The influence of oral anatomy on prey selection during the ontogeny of two percoid fishes, *Lagodon rhomboides* and *Centropomus undecimalis*

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Synopsis

Ontogenetic increases in mouth size and changes in dentition of percoid fishes may affect the size and species of prey selected, thus influencing the fundamental trophic niche. To examine the influence of oral anatomy on prey selectivity by pinfish, *Lagodon rhomboides*, and snook, *Centropomus undecimalis*, two co-occurring percoid fishes with contrasting mouth morphologies, the mouth size, dentition, stomach contents, and available prey during ontogeny were quantified. Based on the presence of prey fragments in stomach contents and direct behavioral observation, prey were categorized by the feeding mode used during capture (suction/ram-feeding or biting). *Centropomus* has a larger size-specific gape than *Lagodon* during all ontogenetic stages. Although both feeding modes were used by *Lagodon* during ontogeny, the amount of prey captured using suction/ram-feeding declined and the amount of prey captured by biting increased with standard length. This change in feeding mode was associated with a change in incisor shape and width: *Lagodon* < 39 mm SL possessed narrow, pointed incisors and strongly selected amphipods, which are captured using suction/ram-feeding; *Lagodon* > 40 mm SL possessed wide, flat-topped incisors and significantly increased their selectivity for polychaetes, which are captured by biting. *Centropomus* used ram-feeding to capture prey at all ontogenetic stages. Size-selective feeding by *Centropomus* was apparent but could not be due to gape-limitation alone, because average prey body depth was only 45% of gape and was not proportional to absolute mouth size increase during ontogeny. Dietary diversity was greatest during the transition from suction/ram-feeding to biting in *Lagodon*. *Lagodon* had a higher dietary diversity at all ontogenetic stages than *Centropomus*, due in part to *Lagodon*'s use of multiple feeding modes.

Introduction

As a result of their complex life histories, the observed trophic niches of fishes usually shift during their ontogeny. Different sizes or life history stages of fishes will feed on different sizes and types of prey (Carr & Adams 1973, Manooch 1977, Grossman 1980, Grossman et al. 1980, Livingston 1982, Clements & Livingston 1983, Sogard 1984, Keast 1985, Kerschner et al. 1985, Grossman 1986, Luczkovich & Stellwag 1993). This ontogenetic shift in food resources used by predatory fishes may be due

to the interaction of changes in external conditions (e.g., predation risk, food supply, habitat) and changes in internal conditions (e.g., physiological demands, anatomical structures, behavior) (for mathematical models predicting these shifts in fishes, see Werner & Gilliam 1984). Of the internal factors, mouth size and oral anatomy appear to determine the fundamental trophic niche (Werner 1974, Wainwright & Richard 1995) and ontogenetic changes in these are often associated with dietary shifts (Stoner & Livingston 1984, Gottfried 1986, MacNeill & Brandt 1990, Meyer 1990, Wainwright 1991). In contrast, ontogenetic changes in feeding behavior or feeding mode used to capture prey appear to be closely related to the ontogenetic change in diet in some species (Schmitt & Holbrook 1984a, Grossman 1986, Eggold & Motta 1992). Behavioral changes in feeding mode may be influenced by mouth morphology, because certain modes (e.g. biting) may be inefficient when used with incompletely developed morphology. Thus, fishes may use multiple feeding modes during ontogeny (Liem 1980), each of which may be optimal for a given set of external conditions (food availability) and internal conditions (morphology). For percoid fishes these modes include: (1) suction-feeding, in which prey are drawn into the mouth of the predator by suction forces (Lauder 1983, Liem 1993), (2) ram-feeding, in which prey are engulfed by the predator as it rapidly swims toward the prey (Norton 1991, Liem 1993), and (3) biting, in which pieces of the prey are cut away from the larger prey or from the substrate where they are attached (Liem 1993).

Prey size should be correlated with oral gape or pharyngeal gape in fishes that use suction and ram-feeding modes, because prey are swallowed whole. Gape limitation has often been inferred when changes in the maximum prey size (measured as the dimension orthogonal to the longest axis of the body) consumed are correlated with the absolute mouth size of the predator (Lawrence 1957, Zaret 1980, Schmitt & Holbrook 1984b, Hoyle & Keast 1987, Hambright 1991, Schael et al. 1991). The average prey size is also correlated with gape but the slope of the regression line calculated for these two variables may be less than 1.0 because of additional intrinsic and extrinsic complications (e.g., optimal foraging constraints, prey size distribution, ontogenetic changes in prey behavior). For these reasons, average prey size may not directly track gape increases during ontogeny.

While gape may be a morphological constraint on diet for fishes that capture prey whole using suction or ram-feeding, it is not a factor limiting prey size for fishes that capture prey by biting, in which large prey are cut or broken into pieces that fit the mouth of the predator (Liem & Osse 1975, Liem 1980, Liem 1984, Stoner & Livingston 1984, Wainwright 1988). Biting may be limited by other aspects of morphology that change during ontogeny, such as presence or absence of cutting teeth or a feeding apparatus developed to generate force (i.e., strong adductor muscles acting on short robust jawbones that allow biting and crushing of prey; see Wainwright & Richard 1995).

The goal of this paper is to compare ontogenetic changes in the diet of two subtropical estuarine fish species, pinfish, *Lagodon rhomboides*, and snook, *Centropomus undecimalis*, with respect to ontogenetic changes in oral anatomy. Both are percoid fishes with similar life histories (spawning offshore, nursery habitat in estuaries); at many sites in Florida they co-occur, but in general juvenile *Centropomus* are more common in mangrove habitats, and juvenile *Lagodon* are most common in seagrass habitats. Within an estuarine system, both species have potential access to the same array of resources. Of the possible underlying causes of ontogenetic changes in diet of these two predators, we will examine a subset of extrinsic factors (e.g., availability of prey of various sizes and taxa) and intrinsic factors (e.g. mouth size, dentition). We will also speculate on the interaction between these extrinsic and intrinsic factors that determine their respective trophic niches.

In both species there are major shifts during ontogeny in the prey taxa that constitute the diets, but these shifts appear to be due to different underlying factors. *Centropomus* is a ram-feeder that does not appear to shift feeding mode during ontogeny; at all sizes it feeds on elusive prey, e.g., calanoid copepods for the smallest individuals or other fishes for the largest individuals. Maximum prey size is less than gape, suggesting that juvenile *Centropomus* are

gape-limited. In contrast, *Lagodon* demonstrates a shift in feeding mode during ontogeny from primarily suction/ram-feeding in small individuals to biting in large individuals. This shift in feeding mode appears to be associated with changes in dentition, which permit prey larger than the gape to be eaten. Because of the difference in the number of feeding modes used by *Lagodon* and *Centropomus*, we tested Liem's (1980) hypothesis that fishes using multiple feeding modes have more diverse diets than fishes using a single mode.

Materials and methods

Morphological measurements of Lagodon, Centropomus, *and prey*

Mouth diameter was measured as the distance between the tip of the premaxilla and the tip of the mandible. These estimates were collected for 50 *Lagodon* [range, 32–145 mm standard length (SL)] and 34 *Centropomus* (range, 29–123 mm SL). Individual measurements on unpreserved specimens (either freshly killed or frozen) were measured by inserting the tips of a dial caliper between the jaws of each individual. In addition, the width of the anterior-most incisors on *Lagodon* jaws from 55 preserved specimens (26–65 mm SL) was measured using a dissecting microscope with an attached video-image-analysis system (JAVA, Jandel Scientific). The standard length (SL) in mm of all specimens examined for stomach content analysis were also measured using a ruler or a dial caliper. Body depth (measured at the widest part of the body) and standard length of individual fishes consumed by *Centropomus* were measured with a dial caliper or an ocular micrometer on a dissecting microscope. Body depths of prey available to *Centropomus* were estimated from standard lengths of all captured prey using regression equations based on 50 specimens of each species. Prey sizes consumed by and available to *Lagodon* were estimated using the sieve fractionation procedure (see below). Regression analyses and analyses of covariance were performed using SYSTAT (Wilkinson 1990).

