overlooked due to their size (approx. 0.25 mm.) and lack of pigment, it is felt that at least a few individuals would have been found since examinations were carried out under magnification.

Rarer Species

Caligus spp. were relatively common in Biscayne Bay, FL (Skinner, 1975), with up to 50 per host reported. In Georgia (Rawson, 1973) and in the present study, they were much less common and were in fact the second rarest parasite encountered at SK with only 4 specimens collected from non-experimental fish. Lernaenicus longiventris, which embeds near the base of fins and commonly extends through the fin between rays, was found at low levels by both of these previous investigators as well as at SK in this study. Apparently only once in all three studies were more than one individual found per host (Rawson, 1973).

Metamicrocotyla macracantha

Metamicrocotyla macracantha was more prevalent at SK (36.2%) than in Biscayne Bay, FL (Skinner, 1975), or in Georgia (Rawson, 1973), where it was reported from 14% and about 26% of the mullet, respectively. Intensity was similar at all three locations: up to 5 per host (Skinner, 1975), a mean of approximately 2 per class I mullet (Rawson, 1973), and a mean of 2.3 and maximum of 18 per host in the present study. Neither of the previous studies addressed the subject of gill arch preference by M. macracantha, which clearly preferred arch 1 in the present study (Table 7). Both Skinner (1975) and Rawson (1973) reported Microcotyle pseudomugilis from striped mullet, but this species was much rarer than M. macracantha in both cases. In fact, apparently only 3 of 83 mullet were infested with 1 specimen each in the former study. It is quite possible that some of the monogeneans in the present study were M. pseudomugilis because many specimens were in poor condition when recovered, the two species are similar in size and general appearance, and both have been reported from striped mullet in the Gulf of Mexico (Hargis, 1956).

Myzobdella lugubris

Myzobdella lugubris was the only parasite that was common at CR but not at SK. Only six of these leeches were recovered from SK mullet and these were from a fish caught on the same day as the single SK mullet with E. versicolor between hemibranchs, suggesting that the group of mullet sampled may have just recently left a freshwater habitat, a

rare action on the part of the fish (except during the spawning season) according to evidence from this study. M. lugubris is considered a fresh and brackish water parasite preferring shallow areas with heavy vegetation (Sawyer et al., 1975), which typifies CR. Apparently the salinity is occasionally too high for it to become established at SK despite the fact that several specimens survived quite well at 25 ppt. on a CR mullet caged at SK for 11 days. No explanation for the negative correlation between intensity and host length found at CR is apparent other than the possibility of host resistance in older fish. However, this hypothesis has no other supporting evidence.

Malmiana philotherma (?)

Because M. philotherma occurred irregularly during experiments no conclusions can be drawn as to how long it survives in freshwater, but Sawyer et al. (1975) consider it a high-salinity parasite. Skinner (1975) identified all leeches from nostrils, mouth, and body surface of striped mullet as Piscicola sp., as did Rawson (1973). In this case there were definitely two species present, and they never overlapped in attachment site.

Contracaecum sp. (?)

While striped mullet have been reported as intermediate hosts for several nematodes, from the size and sites of the encysted nematodes encountered in this study, most if not all are probably Contracaecum sp.,

which Rawson (1973) found sporadically and at low levels in kidneys of mullet in Georgia. Skinner (1975) reported 1 to 6 Thynnascaris sp. from the livers of 43% of mullet examined, but Deardorff and Overstreet (1980) examined the specimens and considered them identical to Contracaecum multipapillatum (= C. robustum). Nematodes of this genus occur as adults in piscivorous birds such as brown pelicans (Pelecanus occidentalis) and double-crested cormorants (Phalacrocorax auritus) according to Deardorff and Overstreet (1980), but it is not known whether mullet become infected from free-living larvae or by feeding on infected copepods. The prevalence of C. multipapillatum in mullet varies according to locality and is probably related to the occurrence of definitive hosts (Deardorff and Overstreet, 1980). Since both prevalence and intensity are positively correlated with host length in SK mullet, adult mullet there are apparently continually re-infected. Neither prevalence nor intensity are correlated with host length in CR mullet, suggesting that re-infection is not continuing in this area. Because both brown pelicans and cormorants are common at SK and at CR, in this case there are probably other limiting factors controlling the nematode population besides presence of the definitive host. It is possible that the freshwater of CR is unsuitable for the survival of larvae and/or a copepod intermediate host, but if CR mullet are only temporary residents of the freshwater habitat this would not seem to make a difference in the acquisition of new infections.

Implications and Conclusions

Polyanski (1958) presented three rules concerning the development of fish parasite fauna: (1) prevalence and intensity of infection increase with age; (2) qualitative changes in the fauna are associated with changes in the habitat or behavior of the host; (3) initial infection of young fish is with parasites that have a direct life cycle or that actively penetrate their host. Rule 3 is not related to this study, and rule 2 is definitely supported. Rule 1, however, may not be as generally applicable as was believed, despite support from other authors (Rawson, 1973; Bortone et al., 1978). Smith (1949) found that ergasilids infest young fish more heavily than old, and Joy (1976) reported a decline in both prevalence and intensity of E. lizae with age (length) of spot (Leiostomus xanthurus). In the present study, prevalence of E. versicolor on filament tips was negatively correlated with length of CR mullet. Regarding intensity, the correlation with length of SK mullet was positive for E. versicolor but negative for E. lizae, and the correlation with length of CR mullet was positive for E. versicolor between hemibranchs but negative for E. versicolor on the distal filaments and for M. lugubris (Table 1).

