

Species-Specific Predation on Amphipod Crustacea by the Pinfish *Lagodon rhomboides*: Mediation by Macrophyte Standing Crop

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Abstract

The amphipod species consumed by *Lagodon rhomboides* represented only a small subset of the amphipod assemblage available at three seagrass habitats in Apalachee Bay, Florida (USA). Predatory preferences were related most closely to the microhabitat of prey species and were unrelated to amphipod abundances. Important prey species were all epifaunal types. Consumption of preferred amphipod species was non-selective at a site with sparse macrophyte cover, but selectivity increased with macrophyte biomass. The amphipod species that were preferentially selected as prey by pinfish correspond with those that have been suggested as being limited by fish predators. It was suggested that mediation of predator behavior by physical structure in seagrass meadows may play an important role in the regulation of species richness and abundances. Species-specific identification of prey is recommended for food-habit studies.

Introduction

The pinfish (*Lagodon rhomboides*: Sparidae) is the most numerous epibenthic fish predator in seagrass habitats of the Gulf of Mexico and the Atlantic coast of the United States of America (Kilby, 1955; Hoese and Jones, 1963; Adams, 1976a; Stoner, 1979). Amphipods are among the most important food items consumed by pinfish (Reid, 1954; Caldwell, 1957; Darnell, 1958; Hansen, 1969; Carr and Adams, 1973; Adams, 1976b) and, in Apalachee Bay, Florida, amphipods consistently make up the largest portion of the stomach contents of juvenile pinfish (Stoner, 1979). Over 30 species of amphipods were collected in a benthic survey of Apalachee Bay (Stoner, in press); 22 of these were found in stomachs of pinfish, and only 7 species individually constituted more than 4% of the amphipods consumed. Furthermore, individual amphipod species appeared not to be taken relative to their abundances in the field. In a study of amphipod abundance patterns and reproductive seasonalities (Stoner, in preparation) it was concluded that amphipod species were

differentially affected by the presence and feeding activities of fish predators (particularly *L. rhomboides*) and that regulation of amphipod populations by predation was mediated by the standing crops of benthic macrophytes at different study sites.

It is well known from models (Emlen, 1966, 1968; MacArthur and Pianka, 1966; Levins and MacArthur, 1969; Pulliam, 1974; Estabrook and Dunham, 1976) and empirical evidence based on predation by fishes (Ivlev, 1961; Zaret and Rand, 1971; Werner and Hall, 1974) that dietary specialization occurs with increasing total prey abundances. A large body of literature is also available on size-selective predation by fishes (Shelbourne, 1962; Brooks and Dodson, 1965; Galbraith, 1967; Brooks, 1968; Ware, 1972; Wong and Ward, 1972; Werner, 1974; Zaret and Kerfoot, 1975; and others). Ware (1972, 1973) concluded that diets of fish are more closely related to physical and behavioral properties of the food organisms than their densities. It is generally accepted that morphological and behavioral limitations of both predator and prey regulate food habits of fishes; however, little is known about the role of habitat structure on predator-prey relationships.

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In laboratory studies, Nelson (1978) found that intensities of predation by fish and shrimp were inhibited by increasing seagrass-blade densities, but only one amphipod species was tested as a prey organism in the experiment. Laboratory studies of Ware (1972) and Stein (1977) were designed to examine the significance of habitat structure on prey selectivity. Ware found that leaf litter provided differential protection to two amphipod species from predation by the rainbow trout *Salmo gairdneri*. Stein reported that selectivity for particular sizes and sexes of crayfish by small-mouth bass varied with substrate type. Field observations appear to confirm Stein's laboratory findings. In the field, the mummichog *Fundulus heteroclitus* was characterized by decreasing predatory efficiency and selectivity with increasing habitat complexity as measured by density of marsh-grass blades (Vince et al., 1976).