Observations on feeding behavior

Lagodon were observed in the field during 28 h of underwater observation from 14 March through 8 Nov 1984 at the Turkey Point Shoal study site (see below, Luczkovich 1987). Feeding modes were determined for individuals using a focal animal technique (Lehner 1979). *Lagodon* were also fed in laboratory aquaria with the various prey collected from the field and notes were made on the feeding modes used. *Centropomus* feeding modes and post-capture manipulations were observed in laboratory aquaria using known sizes of prey.

Lagodon *stomach content analysis*

Two different sampling regimes were used to examine ontogenetic changes in the diet of *Lagodon*. The first, a general survey, covered a broad size range of individuals over one year. The second focused on a narrower size range of individuals that the general survey indicated was undergoing considerable diet shifts. In the second survey, prey selection was determined over a 1-month period by collecting fish for diet analysis and samples of the available prey contemporaneously.

The general survey
In the general survey, *Lagodon* were collected from seagrass meadows at Turkey Point Shoal in St. George Sound (29°53′N, 84°30′W) near the Florida State University Marine Laboratory in Florida. Fish were collected monthly (20 July 1983 through 15 July 1984) with a 5.5 m otter trawl with a 3.2 mm-mesh-liner in a predominantly *Thalassia testudinum* and *Syringodium filiforme* seagrass meadow in 1.5 m deep water (Luczkovich 1987). Fish were preserved in 10% buffered formalin for examination of the stomach contents using a modification of the sieve-fractionation technique of Carr & Adams (1972, 1973). To minimize the effect of differential digestion rates of prey, fish were collected during the middle part of the day when they were actively foraging (Luczkovich 1987) and only stomach contents were examined. The fish from each monthly sample were divided into 10 mm size groups and the

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stomach contents of all individuals in a size class for a particular month were pooled. The pooled stomach contents were passed through a series of sieves (2000, 850, 425, 250, 150, 75 μ). For each prey category (see Table 1), the numerical proportion in each sieve fraction was determined. Each sieve fraction was then dried at 60° C for 48 h and then the dry mass of the whole sieve fraction determined with a precision of 0.00001 g. Dry mass for each prey category was estimated by multiplying its numerical proportion by the total mass of the sieve fraction. The estimated dry masses for each prey category were then summed across sieve fractions and divided by the total dry mass of all sieve fractions (excluding the contribution of sand grains and unidentifiable prey).

Further pooling of the stomach contents was done by calculating the average monthly contribution to the diet (proportional dry mass) of prey identified in the stomach contents within each of four life intervals representing a series of "trophic units" (15–39 mm SL; 40–79 mm SL; 80–119 mm SL; 120–139 mm SL) as previously determined by a clustering strategy (see Stoner 1980, Livingston 1982, Stoner & Livingston 1984, Luczkovich 1987).

In addition to the traditional prey categories as elaborated above, we also examined ontogenetic changes in the importance of different functional categories of prey. Here prey taxa were pooled into two groups based on the feeding mode used by *Lagodon* to capture them (Table 1). These categorizations were based on (1) observations of field feeding behavior, (2) feeding behavior in the laboratory and (3) examination of the stomach contents themselves (especially for prey captured by biting). The two categories were (1) mobile epibenthic and elusive prey captured by suction or ram-feeding (calanoid copepods, harpacticoid copepods, amphipods, isopods, cumaceans, shrimp, and fishes) and (2) sessile prey captured by biting (infaunal polychaetes, hydroids, tunicates, seagrasses, algae, and diatoms). Although suction and ram feeding are distinct feeding modes, they could not be reliably distinguished in this study.

These diet data were used to answer the question: "Does the relative importance of each prey category change among the different size classes of preda-

tors?" Each monthly sample of the diet of a *Lagodon* size class served as a replicate of that size class. We used the nonparametric Kruskal-Wallis test (KW) (Hollander & Wolfe 1973) to determine if there were any significant differences among any size classes of predators. If the KW test was significant, we then applied the nonparametric Jonckheere-Terpstra test statistic (JT test) (Hollander & Wolfe 1973) to determine if these dietary differences (increases or decreases) were consistent as the fish increased in size (e.g., one prey category increasing in importance in each larger size class). In both tests the significance level was set at $p \leq 0.05$. The probability distributions against which the observed values were compared were obtained from 2000 Monte-Carlo simulations of the randomized data using StatXact (Cytel Software Corporation 1989). This is a conservative approach to assess statistical differences; it is warranted in this study because the sample sizes are unequal, small (5–10 monthly replicates) and the underlying distributions are unknown.

Table 1. The feeding mode used by pinfish, *Lagodon rhomboides*, and snook, *Centropomus undecimalis*, to capture various prey. Observations on feeding mode of *Centropomus* were made in laboratory aquaria and from the condition of prey in the stomach contents; observations of *Lagodon* were made in laboratory aquaria, at the collection sites using SCUBA, and from the condition of prey in stomach contents.

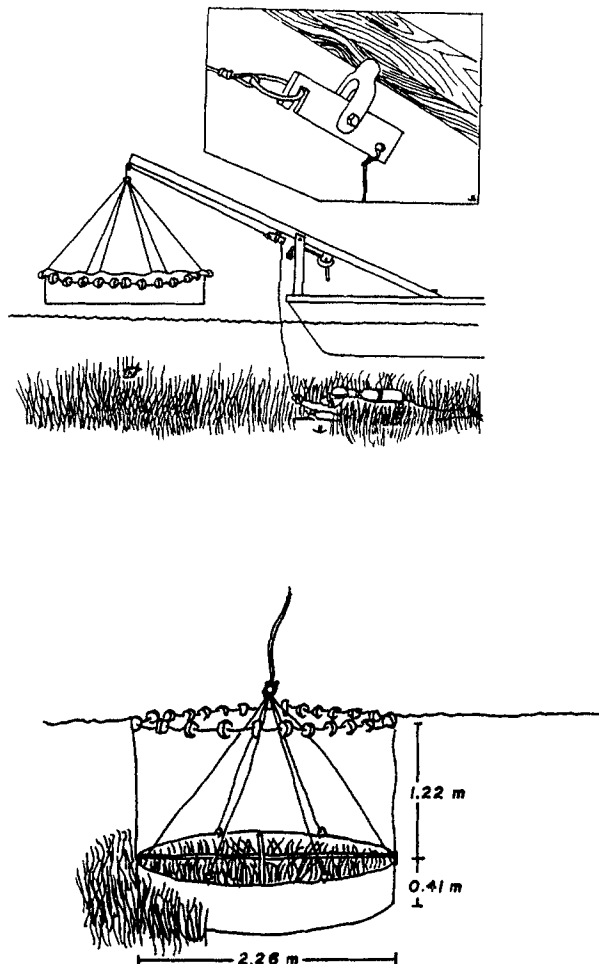| Prey	Lagodon	Centropomus
Calanoid copepods	ram	ram
Harpacticoid copepods	suction	–[1]
Amphipods	suction	ram
Isopods	suction	–[1]
Cumacea	suction	–[1]
Crabs	biting	–[1]
Polychaetes	biting	ram
Colonial tunicates	biting	–[1]
Hydroids	biting	–[1]
Diatoms	biting	–[1]
Algae	biting	–[1]
Seagrass	biting	–[1]
Invertebrate eggs	biting	–[1]
Fishes	ram	ram
Shrimp	ram	ram

[1] Not consumed.