It would seem, then, that no general rule may be drawn relating the length/age of fish with prevalence and intensity of parasites. The biology of each parasite/host combination should probably be regarded separately since parasite and fish probably differ in some aspect of behavior or physiological preference. In addition, the

population structure, diet, and feeding behavior of a fish may differ between habitats (Collins, 1981), and many parasites (Reshetnikova, 1955, as cited by Polyanski, 1958) especially ectoparasites, react in various ways to changes in hydrological and hydrochemical conditions. Thus, the ecology of even one parasite/host combination may differ drastically between habitats.

Previous authors (Bortone et al., 1978; Noble et al., 1963) have noted that in some cases intensity or prevalence of ergasilid infestation is correlated with fish length but lower levels of parasitism occur in the longest size classes of hosts. The same phenomenon with respect to intensity of E. versicolor at SK (Figure 2) and between hemibranchs at CR (Figure 5) was noted in the present study. The most plausible explanations previously proposed are immunity to infestation by the oldest hosts and incorrect inference caused by small samples. The former would not apply, however, to the reciprocal phenomenon noted in the present study; i.e., the intensity of E. lizae at SK and the prevalence of E. versicolor on the distal parts of gill filaments at CR, both negatively correlated with host length, increase in only the longest length class (Figures 3 and 6). In addition, no other evidence for the existence of immunity to these parasites has been produced. The second explanation, while still possible, decreases in probability as more cases of the "aberrant largest hosts" are reported.

The results of this study may be applicable to mariculture operations. Epizootics of some ectoparasites of mullet in brackish water may be controlled by replacing brackish with freshwater, when

appropriate facilities are available. If fish must be held and acclimated in containers, such as during transfer between ponds with different salinities, rapid acclimation is recommended to reduce stress-related mortality. Mullet easily survived salinity changes of 30 ppt. in 4 hrs. at temperatures up to 30°C in the present study. The salinity reduction would probably control infestation by M. macracantha, B. nitidus, and some species of argulids within two weeks. Reducing the salinity would not control epizootics of E. versicolor or E. lizae, but since the eggs of the latter species are lost within six days in freshwater, reproduction of this parasite could be reduced or eliminated and eventual control achieved. While cage culture of mullet is not commonly practiced, there may be regions where this fish is an important dietary component of humans but cannot be caught at certain times, such as during the spawning season. In this case, the holding of mullet in simple cages or enclosures would ensure access to a steady supply of fish. Abnormally high parasite loads were noted on only a few caged individuals, and fish held in brackish water remained in good condition through 40 days in the present study. Thus, groups of mullet could probably be held in cages for extended periods without high mortality in at least some localities.

SUMMARY

At CR (freshwater) the comparatively depauperate fauna included only two commonly encountered ectoparasites: E. versicolor and M. lugubris. At the brackish study site (SK) E. versicolor, E. lizae, N. lizae, B. nitidus, M. macracantha, and argulids were common, and several other copepods and a leech (Malmiana philotherma ?) were recorded. The most common ectoparasite at both study sites, E. versicolor was found most often proximally between gill hemibranchs of hosts in freshwater, apparently the first time this has been reported, but infested only the distal tips of the filaments in brackish water. Pathological host response to this parasite was noted for those at filament tips but not between hemibranchs. Experimental translocation of mullet between the study sites showed that the distribution of E. versicolor changed. This change was not caused by the already attached E. versicolor moving from between hemibranchs to distal tips or vice versa as the salinity changed, but by new infestations on the portion of the gills typically parasitized at that study site.

Ergasilus lizae, N. lizae, and M. macracantha survived at least two weeks on mullet held in freshwater, but the eggs of E. lizae and N. lizae were lost. Adult argulids survived at least 12 days of exposure to freshwater, but immature argulids, found only on tips of

gill filaments, were not found after three days. Bomolochus nitidus had the lowest tolerance to freshwater and was never found on translocated mullet.

A group of larger mullet, primarily females, may be semi-permanent residents of the freshwater river. Evidence for this theory includes (1) freshwater mullet are larger and more often females than mullet caught in brackish water (Collins, 1981); (2) the five mullet caught in freshwater that were infested with ectoparasites typical of the brackish habitat (E. lizae, M. macracantha, M. philotherma) were all small (≤ 270 mm. SL), a size more typical of brackish than freshwater; (3) neither prevalence nor intensity of the larval nematode Contracaecum multipapillatum (?) was correlated with length of mullet caught in freshwater, but in fish from brackish water prevalence was 100% and intensity was positively correlated with host length, suggesting that mullet caught in freshwater, where the life cycle of C. multipapillatum probably is not completed, spend extensive amounts of time there; (4) prevalence of E. versicolor at distal tips of filaments was 100% and intensity was positively correlated with host length at SK, but at CR both prevalence and intensity were negatively correlated with host length, suggesting that the longer mullet spend more time in freshwater. Commercial fishing is not permitted in most of Florida's freshwater rivers. If groups of large mullet do in fact reside semi-permanently in these habitats, they may constitute breeding stock reservoirs ensuring that populations of this commercially important species are not depleted by over-fishing.

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BIOGRAPHICAL SKETCH

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Frank J. Maturro, Jr.

Frank J. Maturro, Jr.
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Frank G. Nordlie

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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