Because field data suggest that fish and decapod predators limit abundances of amphipods in seagrass meadows (Young et al., 1976; Young and Young, 1977, 1978; Nelson, 1978; Stoner, in preparation) species-specific predation by numerically dominant predators may exert considerable influence on the composition of amphipod assemblages. This study was initiated to test the hypothesis that prey selectivity by *Lagodon rhomboides* is mediated by seagrass biomass. Some of the amphipod population data obtained earlier (Stoner, in preparation) are discussed in terms of the findings reported here.

Materials and Methods

As described earlier (Stoner, 1979), *Lagodon rhomboides* were collected by monthly trawling at four permanently marked stations in Apalachee Bay, Florida (USA). For the topic of the present paper, only fish collected for the 6 month period from April, 1977, through September, 1977, were examined since this was the period during which high numbers of juvenile pinfish (16 to 80 mm standard length) were available. Over 400 pinfish for each of 3 vegetated stations were examined; however, the unvegetated site produced too few pinfish for satisfactory evaluation of species-specific predation, and this site was therefore eliminated from the analysis presented here. During the 6 month sampling period, benthic macrophyte biomass was relatively constant at each of the three vegetated sites (Fenholloway 12, Econfina 10, and Econfina 12). These stations will be

referred to as the sites of low (166 g dry weight m^{-2} , standard deviation = 57), medium (266 g dry weight m^{-2} , SD = 65), and high (399 g dry weight m^{-2} , SD = 129) macrophyte biomass, respectively. The stations were all polyhaline, with salinities ranging from 19 to 34‰, and were characterized by similar water quality (see Stoner, in preparation).

The procedures for fish-stomach analysis have been described previously (Stoner, 1979). This included the gravimetric sieve fractionation method developed by Carr and Adams (1972) for use with small fishes. All amphipods in stomachs of pinfish were counted and identified to species except where broken beyond recognition.

Amphipods were collected at each field site on each of the dates that fish were collected. Data on amphipod abundances were taken from a parallel study (Stoner, in preparation).

Results

The relative frequencies of occurrence of 22 amphipod species in the stomachs of *Lagodon rhomboides* varied widely among the three study sites (Table 1). During the 6 month period, *Cymadusa compta* (Amphithoidae) was the most frequently consumed species over all stations (24.4% of occurrences); however, frequency of occurrence ranged from 16.0% at the heavily vegetated site (Econfina 12) to 35.8% at the site with medium vegetation (Econfina 10). Three other amphipods individually contributed over 10% of the overall occurrences: *Lembos* sp. A (Aoridae), *Elasmopus levis* (Melitidae), and *Paracaprella tenuis* (Caprellidae). Differences among stations were most obvious in the consumption of *P. tenuis*, which was lowest at Econfina 10, and *Lembos* sp. A, which was the most important amphipod consumed by pinfish at the heavily vegetated site (Econfina 12). Only three other species individually contributed more than 4% of the total. *Gitanopsis* sp. A (Amphilochoidea) had the highest frequency of occurrence in stomachs of fish from the heavily vegetated site (12.3%), but contributed only 2.5% of the amphipods consumed at Econfina 10. *Rudilemboides naglei* (Aoridae) was an important food species at the two most heavily vegetated sites (8.7 and 9.6%), but made up only 1.3% of the occurrence at the site with sparse vegetation. *Batea catharinensis* (Bateidae) contributed from 3.2 to 5.3% of the amphipods consumed at the three stations. Fifteen other amphipod species were found in pinfish stomachs, but none of these species contributed more than 2.8%

Table 1. Amphipod species consumed by juvenile pinfish (*Lagodon rhomboides*) at 3 stations in Apalachee Bay, Florida. *N* = number of observations