Fig. 1. The drop-net used to capture *Lagodon rhomboides* in the prey selectivity study. A 4.0 m^2 circular metal frame drop-net was suspended from a pontoon boat and released by a diver after *Lagodon rhomboides* were observed feeding in a seagrass meadow. After the diver released the trigger mechanism (detail, top panel) by pulling a cord, the net fell to the substrate, the attached barrier net floated to the surface, and the fish were captured using rotenone and dipnetting. Prey availability samples (0.064 m^2) were taken with a suction dredge sampler at the locations where fish were observed to feed.

Prey selection by Lagodon

In the second survey, we compared the diets of *Lagodon* with sizes and abundances of the potential invertebrate prey available at this site in order to study prey selection. On seven occasions during April and May 1985, a 4.0 m^2 drop-net was used to surround actively foraging pinfish after the senior author had observed them feeding for 1 h while SCUBA diving (Fig. 1). After dropping the net, a circular 0.064 m^2 area of seagrass meadow was isolated using an inverted, weighted bucket. Rotenone was applied within the drop-net and all the fishes inside were collected by dipnetting. A suction-dredge sampler (Brook 1979) with a 500 μ collection bag was then used to collect all invertebrates inside the quadrat (Luczkovich 1987). For each of the 7 drop net samples, the *Lagodon* collected were separated into 3 size categories (20–29 mm, 30–39 mm, 40–49 mm SL). The diets of each size category were analyzed as described in the general survey (e.g., sieving, counting, dry weights, etc.); prey constituting less than 3% of the diet or less than 5% of available prey were excluded. This resulted in two prey categories that are captured using differ-

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ent feeding modes: (1) polychaetes, which were in pieces in the stomach contents and thus captured by biting; and (2) amphipods, which were found whole in stomachs and thus are taken by ram-suction feeding. In each suction-dredge sample, potential prey items were separated from inorganic material and detritus, sorted into the above categories, passed through a series of nested sieves (2000, 850, 450 μ), and then dried to a constant biomass for 48 h at 60° C.

Selective feeding by *Lagodon* was determined by comparing the proportional biomass of prey that were in stomach contents to the proportional biomass of prey that were available. For each *Lagodon* size class and prey category, we estimated average prey selectivity (Manly's α) using drop-nets and suction dredge samples as replicates. Manly's α was calculated as follows (Chesson 1978, Krebs 1989):

$$\alpha_i = (r_i/n_i) * (1/ \sum_{j=1}^{m} (r_j \cdot n_j)),$$

where α_i = Manly's alpha for prey type i; r_i, r_j = proportion of prey type i or j in the diet (i and j = 1, 2, 3, ...m); n_i, n_j = proportion of prey type i or j in the environment; and m = number of prey types possible.

Centropomus *stomach content analysis*

Juvenile *Centropomus* and samples of potential prey were collected in mangrove impoundment 16A in Saint Lucie County, Florida (27°30′N, 80°19′W). Fishes and invertebrates were collected at six stations inside the impoundment dike using a specially designed pull-net (2.5 × 1.8 m bag, 2.5 × 6.2 m side panels, 3.2 mm mesh netting[1]). Separate day and night samples were taken at each station every 2 weeks from 19 June 1985 through 24 January 1986. However, for this analysis day and night samples from the same station were pooled. All fishes

and invertebrates were preserved in 10% formalin in the field and transferred to 70% ethanol for storage.

Diet analysis for *Centropomus* was based on 258 individuals (5–119 mm SL). Only stomach contents were examined for identification and measurements of prey items, minimizing the effect of differential digestion rates. Size measurements (length, width, and depth) were taken for each prey item ingested by a predator if relatively few or from a random subsample of 50 prey if copepods were consumed; an ocular micrometer or a ruler was used for these measurements. To determine the numerical importance of each prey category, prey were sorted into taxonomic groups and counted. To determine the gravimetric importance, the sorted prey categories were individually dried and then weighed. The dry mass of the smaller prey categories (e.g., copepods) was estimated by multiplying the counts of these prey in stomachs by estimates of the mean mass of an individual prey item (determined from larger diet samples). As with *Lagodon*, stomach contents were examined for increases or decreases in the importance of taxonomic and functional groups of prey (as determined by the feeding mode used to capture them; see Table 1) across four *Centropomus* size classes (5–14 mm, 15–39 mm, 40–79 mm, and 80–119 mm SL). Statistical analyses were as noted above for *Lagodon*, using non-parametric Kruskal-Wallis and Jonckheere-Terpstra tests (Cytel Software Corp)[2] to compare size classes and Systat to perform regression analyses (Wilkinson 1990).

The relative abundance and size estimates of major categories of potential prey in the environment were compared with the abundance and size of these species in the stomach contents of *Centropomus* collected in the same pull-net samples. Numerical abundance of the three prey fishes in the diet (*Gambusia holbrooki*, *Poecilia latipinna*, and *Cyprinodon variegatus*) was estimated using catch-per-unit-effort (CPUE), which was determined by dividing the total number of fish collected in a given

[1] Gilmore, R.G., P.B. Hood, R.E. Brockmeyer & D.M. Scheidt. 1986. Impoundments No. 16A and 24, St. Lucie County, John Smith Impoundment, Brevard County, Florida: water control systems and their hydrological impact. Florida Department of Health and Rehab. Serv., Final Report for Contract No. LD704. 63 pp.

[2] Cytel Software Corporation. 1989. StatXact: statistical software for exact nonparametric inference. User manual, Cytel Software Corporation, 137 Erie Street, Cambridge.
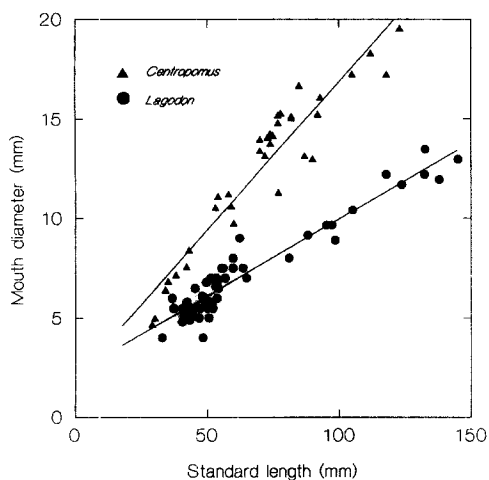
Fig. 2. The mouth diameter (gape) in mm of *Lagodon rhomboides* and *Centropomus undecimalis* plotted against standard length (SL) in mm. Regression equations: *Lagodon*: gape = 0.0762 (SL) + 2.3547, R^2 = 0.924; *Centropomus*: gape = 0.149 (SL) + 1.982, R^2 = 0.896.
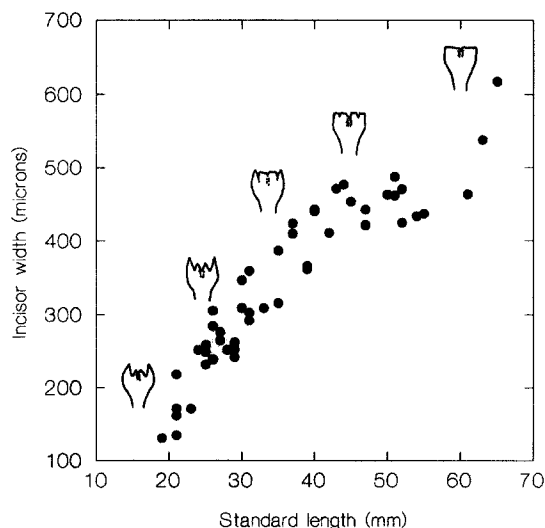

