HELMINTH PARASITISM OF THREE LARVAL FISHES IN THE NORTHERN GULF OF MEXICO¹

Helminth infections of the pelagic larvae of marine fishes are ecologically germane to fisheries biology for two important reasons. First, endoparasites, although not likely to actively kill host larvae, may passively contribute to larval mortality by competing for nutrients and space in the alimentary canal (Rosenthal 1967) or by causing pathological lesions (Yamashita 1979), thereby compromising growth (May 1983). Because growth abets both feeding success and predator avoidance, it is linked with survival and therefore is an important factor in determining cohort size (Hunter 1981). Second, helminth infections can be useful indicators of trophic relationships because the life stages of cestodes and trematodes are transmitted through intermediate hosts before infection of the definitive host (see review in Campbell et al. 1980).

Given that larval fishes eat copepods, the vectors of many marine helminth infections (Cheng 1964; Gibson and Bray 1979), it should not be surprising that they are infected with cestodes and trematodes. Yet, despite extensive laboratory and field studies of larval fish feeding (see review in Hunter 1981), there are only incidental reports, none comprehensive, of helminth infections (Lebour 1918; Ogilvie 1927; Hentschel 1950; Bowers and Williamson 1951; Rosenthal 1967; Marak 1974; Mackenzie 1974; Yamashita 1979). Herein I report the prevalence and temporal variation of cestode and trematode infections in three species of larval fishes collected in the northern Gulf of Mexico: gulf menhaden, Brevoortia patronus Goode; spot, Leiostomus xanthurus Lacepède; and Atlantic croaker, Micropogonias undulatus (Linnaeus).

Methods

Larvae of gulf menhaden, spot, and Atlantic croaker were collected on four cruises in the northern Gulf of Mexico in December 1979, February 1980, December 1980, and February 1981. Cruises generally occupied three stations (at the 5.5, 27, and 55 m isobaths) along each of three transects (off of Galveston Bay, the Mississippi Delta, and Cape San Blas). Collections from three discrete depths taken at 0001, 0600, 1200, and 1800 h (CST) at each station with a Multiple Opening/Closing Net and Environmental Sensing System² (MOCNESS) (Wiebe et al. 1976) were fixed in 5% Formalin buffered with sodium borate. Nominal depths of the MOCNESS samples corresponded to strata just above the thermocline, in the middle of the upper mixed layer, and just below the surface. The MOCNESS was equipped with nine 1.0 by 1.4 m, 505 μ m mesh nitex nets and with 0.25 by 0.35 m, 67 μ m mesh nets "nested" inside.

Larvae of all three species were removed from MOCNESS samples, measured (notochord or standard length), and dissected, except when the total number of a species exceeded 30 larvae. In these cases, 30 larvae were chosen randomly from a numbered grid by consulting a table of random numbers. Contents of the entire alimentary canal, including parasites, were identified and enumerated. Helminths were stained with Mayer's paracarmine and mounted to aid in identification.

The cooccurrence of cestodes and trematodes was assessed by the index of affinity (Fager 1957; Fager and McGowan 1963). Independence in the prevalence of helminth infections was assessed by constructing four-way contingency tables (species of fish larvae \times cohort \times month \times prevalence of infection) and by referring G² to a chi-square distribution (Fienberg 1970). In this log likelihood ratio test, 1×10^{-7} was added to each observed value in order to allow the use of natural logarithms with observed zero incidences.

Results and Discussion

Parasites

Two taxa of helminths were identified, a tetraphyllidean cestode of the *Scolex pleuronectis* complex and a digenean hemiurid trematode *Aphanurus* sp. All specimens of *S. pleuronectis* were plerocercoids with the exception of one juvenile that had undergone strobilization. *Aphanurus* sp. were late metacercariae or adults; gonads were developed but ova were never visible.

Helminths occurred primarily in the midgut; only 4 of 64 (6.2%) gulf menhaden and none of the spot and Atlantic croaker larvae had helminths in the hindgut (sensu Iwai 1969). Usually a single larva was infected by only one cestode and/or one trematode; 8 of 64 (12.5%) gulf menhaden larvae were infected simultaneously by as many as three helminths.

Cestode plerocercoids of the S. pleuronectis com-

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²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

plex are ubiquitous endoparasites of adult fishes (Appey and Burt 1982) including *Brevoortia tyrannus* (Meyers 1978). They also have been reported in the alimentary canal of *Clupea harengus* larvae (Rosenthal 1967). Plerocercoids of the *Scolex polymorphus* complex, a systematic composite that is similar to *S. pleuronectis*, infect a variety of fishes and invertebrates in the northern Gulf of Mexico (Overstreet 1978). Digenean hemiurid trematodes, but none of the genus *Aphanurus* (Lebour 1918; MacKenzie 1974; Yamashita 1979), have been reported in larval fishes of disparate taxa. *Aphanurus* sp. also infects adult *B. tyrannus* (Meyers 1978).