Prey species	Fenholloway 12		Econfina 10		Econfina 12		Total	
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
<i>Cymadusa compta</i>	34	22.5	58	35.8	30	16.0	122	24.4
<i>Lembos</i> sp. A	16	10.6	22	13.6	38	20.3	76	15.2
<i>Elasmopus levis</i>	22	14.6	18	11.1	21	11.3	61	12.1
<i>Paracaprella tenuis</i>	18	11.9	7	4.3	25	13.4	50	10.0
<i>Gitanopsis</i> sp. A	8	5.3	4	2.5	23	12.3	35	7.0
<i>Rudilemboides naglei</i>	2	1.3	14	8.7	18	9.6	34	6.8
<i>Batea catharinensis</i>	8	5.3	7	4.3	6	3.2	21	4.2
<i>Corophium</i> sp. A	8	5.3	6	3.7	0	0	14	2.8
<i>Pontogenia</i> sp. A	6	4.0	2	1.2	6	3.2	14	2.8
<i>Melita appendiculata</i>	12	7.9	0	0	0	0	12	2.4
<i>Ampelisca vadorum</i>	1	0.7	6	3.7	4	2.1	11	2.2
<i>Corophium louisianum</i>	5	3.3	5	3.1	0	0	10	2.0
<i>Lysianopsis</i> spp. (2)	1	0.7	4	2.5	4	2.1	9	1.8
<i>Carinobatea carinata</i>	0	0	2	1.2	5	2.7	7	1.4
<i>Erichthonius</i> sp. A	0	0	4	2.5	3	1.6	7	1.4
<i>Synchelidium americanum</i>	5	3.3	0	0	2	1.1	7	1.4
<i>Cerapus</i> sp. A	2	1.3	0	0	2	1.1	4	0.8
<i>Gammarus</i> spp. (2)	1	0.7	2	1.2	0	0	3	0.6
<i>Ampelisca verrilli</i>	2	1.3	0	0	0	0	2	0.4
<i>Paraphoxus</i> sp. A	0	0	1	0.6	0	0	1	0.2

Table 2. Abundances of amphipods at 3 stations in Apalachee Bay, Florida, from April through September, 1977. *N m*⁻² = mean number of amphipods per square meter based on monthly sampling

Species	Fenholloway 12		Econfina 10		Econfina 12	
	<i>N m</i> ⁻²	%	<i>N m</i> ⁻²	%	<i>N m</i> ⁻²	%
<i>Cymadusa compta</i>	129	9.7	397	16.9	201	17.4
<i>Lembos</i> sp. A	79	5.9	132	5.6	91	7.9
<i>Elasmopus levis</i>	230	17.3	532	22.6	170	14.8
<i>Paracaprella tenuis</i>	32	2.4	22	0.9	35	3.0
<i>Gitanopsis</i> sp. A	38	2.9	63	2.7	6	0.5
<i>Rudilemboides naglei</i>	35	2.6	205	8.7	245	21.3
<i>Batea catharinensis</i>	54	4.2	35	1.5	38	3.3
<i>Corophium</i> sp. A	25	1.9	3	0.1	0	0
<i>Pontogenia</i> sp. A	63	4.7	82	3.5	67	5.8
<i>Melita appendiculata</i>	101	7.6	41	1.7	3	0.3
<i>Ampelisca vadorum</i>	82	6.2	183	7.8	94	8.1
<i>Corophium louisianum</i>	13	1.0	38	1.6	0	0
<i>Lysianopsis alba</i>	183	13.8	315	13.4	32	2.8
<i>Lysianopsis hirsuta</i>	16	1.2	25	1.1	0	0
<i>Carinobatea carinata</i>	47	3.5	69	2.9	104	9.0
<i>Erichthonius</i> sp. A	16	1.2	16	0.7	0	0
<i>Synchelidium americanum</i>	47	3.5	13	0.5	10	0.9
<i>Cerapus</i> sp. A	41	3.1	16	0.7	16	1.4
<i>Gammarus macromucronatus</i>	0	0	0	0	3	0.3
<i>Gammarus mucronatus</i>	0	0	3	0.1	0	0
<i>Ampelisca verrilli</i>	0	0	113	4.8	25	2.2
<i>Paraphoxus</i> sp. A	16	1.2	32	1.4	0	0
<i>Colomastix</i> sp. A	0	0	6	0.2	0	0
<i>Leucothoe</i> sp. A	0	0	6	0.2	0	0
<i>Listriella</i> sp. A	3	0.2	0	0	0	0
<i>Listriella</i> sp. B	3	0.2	0	0	0	0
<i>Stenothoe</i> sp. A	6	0.5	6	0.2	6	0.5
<i>Tiron tropakis</i>	69	5.2	3	0.1	6	0.5