Fig. 3. The incisor width of *Lagodon rhomboides* plotted against standard length (mm). Incisor morphology redrawn from Stoner & Livingston 1984.

sample by the number of pull-nets made to collect the sample. For each of these prey species, the numerical proportion in the environment (n_i) was compared with the numerical proportion in the stomach contents (r_i) of the *Centropomus* size classes. Selective feeding was measured using Manly's α (see above). Separate α_i values were calculated for each prey species and *Centropomus* size class on each collection date (all stations pooled) and average α calculated using dates as replicates.

Results

Ontogenetic changes in oral anatomy of Lagodon and Centropomus

The oral anatomy of both species changed during ontogeny. Although there was a continuous increase in gape for both *Lagodon* and *Centropomus* during ontogeny, *Lagodon* gape was smaller than *Centropomus* at all sizes examined (Fig. 2). As standard length increased, the difference in gape between the species increased significantly (slopes of the regression differed significantly; ANCOVA $t_{1,80}$ = 8.9308, p < 0.00001, R^2 = 0.946, n = 84). On the average, the oral gape of a 20 mm SL *Centropomus*

exceeded a similarly sized *Lagodon* by 1.2 mm, and the gape of a 70 mm SL *Centropomus* exceeded a same-sized *Lagodon* by 4.8 mm. In addition, *Lagodon* incisors increased in width (Fig. 3) and changed in shape (similar to that described by Stoner & Livingston 1984). *Centropomus* had small conical teeth that did not change in shape during ontogeny (Fraser 1968, Lau & Shafland 1982).

Lagodon stomach content analysis

The general survey
When prey are categorized on the basis of mode of capture, prey taken by suction or ram feeding decreased as a percentage of the diet during ontogeny. *Lagodon* consumed decreasing amounts of calanoid and harpacticoid copepods with increasing fish SL (JT test, p = 0.001; Fig. 4a). Amphipods, isopods, and cumaceans declined significantly as a proportion of the diet as fish size increased (JT test, p = 0.0004). There was no consistent increase or decrease in the proportion of the diet formed by shrimp and fish as *Lagodon* increased in size (JT test, p = 0.1075). Overall, *Lagodon* captured a decreasing amount of prey using suction or ram-feed-
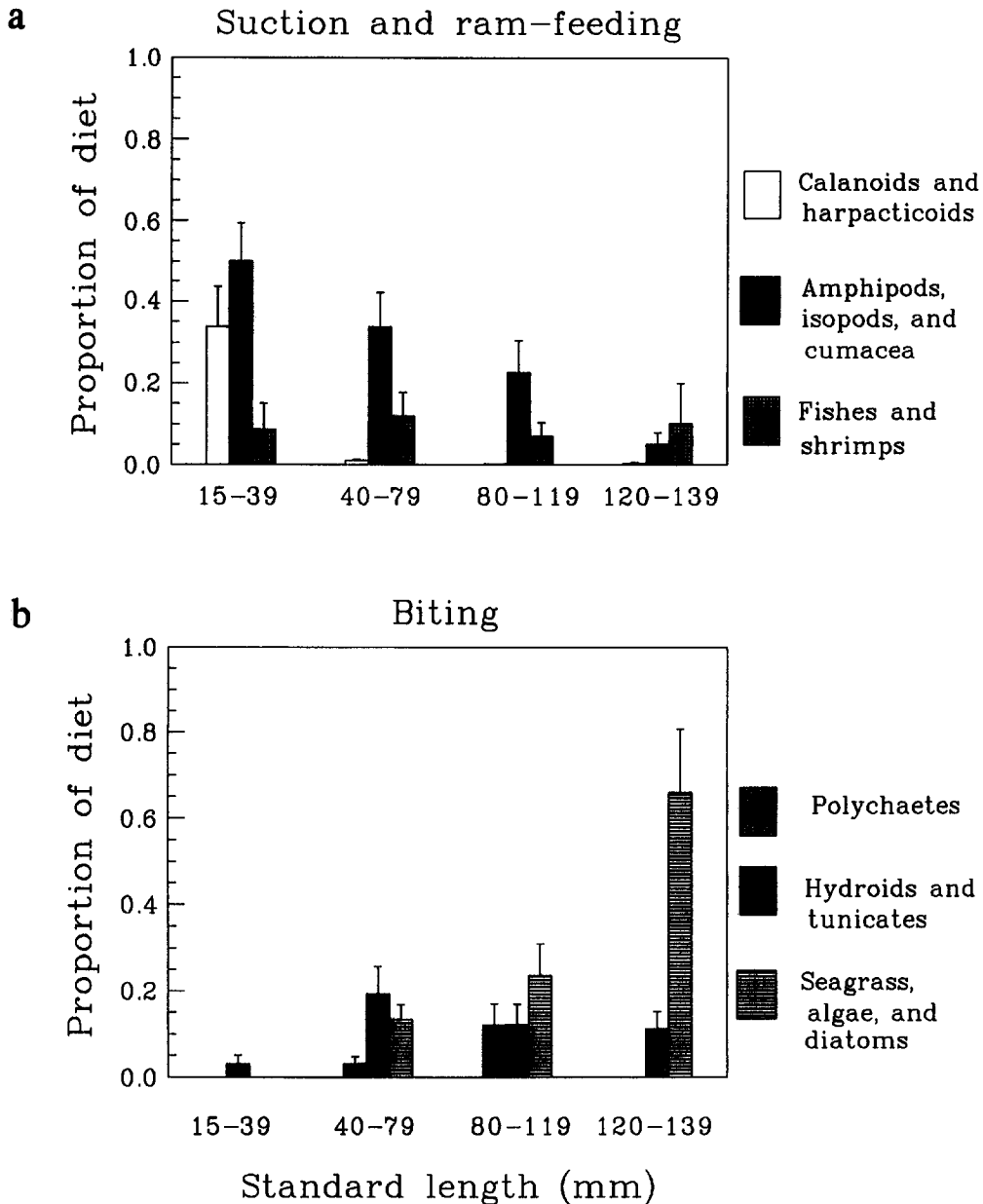
Fig. 4. The mean (± 1 S.E.) proportion of dry biomass of prey categories in the stomach contents of *Lagodon rhomboides* in four standard length classes (mm) collected in the general diet study: a – prey captured by suction or ram-feeding (amphipods, cumaceans, isopods, copepods, and shrimps); b – prey captured by biting (hydroids, tunicates, algae, seagrasses, polychaetes).

ing during ontogeny (all prey pooled by method of capture, JT test, p = 0.0011; Fig. 4a).