Prevalence of Infections

The cooccurrence of cestodes and trematodes in larval gulf menhaden did not indicate affinity. Scolex pleuronectis and Aphanurus sp. cooccurred in only 2 of 64(3.1%) infected gulf menhaden larvae and never in the 1 spot or the 4 Atlantic croaker larvae; the theoretically expected coincidence of infection was 15%. The index of affinity was -0.02 where an index >50 is expected if species show positive affinity (Fager and McGowan 1963). Whereas Ogilvie (1927) reported that most C. harengus larvae in the North Sea were infected simultaneously with both a cestode and a trematode, Hentschel (1950) reported only cestode infections of C. harengus in the North and Baltic Seas. The present lack of affinity suggests that S. pleuronectis and Aphanurus sp. do not share a common intermediate host.

The prevalence of infections (Table 1) differed significantly among the three species of fishes (Tables 2, 3). Scolex pleuronectis infected 26 of 1,067 (2.4%) gulf menhaden and 2 of 235 (0.8%) Atlantic croaker larvae examined. No S. pleuronectis were found in spot larvae. Aphanurus sp. infected 38 (3.6%) gulf menhaden, 1 (0.5%) spot, and 2 (0.8%)Atlantic croaker larvae. The high prevalence of infection by both the cestode and the trematode in gulf menhaden larvae and the corresponding low or complete lack of infection by the cestode in spot and Atlantic croaker larvae imply that diets differ. The diets of these three species did differ significantly with the diet of gulf menhaden larvae the most distinct (Govoni et al. 1983). Gulf menhaden larvae ate a more diverse diet that included phytoplankters (mainly dinoflagellates) as well as zooplankters (including tintinnids, pelecypods, pteropods, and all stages of copepods). The diets of larval spot and Atlantic croaker were restricted to zooplankton. Significant differences in diet notwithstanding, the lack of adequate systematic definition (the S. pleuronectis complex), and the lack of tetraphyllidean and hemiurid host specificity confound relationships between helminth infections and diet among these larval fishes.

The prevalence of infections (Table 1) was lower than previously reported helminth infections of larval fishes caught at sea (Lebour 1918; Hentschel 1950; MacKenzie 1974). Previous reports have dealt with larger fish larvae that were exposed to helminth infection for longer periods (MacKenzie 1974) and

Species	Winter	Month	Cestodes		Trematodes		Larvae examined	
			Infected	Uninfected	Infected	Uninfected	Number	Totals
Brevoortia patronus	1979-80	Dec. Feb. Σ	1	163	2	162	164	
			21	319	35	305	340	
			22	482	37	467	504	
	1980-81	Dec.	0	177	0	177	177	
		Feb. Σ	4	382	1	385	386	
			4	559	1	562	563	1.067
Leiostomus xanthurus	1070.00				_			.,
	1979-80	Dec.	0	13	0	13	13	
		reo.		12	_1		12	
		2	0	25	1	24	25	
	1980-81	Dec.	0	134	0	134	134	
		Feb. Σ	_0	37	0	37	37	
			0	171	0	171	171	
								196
Micropogonias undulatus	1979-80	Dec.	1	16	2	15	17	
		Feb.	0	18	0	18	18	
		Σ	1	34	2	33	35	
	1980-81	Dec.	0	151	0	151	161	
		Feb.	ĩ	48	õ	49	49	
		Σ	1	199	0	200	200	235

 TABLE 1.—The prevalence of cestode (Scolex pleuronectis) and trematode (Aphanurus sp.). infection in larval cohorts of Brevoortia patronus, Leiostomus xanthurus, and Micropogonias undulatus in the northern Gulf of Mexico.

TABLE 2.—Tests of independence in the prevalence of cestode (Scolex pleuronectis) infection among larval Brevoortia patronus, Leiostomus xanthurus, and Micropogonias undulatus collected in December 1979, February 1980, December 1980, and February 1981 in the northern Gulf of Mexico.

		Partial asso	Marginal association		
Variable	df	G²	Probability (%)	G²	Probability (%)
Prevalence (P)	1	1,798.33	<0.001		
Month (M)	1	23.15	<0.001		
Cohort (C)	1	92.34	<0.001		
Species (S)	2	899.60	< 0.001		
PM	1	12.09	<0.001	19.4	<0.001
PC	1	16.73	<0.001	23.83	<0.001
PS	2	2.38	>0.050	10.77	=0.010
MC	1	0.93	>0.050	32.80	< 0.001
MS	2	181.92	< 0.001	215.08	<0.001
CS	2	127.76	<0.001	160.98	<0.001
PMC	1	4.43	>0.050	1.34	>0.050
PMS	2	4.33	>0.050	0.81	>0.050
PCS	2	2.20	>0.050	0.00	>0.050
MCS	2	17.49	<0.001	15.34	<0.001
PMCS	2	0.05	>0.050		

TABLE 3—Tests of independence in the prevalence of trematode (Aphanurus sp.) infection among larval Brevoortia patronus, Leiostomus xanthurus, and Micropogonias undulatus collected in December 1979, February 1980, December 1980, and February 1981 in the northern Gulf of Mexico.