of the total. The 7 species which contributed over 4% of the overall frequency of occurrence will be considered the "preferred" prey species. All are epifaunal forms, either free-living or domicolous (tube-dwelling). Infaunal species, including members of the genera *Corophium*, *Lysianopsis*, *Ampelisca*, and *Paraphoxus*, contributed little to the diets of pinfish.

Relative abundances of amphipod species in the field (Table 2) varied considerably from relative frequencies found in pinfish stomachs (Table 1). Although common in the field, certain amphipods such as *Ampelisca vadorum* (Ampelis-

cidae), *Lysianopsis alba* (Lysianassidae), and *Carinobatea carinata* (Bateidae) were not common food items of *Lagodon rhomboides*. On the other hand, certain species such as *Cymadusa compta*, *Paracaprella tenuis*, and *Gitanopsis* sp. A were much more common in fish stomachs than in the field. Many of the rare amphipods were never consumed by pinfish, as might be predicted.

Upon first examination, consumption of an amphipod species by pinfish appeared to depend on two characteristics of the prey: (1) microhabitat (i.e., infaunal, epifaunal, domicolous, etc.), and (2) abundance in the field. To examine the effects of benthic macrophyte biomass on amphipod selectivity by pinfish, only those species known to occupy microhabitats appropriate for capture by pinfish were considered. Because of constraints placed on the predator by its morphology and behavioral capabilities, certain amphipod types (e.g. infaunal burrowers) were never consumed despite high abundance in the field; therefore, only the 7 "preferred" epibenthic species were included in further analysis. Other epifaunal species including *Melita appendiculata*, *Carinobatea carinata*, and *Gammarus* spp. were too rare in the field and in stomachs to provide reliable information on their selectivities by pinfish, and since there is general agreement in the literature that whether or not a food item is taken depends only on the abundance of higher ranking prey (Pyke et al., 1977), analysis of species-specific selectivity limited to the 7 "preferred" species of amphipods is justified. Except for *Rudilemboides naglei*, relative field abundances of the 7 "preferred" prey species were similar at the three locations; however, the relationship between the relative abundance of