In contrast, prey taken by biting increased as a percentage of the diet during ontogeny. *Lagodon* 15–39 mm SL ate few hydroids and tunicates (3% of diet); hydroids and tunicates increased significantly

in the diet of 40–79 mm SL fish (19% of diet), then declined slightly in the 80–119 mm SL (12% of diet) and 120–139 mm SL (11% of diet) size classes (KW test, p = 0.0015; Fig. 4b). Algae and seagrass increased in the diet from 0% of the dry biomass of the stomach contents in fish 15–39 mm SL to 66% in

fish 120–139 mm SL (JT test, p = 0.0011). Although the percentage of the diet consisting of polychaetes increased from 0% in 15–39 mm SL fish to 12% in 80–119 mm SL fish, the percentage of the diet consisting of polychaetes did not increase significantly as fish grew (JT test, p = 0.148). The total amount of prey captured by biting increased significantly from 9% of the diet in 15–39 mm SL fish to 81% in 120–139 mm SL fish (JT test, p = 0.0011).

Prey selection by Lagodon

Based on the results of the morphological analyses and the general diet survey, it was apparent that *Lagodon* > 40 mm SL had undergone a change in diet (from water-column feeding on calanoid copepods to seagrass benthos) as well as a change in tooth morphology (pointed to flat-topped incisors). During this transitional size range, we estimated selectivity toward polychaete and amphipod prey by determining proportional prey biomass in the stomach contents of actively feeding fish collected using the drop-net and prey biomasses available in the feeding environment using the suction-dredge sampler. Polychaetes constituted the greatest biomass, or 68.7% (range: 48.4–79.1%) of the available prey, while amphipods constituted 16.7% (range: 9.3–26.1%) of the available prey. Other potential prey were present (isopods, cumacea, shrimps, and crabs), but none of these prey constituted more than 5% of the available prey samples.

The smallest *Lagodon* captured in the drop nets consumed amphipods, but the largest consumed polychaetes as well as amphipods. *Lagodon* 20–29 mm SL and 30–39 mm SL consumed mostly amphipods (31.6% and 49.7% of stomach contents, respectively), but few polychaetes (5.2% and 2.2% of stomach contents, respectively; Fig. 5a). *Lagodon* 40–49 mm SL consumed polychaete and amphipod prey in the same approximate proportion (29% and 32% of diet, respectively). Although amphipods comprised more than 30% of the diet of all three size classes of *Lagodon*, there was a significant decline in selectivity (as estimated by Manly's α) for amphipods by *Lagodon* 40–49 mm SL (KW test, p = 0.037; Fig. 5b). There was a significant increase in polychaetes consumed by *Lagodon* 40–49 mm SL
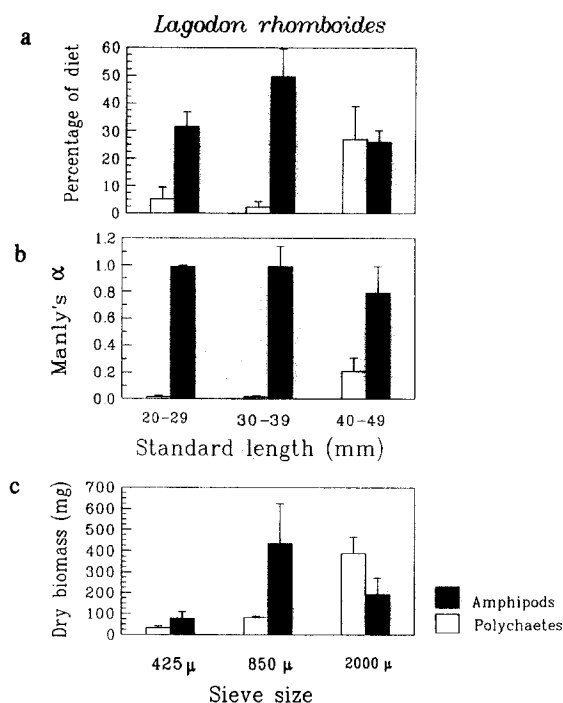

Fig. 5. a – The mean (± 1 S.E.) percentage of amphipods and polychaetes in the dry biomass of the stomach contents. b – The mean (± 1 S.E.) Manly's α selectivity index calculated for three standard length classes (mm) of *Lagodon rhomboides* collected in the prey selectivity study. c – The mean (± 1 S.E.) biomass of amphipods and polychaetes retained on 425, 850, and 2000 μ sieves used to screen prey collected with the suction dredge in the prey availability study for *Lagodon rhomboides*. Means were calculated by pooling all individuals in a size class within a drop-net collection and averaging across the drop-net samples for each size class: 20–29 mm SL fish (43 individuals total, n = 7 drop nets); 30–39 mm SL fish (24 individuals total, n = 6 drop nets); and 40–49 mm SL fish (11 individuals total, n = 5 drop nets).

(KW test, p = 0.058) and a significant increase in selectivity for polychaetes (KW test, p = 0.039).

The ontogenetic shift by small *Lagodon* from amphipod to polychaete prey represented a shift to a larger prey type. The size of available polychaetes was large relative to the amphipod prey, because most amphipods were between 850 μ and 2000 μ, whereas most polychaetes were > 2000 μ in diameter, based on the biomasses of available prey retained on three nested sieves (2000, 850, 425 μ screens; Fig. 5c).
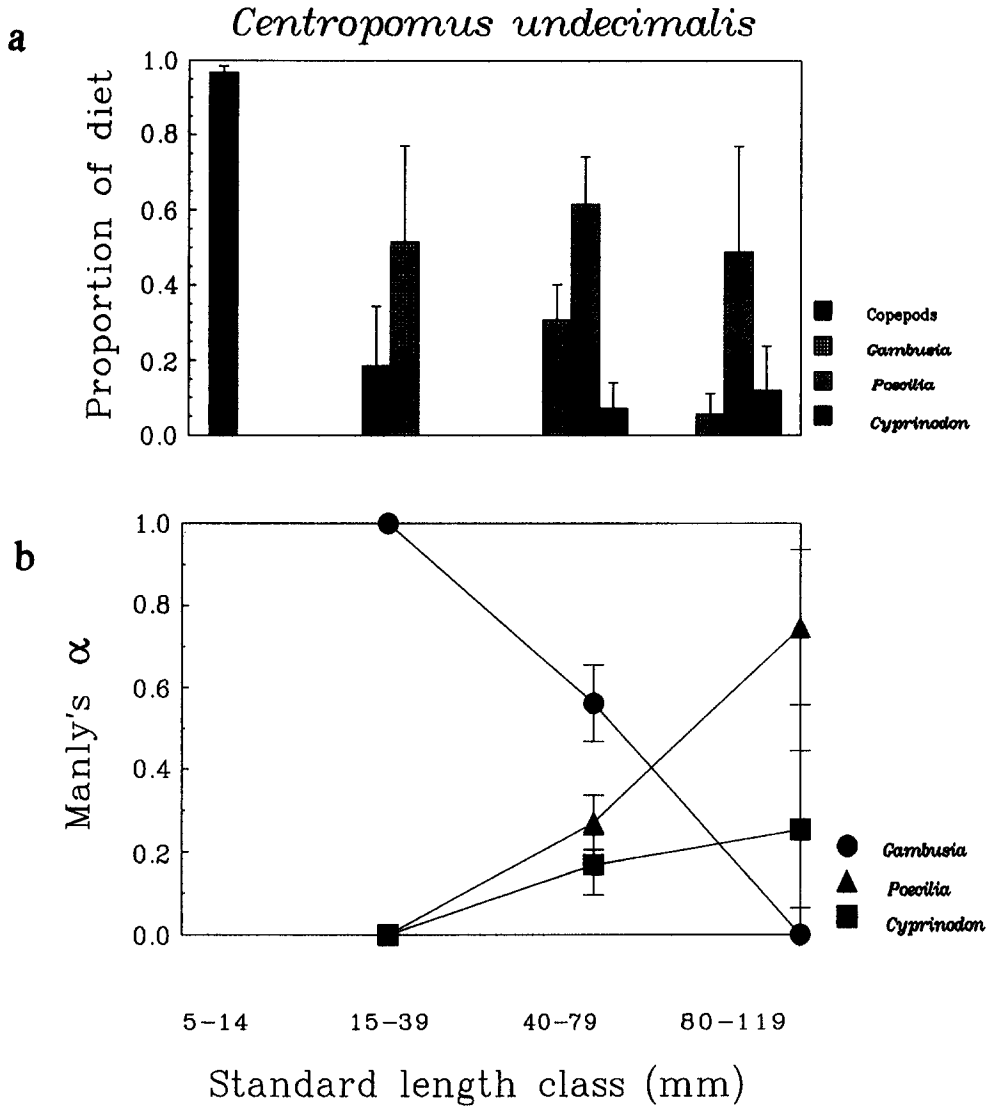
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Centropomus undecimalis