		Partial asso	Marginal association			
Variable	df	G²	Probability (%)	G²	Probability (%)	
Prevalence (P)	1	1,700.74	<0.001			
Month (M)	1	23.15	<0.001			
Cohort (C)	1	92.34	<0.001			
Species (S)	2	899.60	<0.001			
PM	1	13.87	<0.001	23.57	<0.001	
PC	1	58.80	<0.001	71.46	<0.001	
PS	2	0.08	>0.050	12.24	<0.010	
MC	1	0.39	>0.050	32.80	<0.001	
MS	2	183.17	<0.001	215.08	<0.001	
CS	2	126.11	<0.001	160.98	<0.001	
PMC	1	0.10	>0.050	0.34	>0.050	
PMS	2	8.71	>0.050	6.01	=0.050	
PCS	2	0.14	>0.050	0.68	>0.050	
MCS	2	18.04	<0.001	15.34	< 0.001	
PMCS	2	0.00	>0.050			

that ate greater numbers of copepods (Hentschel 1950). Copepods are the intermediate hosts of tetraphyllidean cestodes (Cheng 1950) and digenean hemiurid trematodes (Gibson and Bray 1979).

Although the prevalence of infections was low for all species, it became greater in gulf menhaden and Atlantic croaker larvae as length increased. No helminths were found in larval gulf menhaden or Atlantic croaker shorter than 5.01 mm. Scolex pleuronectis infected only 2 of 557 (0.4%) gulf menhaden larvae <15.01 mm long but 24 of 386 (6.2%) larvae between 15.01 and 20.00 mm; Aphanurus sp. infected no gulf menhaden larvae <15.01 mm, but 37 of 386 (9.6%) larvae between 15.01 and 20.00 mm.

The prevalence of S. pleuronectis and Aphanurus sp. infections (Table 1), being significantly (Tables 2,

3) greater in February than in December, particularly for gulf menhaden, may be related to differences in the corresponding size of larvae and to ontogenetic changes in their diets. Larger larvae, which had a higher prevalence of infection, were more abundant in February than in December. Spawning of gulf menhaden during these years was bimodal with peaks in late December and late January,³ thus growth of cohorts resulted in longer larvae in February collections. Inasmuch as gulf menhaden larvae did not eat appreciable numbers of adult copepods until they had grown longer than 5.01 mm², one would expect a higher prevalence of helminth infection in months when larger larvae were more abundant. Since the length of the spot and Atlantic croaker larvae collected changed little from December to February, a seasonal trend in the prevalence of infection would not be expected.

Larval cohorts collected in the winter of 1979-80 (Table 1) showed a significantly greater prevalence of infection than larvae collected in 1980-81 for both S. pleuronectis (Table 2) and Aphanurus sp. (Table 3), but shifts in diet do not explain this difference. Gulf menhaden larvae exemplified this annual difference in infection owing to the greater number of larger larvae (>5.01 mm) collected and examined from both winters. Larval gulf menhaden ate a greater number and a greater diversity of copepods in the winter of 1980-81 than in 1979-80 (Govoni et al. 1983).

Whether gulf menhaden, spot, and Atlantic croaker larvae are definitive or paratenic (auxiliary) hosts for members of the *S. pleuronectis* complex or *Aphanurus* sp. are not known, due in part to the lack of systematic definition. In either case, the levels of infection in terms of the prevalence of infection as well as the parasite loads on individual larvae are lower than those that directly cause death of larval seabream (*Pagulus* = *Chrysophrys major*) in the laboratory (Yamashita 1979). Indirect effects of helminth infections (May 1983) on larval fish cohorts are not yet clear.

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EMPIRICAL USE OF LONGEVITY DATA TO ESTIMATE MORTALITY RATES

Various investigators have utilized compendia of life history parameters to develop equations for predicting values of difficult-to-estimate parameters from easily measured or estimated quantities. For example, Pauly (1979) developed multiple regressions to predict the natural mortality rate of fish from growth parameters and mean water temperature. Ohsumi (1979) developed linear regressions for estimating natural mortality of cetaceans from maximum length or maximum age. In this paper, a general regression equation is developed to predict the total mortality rate of fish, cetacean, and mollusk stocks from the maximum age.

It seems intuitive that longevity and mortality rate in a species should be inversely related since animals from a population with a high mortality rate would not survive long enough to reach old age. The nature of the relationship between mortality and maximum age is explored below.