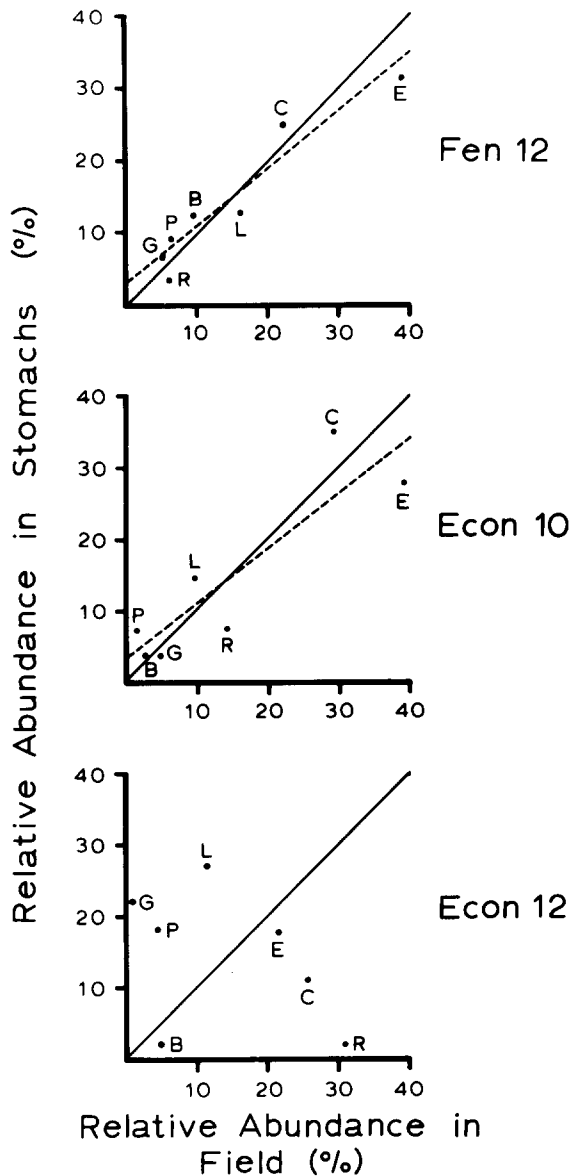


Fig. 1. Relative abundance of preferred amphipod species in stomachs of *Lagodon rhomboides*, shown as a function of amphipod abundances at 3 field stations in Apalachee Bay, Florida, USA. Continuous line: response predicted for a non-selective predator; broken line: significant ($P < 0.01$) linear regression equations fitted to the data. B: *Batea catharinensis*; C: *Cymadusa compta*; E: *Elasmopus levis*; G: *Gitanopsis* sp. A; L: *Lembos* sp. A; P: *Paracaprella tenuis*; R: *Rudilemboides naglei*

amphipod species in the field and in fish stomachs was different at the three field sites (Fig. 1). The degree of species-specific selectivity was a function of macrophyte biomass at the study site. Where vegetation was sparse (Fenholloway 12) amphipods were consumed by pinfish in proportions very close to those found in the field (i.e., no selectivity among

the "preferred" species was found). The relationship between amphipod abundance (x) and amphipod consumption (y) at Fenholloway 12 is explained by the equation:

$$y = 0.791(x) + 2.958 \quad (r = 0.946, P < 0.01),$$

which is close to the predicted response. With intermediate macrophyte cover (Econfina 10) amphipod consumptions were still closely related to field abundances; however, consumption rates diverged from predicted values more than those at the sparsely vegetated site. The relationship at Econfina 10 is explained by the equation:

$$y = 0.775(x) + 3.224 \quad (r = 0.884, P < 0.01).$$

At Econfina 10, *Cymadusa compta*, *Lembos* sp. A, and *Paracaprella tenuis* were taken more frequently than predicted according to field abundances. *Elasmopus levis* and *Rudilemboides naglei* were taken less frequently than predicted. At Econfina 12, where vegetation was very heavy, amphipod consumption diverged dramatically from that predicted from field abundances of amphipods, and no linear model fits the relationship. *Lembos* sp. A, *P. tenuis*, and *Gitanopsis* sp. A were heavily selected at this station while *C. compta* and *R. naglei* were underutilized despite high field abundances. *E. levis* and *Botea catharinensis* were close to, but below predicted consumption frequencies.

Discussion

Data presented in this paper show that only a small subset of the amphipod assemblage in Apalachee Bay is used as prey by *Lagodon rhomboides*. Amphipods consumed most frequently were epifaunal types, either free-living or domicolous. This finding was not surprising since, during field observations, I found that young pinfish normally swim and feed among seagrass blades. They rarely venture beyond seagrass-covered habitats into sand patches and, except at night, rarely approach the sediment between plants. I never observed pinfish picking up sediments, and polychaetes found in stomachs (Stoner, 1979) were all epifaunal types (e.g. *Platynereis dumerilii*, syllids, and serpulids which live on seagrass blades). The morphology, natural history, and microhabitat of an animal is well known to determine which predators normally consume it (Ricker, 1937; Royama, 1970; Ware, 1973; Hughes, 1979), yet few researchers working with small predators identify prey organisms to the species or even generic levels. Keast (1970) and Kislalioglu and Gibson (1977) also pointed out the importance