Fig. 6. a – The mean (± 1 S.E.) proportion of dry biomass of prey categories in the stomach contents of *Centropomus undecimalis* in four standard length classes. b – The mean (± 1 S.E.) Manly's α for *Gambusia holbrooki, Poecilia latipinna*, and *Cyprinodon variegatus* plotted against three *Centropomus undecimalis* standard length classes.

Dietary analyses of Centropomus

In the laboratory and field, juvenile *Centropomus* used only ram-feeding to capture prey; all prey in stomachs appeared to have been consumed whole. Therefore, prey are categorized below taxonomically and on a prey size basis because there is no evidence that *Centropomus* uses more than one feeding mode.

Juvenile *Centropomus* consumed mostly cala-

noid and cyclopoid copepods when small and fishes (*Gambusia holbrooki, Poecilia latipinna*, and *Cyprinodon variegatus*) when large (Fig. 6a). Small amounts of decapod zoeae, shrimp (*Palaemonetes intermedius*), amphipods, and polychaetes were also consumed, but none of these prey exceeded 3% of the diet by dry biomass. The proportion of diet that consisted of copepods (JT test, p = 0.0003) decreased significantly with increased fish size, whereas the proportion that consisted of fishes increased
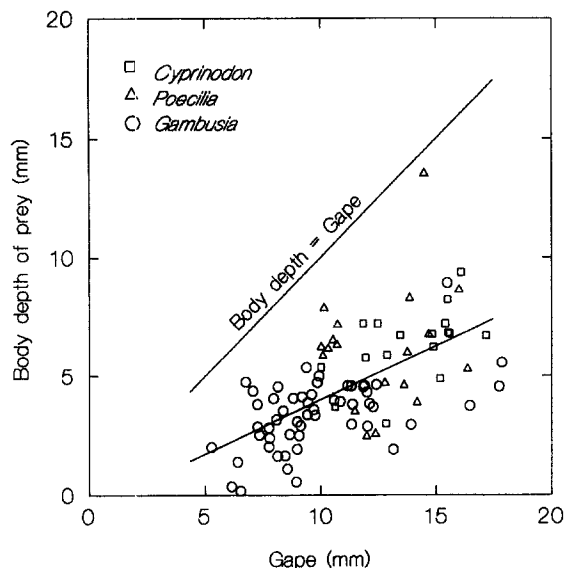
Fig. 7. Body depths of the *Gambusia holbrooki, Poecilia latipinna*, and *Cyprinodon variegatus* consumed as a function of the gape of *Centropomus undecimalis*. The overall regression equation between prey body depth and gape is: body depth in mm = 0.452* (gape in mm) − 0.519 (R^2 = 0.396).

in larger fish (JT test, p = 0.007). Although the proportion of the diet consisting of *Gambusia* increased from 0.0 to 5–14 mm SL fish to 0.52 in 15–39 mm SL fish, this prey type did not differ significantly among all size classes (KW test, p = 0.090). The proportion of the diet constituted by *Poecilia* (JT test, p = 0.0049) and *Cyprinodon* (JT test, p = 0.00048) increased significantly with *Centropomus* size.

Centropomus *prey selectivity*

Both the maximum and average prey size consumed by juvenile *Centropomus* increased during

ontogeny, but the increase in average size was less than would be expected by an increase in gape alone. The average body depth of prey fishes consumed by *Centropomus* increased linearly with gape (Fig. 7), but the slope of the regression line (0.452) was significantly < 1.0, suggesting that smaller fish are feeding closer to the maximum gape than larger fish (comparison of slopes, t = − 9.229, p < 0.0001).

The mouth size of *Centropomus* appears to have influenced the species of prey selected from the assemblage of fishes available in the environment. Small narrow-bodied fishes were consumed disproportionately by small *Centropomus* and deep-bodied fishes selected by large *Centropomus*. Small *Centropomus* (< 50 mm SL and < 10 mm gape) consumed only *Gambusia*, which are the most abundant fish available (Table 2) and also have the narrowest length-specific body depth of the three prey fishes [regressions of prey body depth in mm (BD) on prey standard length in mm (SL): *Gambusia*, BD = 0.272986 (SL) - 0.64974, R^2 = 0.93; *Poecilia*: BD = 0.356271 (SL) - 0.87894, R^2 = 0.95; *Cyprinodon*: BD = 0.467339 (SL) - 2.47832, R^2 = 0.95; the slopes of these regressions differ significantly, ANCOVA, $F_{2,117}$ = 501.9, p < 0.0001]. Selectivity (Manly's α) was greatest for narrow-bodied *Gambusia* when *Centropomus* were less than 40 mm SL and declined significantly with increasing size classes (JT test, p = 0.0011; Fig. 6b). In contrast, prey selectivity for deep-bodied *Poecilia* rose significantly with increasing fish size (JT test, p = 0.0011). Selectivity for *Cyprinodon* increased, but not significantly (JT test, p = 0.1100). It is apparent that the smallest individuals of all three fish species were selected from the available prey by *Centropomus* (Fig. 8), suggesting that gape limited the size of prey fishes that could by consumed by small *Centropomus* regard-

*Table 2.*The catch-per-unit-effort (CPUE), mean body depth (BD) in mm estimated from regression equations (see text), and mean standard length (SL) ± 1 S.E. in mm of the three most numerous potential prey fishes collected with the pull-net in the mangrove impoundment June 1985 through January 1986. Species are ranked from largest to smallest by mean standard length.

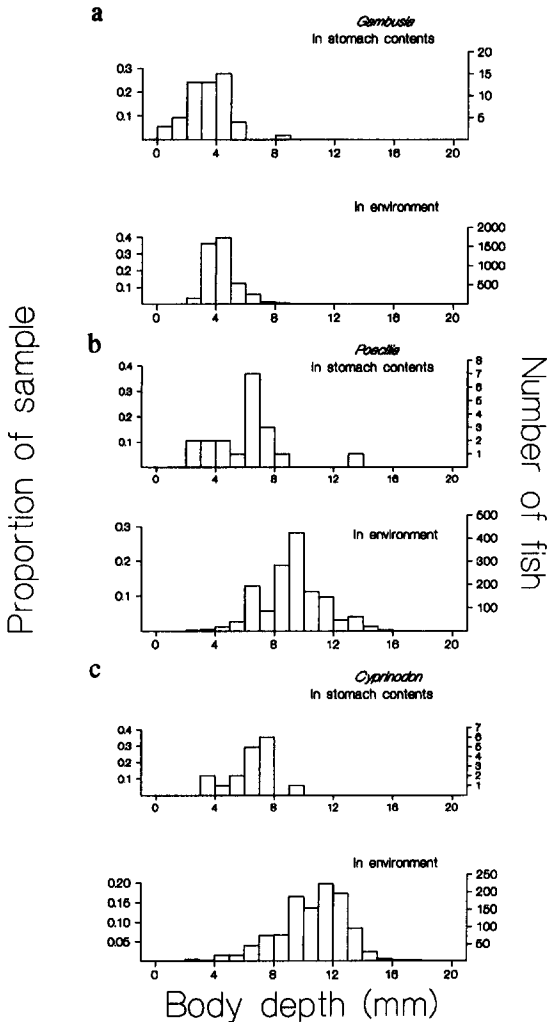| Species	CPUE	BD	SL	(± S.E.)	n
Poecilia latipinna	62.51	9.3	28.5	0.15	1501
Cyprinodon variegatus	32.05	10.7	28.2	0.25	1134
Gambusia holbrooki	199.37	4.5	18.7	0.10	4355

Fig. 8. The proportional frequency and total abundance of 1 mm body-depth classes of a – *Gambusia holbrooki*, b – *Poecilia latipinna*, and c – *Cyprinodon variegatus* in stomach contents of *Centropomus undecimalis* and the available prey collected in pull-net samples at six stations in the mangrove impoundment September 1985 through January 1986.

less of species. Although many large individuals were present in the environment, *Poecilia* and *Cyprinodon* were rarely consumed if they were > 12 mm in body depth.

Comparison of taxonomic diversity of Lagodon *and* Centropomus *diets*
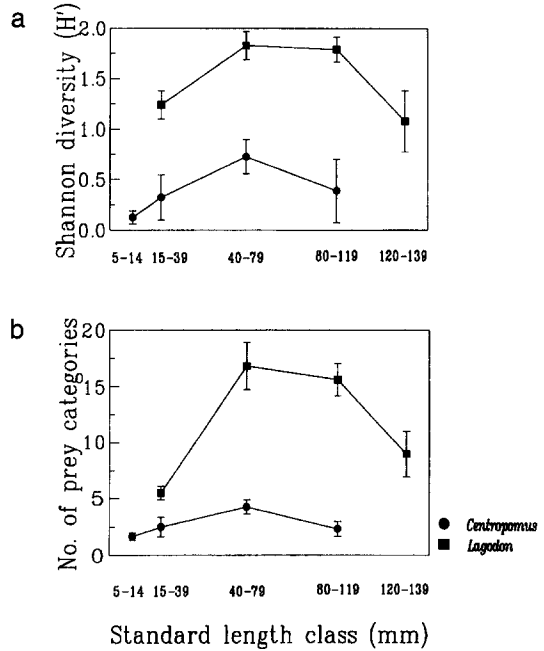
Lagodon had a much broader diet than *Centropo-*

Fig. 9. Diversity of the trophic niche in *Lagodon rhomboides* and *Centropomus undecimalis*: a – the Shannon diversity (H') of each of the size classes of *Centropomus* and *Lagodon* studied; b – the number of prey categories consumed by each of the size classes.

mus throughout ontogeny. Over all size classes, Shannon diversity (H') averaged 1.58 in *Lagodon*, with an average of 13 prey categories being consumed. Shannon diversity of *Lagodon*'s diet was greatest in intermediate size classes (40–79 mm SL and 80–119 mm SL), during the transition from suction/ram-feeding to biting, and lowest when predominantly one feeding mode was being used (KW test, p = 0.0065; Fig. 9a). The same was true for the number of prey categories consumed (KW test, p = 0.0011, Fig. 9b). In contrast, Shannon diversity averaged 0.411 over all *Centropomus* size classes, with an average of 3 categories of prey consumed. *Centropomus* dietary diversity did not change significantly among size classes (KW test, p = 0.303 for H' and p = 0.147 for number of prey categories). Thus, dietary diversity was greatest for *Lagodon*, especially in size classes that used multiple feeding modes, and least for *Centropomus*, which used a single feeding mode during ontogeny.

Discussion

Differences in oral anatomy determined the fundamental trophic niche of these two percoid species. In *Lagodon*, changes in dentition were associated with a shift in feeding mode used to capture prey during ontogeny, thus broadening the trophic niche. In *Centropomus*, gape appeared to limit the body depth of prey that could be consumed, thus influencing the species of prey consumed. In both cases, the diet changed when abundant large prey were consumed following an increase in gape (*Centropomus*) accompanied by a change in dentition (*Lagodon*). Although other intrinsic factors, such as changes in nutritional requirements and swimming abilities, and extrinsic factors, such as changes in prey abundance and risk of predation, must also interact to determine the realized niche (Werner et al. 1983, Werner & Gilliam 1984, Gilliam & Fraser 1987, Holbrook & Schmitt 1988), it appears that mouth size and dentition play a central role in determining diet in these two fish species.

Lagodon in this study showed a significant increase in the consumption of sessile prey obtained by biting at approximately 40 mm SL. *Lagodon*'s diet at sizes < 40 mm SL may be limited by morphology because: (1) incisors with cutting edges are absent; (2) gape is small relative to the most abundant prey, polychaetes, and (3) biting forces generated by the feeding apparatus maybe insufficient to cut through large available prey. During ontogeny, the small incisors found in < 40 mm SL *Lagodon* are replaced by wider, flat-topped incisors that form a cutting edge (Caldwell 1957, Stoner & Livingston 1984, Luczkovich et al. unpublished). Incisors measured in the current study were much wider than reported by Stoner & Livingston (1984). The widths reported by those authors (10–86 μ width for *Lagodon* 15–100 mm SL) are approximately one order of magnitude too low, and are probably in error. Tooth replacement in *Lagodon* has not been studied in sufficient detail, so that the number of times teeth are replaced during ontogeny is unknown. Mouth size did not constrain the prey size consumed by juvenile *Lagodon* > 40 mm SL, which appeared to compensate for their small gape by biting off pieces of prey that were too large to fit in their mouths

(polychaetes, colonial tunicates, hydroids, macroalgae, and seagrasses).

Subtle differences between size classes in biting strength may be responsible for some of the variation in food acquired by *Lagodon*. For example, although seagrasses were present in large abundance in the environment, *Lagodon* did not begin to consume substantial quantities of this resource until reaching 120 mm SL (see also Motta et al. 1995). Different prey types will differ in the materials of which they are composed (e.g., collagen, cellulose) and these materials will cause prey to have different toughness. The toughness of prey is typically not correlated with its size, but with the mechanical properties of the materials of which it is composed. Once a predator can muster enough force in the feeding apparatus to overcome the material toughness, it can feed on any size prey of that type by biting. In the future, the forces generated by *Lagodon* of different sizes during a bite should be measured and compared against the toughness of available prey.

The behavioral shift in feeding mode in *Lagodon* may have been a function of the change in tooth morphology during ontogeny, which changed the relative profitability of different prey types. In the case of small < 40 mm *Lagodon*, the energetic return for feeding on sessile prey may be low, because the teeth required to bite such prey have not developed. In larger *Lagodon* (> 40 mm), the energetic return for feeding on elusive prey may be low, because ram-feeding is difficult (results in low capture success) for fish with relatively small mouths (Norton 1991). I a similar way, changes in the feeding modes used by zooplanktivorous clupeids, scombrids, and engraulids have been interpreted as being due to the maximization of energetic return (Crowder 1985). Other external factors, such as piscivores in the environment (both species coexist with many large predators), could have influenced the feeding mode shift, if small individuals modified their prey choice and habitat selection in response (Grossman 1980, Werner et al. 1983, Gilliam & Fraser 1987, Holbrook & Schmitt 1988).