of species-specific gut analysis. Prey organisms are generally categorized in taxonomic groups far too broad for usefulness; consequently, selection patterns are obscured. Kislalioglu and Gibson found that food partitioning among fishes in Loch Etive, Scotland, was discovered only when food habits were examined at the species level. Also, since the abundance of predators or their food habits are often examined as a function of prey availabilities, information must be available on the abundances of true prey species. For example, only about 50% of the amphipod numbers at Apalachee Bay stations were potential prey items for *L. rhomboides*, and overall patterns of amphipod abundance did not always reflect abundance of prey species. Knowledge of prey species is especially important where many species are found among particular benthic assemblages such as occur in seagrass habitats. I assert that the researcher who conducts feeding studies must be thoroughly familiar with the taxonomy of the prey organisms unless only the most gross evaluation of food habits is required.

At given sampling sites, the degree of selectivity for amphipod species was shown to be a function of macrophyte standing crop. At low macrophyte densities, preferred amphipod species were consumed in frequencies very close to those found in surveys of the benthos. With increasing vegetation, certain species were consumed in frequencies greater than those in the field (e.g. *Lembos* sp. A, *Paracaprella tenuis*, and *Gitanopsis* sp. A. Other amphipods appeared to be protected from pinfish predation by denser vegetation, especially *Cymadusa compta* and *Rudilemboides naglei*. In another paper (Stoner, in preparation), I noted a dramatic decline in the population densities of *Lembos* sp. A at the heavily vegetated station (Econfina 12) following spring migration of pinfish to the grassbeds. Since *Lembos* sp. A is reproductively active during the summer, I attributed the population decline to fish predation. I also suggested that *P. tenuis* and *Gitanopsis* sp. A were limited by predators which invaded the shallow seagrass flats during spring and summer. Selectivity for *Lembos* sp. A, *P. tenuis* and *Gitanopsis* sp. A shown in this paper seem to bear out my earlier hypotheses concerning population dynamics of these amphipods. I also suggested that population densities of *C. compta*, *Elasmopus levis* and *R. naglei* appeared not to be affected by fish predation. Data presented here show that these species are not positively selected as prey by pinfish.

Since the exact microhabitats and behaviors of the 7 preferred amphipod species are unknown, one may only speculate as to mechanisms involved in differential prey selectivity with increasing macrophyte biomass. Both groups of amphipods, those selected positively and those selected against, included free-living and domicolous forms. Neither type appears to be better protected by macrophyte cover. Schoener (1971) and Werner (1974) found that prey of small size were taken by predators in order of their size, but since large and small amphipods were found in both positively and negatively selected groups, size does not appear to be a particularly important factor in the prey selectivity process in pinfish. *Cymadusa compta* is heavily pigmented and may be well hidden by vegetation, but *Lembos* sp. A, a preferred species, is also darkly pigmented at times. One can only conclude that behavioral characteristics of the amphipods probably determine whether or not they are taken by pinfish in heavy vegetation. The exact relationship of an amphipod to a seagrass blade or sediment surface may determine its accessibility to predators. Similarly, certain diel patterns in locomotory activities (see Robertson and Howard, 1978) may make different species more or less vulnerable to predation. As a complicating factor, the possibility that certain amphipod species behave differently in various seagrass densities cannot be ruled out. Until further information is available on the behavior of the prey species, the ecological machinery involved in the prey selection process can only be hypothesized.

Few studies have tested the influence of habitat structure on prey selectivity by fishes (Ware, 1972; Vince *et al.*, 1976; Stein, 1977; and present study), yet these data further demonstrate my conclusion (Stoner, 1979) that food webs and predator-prey relationships are not static systems. Variation in habitat structure over space and time may dramatically alter not only the behavior of the predator, but undoubtedly influences patterns of abundance and species richness in both prey and predator groups. The physical structure of the habitat is, therefore, inextricably related to the population and community dynamics of its inhabitants.

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