During ontogeny in *Lagodon*, there was an increase in the biomass of seagrass and algae consumed; a transition from a predominantly carnivo-

rous diet to predominantly herbivorous diet has been shown previously for *Lagodon* (Stoner 1980, Livingston 1982, Stoner & Livingston 1984, Luczkovich & Stellwag 1993). This trend also occurs in other fishes in the family Sparidae (*Diplodus, Sparus, Archosargus*) (Christensen 1977, Vaughan 1978). In all of these sparids, relative intestine length increases during ontogeny, which may provide an increased surface area for digestion and absorption of plant remains (Christensen 1977, Vaughan 1978, Stoner & Livingston 1984). In *Lagodon*, the abundance of cellulolytic intestinal bacteria also increases during ontogeny (Luczkovich & Stellwag 1993). Increased use during ontogeny of algae and seagrasses, which appear to be an underutilized trophic resource in great abundance, would be impossible without these complex adaptations involving changes in digestive physiology, oral and intestinal anatomy, ecological relationships with symbionts, and feeding behavior. Nevertheless, *Lagodon* and the other sparids are opportunistic predators with broad diets and are able to switch to energy- and protein-rich animal prey, especially if such prey are abundant, are in low complexity habitats, or avoid capture poorly (Main 1985, 1987). The ability to switch feeding modes between biting and suction/ram-feeding in response to changes in prey availability allows *Lagodon* to occupy a broad trophic niche.

Although prey taxa changed during ontogeny, *Centropomus* always fed on elusive prey and the prey selected followed a sequence based on size of prey. Small individuals consumed the smallest available elusive prey (calanoid and cyclopoid copepods) and gradually added larger elusive fishes to their diet as they grew. This shift toward larger fish prey during ontogeny is due in part to the effects of gape-limitation because maximum prey size was less than gape, prey consumed were among the smallest available, and selectivity for deep-bodied prey increased with predator size. However, other factors in addition to gape-limitation could have also limited prey size, because average prey body depths were significantly less than the gape and did not increase proportionately with gape. Although prey fishes less than the maximum body depth (89% of oral gape) were abundant at the collection site, they were not consumed frequently by *Centropomus*. It is possible that large *Poecilia* and *Cyprinodon* avoided capture, were not attacked, or may have escaped following capture while being manipulated in the jaws for swallowing (Reimchen 1991a, 1991b), leading to the observed pattern of average prey body depth being both smaller than gape and the average size of prey in the environment. The relationship between average prey body depth and gape may also be influenced by the limits imposed by pharyngeal gape during swallowing (Wainwright 1988), rather than oral gape during prey capture, and thus reflect the size and species of prey that can be easily swallowed by *Centropomus*. Because pharyngeal gape was not measured in this study, it is unknown if this measure is a better predictor of prey size and species consumed. It is known that handling time increases with relative prey size (Werner 1974, Hoyle & Keast 1987), and *Centropomus* may have considered this cost when selecting fishes for consumption, avoiding large fish (> 89% of gape). Factors other than absolute mouth size constraints, such as relative swimming abilities of the predator and its prey (e.g. Webb 1986) and the presence of erectable spines on prey (Hambright 1991) may explain some of the selectivity for the fishes consumed by *Centropomus*. Interestingly, none of the prey fishes consumed by *Centropomus* in this study have dorsal spines, even though species such as *Diapterus auratus* (Gerreidae), which have large dorsal spines, were present in the environment.[1]

Liem's (1980) hypothesis that use of multiple feeding modes leads to greater dietary diversity is supported by this study. Based on feeding mode observations in the laboratory and field, and dietary characterization of freely foraging individuals in the field, it is clear that *Lagodon* used at least 2 modes of feeding (biting and suction/ram-feeding), whereas *Centropomus* used one mode (ram-feeding). *Lagodon* probably uses more modes, although we could not reliably distinguish them in the current study. Dietary diversity of *Lagodon* exceeded that of *Centropomus* at all life intervals examined. Thus, in spite of its relatively small mouth, *Lagodon* occupies a broader ecological feeding niche than *Centropomus*. An alternative explanation for this result

is that the seagrass meadow where the *Lagodon* were collected had greater prey diversity available than the mangrove impoundment where the *Centropomus* were collected. We cannot test this hypothesis because equivalent-effort prey availability samples in the mangrove impoundment and seagrass meadow are lacking. Nevertheless, *Centropomus* was never observed to use biting in the laboratory feeding trials and did not consume any of the sessile prey which occurred on the red mangrove prop roots at the collection site, thus suggesting its diet is restricted by the limited ability to generate force by biting. Seagrass meadows are available to small *Centropomus*, but these habitats are rarely used by individuals < 100 mm SL (Gilmore et al. 1983, McMichael et al. 1989) and mangroves may provide more profitable foraging habitats for small *Centropomus*. A reciprocal transplant experiment, in which dietary diversity of *Lagodon* and *Centropomus* could be measured while they were foraging in the same environment (mangrove impoundment or seagrass meadow) with an equal diversity of prey available, is required to be certain of this result.

Mouth size and dentition, the intrinsic factors measured in this study, set the limits of the fundamental trophic niche for juvenile *Lagodon* and *Centropomus*; other intrinsic and extrinsic factors should be studied in more detail in the future, because these will interact with mouth morphology to produce the realized niche. Capture success should be measured for various prey species and sizes in the laboratory under equal availability conditions for both *Lagodon* and *Centropomus*. Detailed high-speed kinematic studies of *Centropomus* and *Lagodon* at different ontogenetic stages are needed to fully appreciate the capture success for various species of elusive prey during predatory attacks. Behavioral studies in the laboratory and field are also needed to measure prey selectivity by *Lagodon* and *Centropomus* under conditions of changing prey availabilities and predation risk. Until such studies are completed, the relative contribution of morphology and behavior to ontogenetic changes in resource use cannot be separated.

In summary, it is not surprising to find that fishes change the taxonomic groups on which they feed during ontogeny. These taxonomic shifts may be of two types. Gape-limited feeders shift because within any taxonomic group there is a limited size range of prey, and predators are shifting ontogenetically from taxonomic groups dominated by small individuals to taxonomic groups dominated by large individuals. This was the case with *Centropomus*, where the changes in taxonomic composition were not accompanied by changes in the functional group of the prey, that is, elusive prey such as calanoid copepods were replaced by elusive prey such as small fishes. Fishes with mouth shapes similar to *Centropomus* should also be gape-limited and unable to consume prey larger than some threshold, which increases during ontogeny. A second cause of taxonomic shifts can be observed in *Lagodon*, where the functional group of prey eaten differs during ontogeny, that is, small *Lagodon* capture amphipods using suction/ram-feeding, and large *Lagodon* bite pieces out of large sessile prey like polychaetes, hydroids, tunicates, algae, and seagrasses. Fishes with mouths similar to *Lagodon* may be gape-limited when they are small and capable of biting pieces from prey when they are large. Fishes with biting mouth morphology are thus not limited by prey size, but instead by the biting strength and their ability to cut through tough, large prey.

Acknowledgements

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